The Peruvian Anchoveta and Its Upwelling Ecosystem: Three Decades of Change

Edited by

D. Pauly and I. Tsukayama

1987

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Cover: Time series of turbulence *(above)* and sea surface temperature *(below)*, combined with pre-hispanic representation of Peruvian fisherman, adapted from IMARPE report entitled "Research on the Anchovy: Models and Reality" (1975).
Artwork by Ovidio F. Espiritu, Jr.

PROCOPA Contribution No. 46.

ICLARM Contribution No. 391.

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Indexes ●*V.C. Sambilay, Jr.*[*]

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[*] College of Fisheries, University of the Philippines in the Visayas, Diliman, Quezon City, Philippines.

IMARPE Foreword

R. VILLANUEVA
Executive Director
Instituto del Mar del Peru

The marine fisheries are vital to Peru and hence responsible management of our marine fish resources should be one of our national priorities.

Much has been achieved as far as understanding the fishery biology of the various fish species inhabiting the Peru Current System is concerned; the life-histories of the major species have been largely elucidated, the fishery monitored and the gross effect of successive El Niño events well documented.

Our major impediment in this research effort and hence in formulating optimal management options has been, however, the piecemeal nature of much of our research largely due to lack of continued funding for sustained efforts.

This has resulted in many of our valuable results remaining disconnected, delaying the emergence of a broad view of the upwelling ecosystem along our shores, both in the heads of some of our scientists and of some of our fishery managers. How else can we explain, over 30 years after the onset of the anchoveta fishery, the lack of a management plan which would *simultaneously* consider the exploitation of the anchoveta, of its major predators and competitors (bonitos, mackerels, horse mackerels, sardine) as well as the conservation of the guano birds and seals?

I was therefore very pleased when I first heard about the project initiated by Ms. Isabel Tsukayama, then Chief of IMARPE's Pelagic Resources Division, by Dr. Pauly of ICLARM and by PROCOPA staff and have since given it as much support as I could, both by encouraging IMARPE staff to participate in it and by encouraging other institutions to release data.

I now feel satisfied that this project has produced the elements needed to reach a global view of the Peruvian ecosystem and I have no doubt that future generations of Peruvian researchers will find this book useful as inspiration and/or as source of background data for their research.

With this volume, which includes in table or graphic form an extremely large amount of time series data, our Institute also provides the international scientific community with material that can be used to test various hypotheses on the dynamics of upwelling ecosystems and of their pelagic resources. We have convinced ourselves, during this exercise, that we held in our files, drawers and unpublished reports more and better data than we thought was the case. We hope others with social and economic constraints such as ours will also inspect their files and drawers - and put together the data, as was done in this book.

Finally, I wish to thank GTZ and ICLARM. Without their support and active involvement, this book could not have been written. This applies especially to Dr. Bilio, who approved the whole idea, and to Dr. Arntz and Dr. H. Salzwedel, the successive team leaders of PROCOPA, who so often acted as bridge between us and faraway ICLARM. This applies also to the latter organization and its Director General, Dr. I.R. Smith, for hosting a young Peruvian scientist involved in the project and especially for their support of Dr. D. Pauly, whose communicative enthusiasm certainly was a major element to the success of this project.

Callao, June 1987

GTZ Foreword

DR. M. BILIO
Fishery and Aquaculture Section, GTZ

Peruvian-German cooperation in fisheries research is getting close to the completion of its first decade of existence, while cooperation in the fisheries sector in general is even older. Research cooperation is being conducted through the Programa Cooperativo Peruano-Alemán de Investigación Pesquera (PROCOPA) at the Instituto del Mar del Perú (IMARPE) in Callao. The main purpose of this project is to provide assistance in research areas that could not be covered sufficiently by Peruvian scientists alone, due to the restricted means available from national resources.

PROCOPA, dealing with fishery resources largely dependent on the productive conditions connected with the Peruvian upwelling system, has from the start aimed to include species other than anchoveta in its research program. In this context, emphasis was put on the stock assessment of fish species in demand, or at least highly suitable, for human consumption. The final objective of the German contribution was the integration of all available and newly acquired knowledge into a model of the ecosystem. Such a model should enable us to understand the essential interactions among the major components of the system and, hence, to predict changes due either to natural causes, such as "El Niño" events, or to the exploitation of parts of the system by a fishery.

Collaboration of Peruvian and German scientists has produced a respectable series of reports and publications culminating in the publication of "El Niño, Su Impacto en la Fauna Marina", edited by W. Arntz, A. Landa and J. Tarazona (Boletín del Instituto del Mar del Perú, special volume, Callao 1985). However, PROCOPA has not only involved Peruvian and German researchers. It has, indeed, included a considerable number of internationally renowned scientists from other countries, in particular the USA and the UK, and derived benefit from their participation, which is also documented in PROCOPA's list of publications. One of the foreign scientists who participated in PROCOPA's activities already at an early stage was Dr. Daniel Pauly of ICLARM who was invited in 1981 by Dr. W. Arntz, then PROCOPA team-leader, for what was planned to be a brief consulting exercise on single-species population dynamics and a series of lectures to IMARPE staff. The present book documents into what Dr. Pauly's collaboration has grown!

The involvement of ICLARM in PROCOPA is in line with the close cooperation between GTZ and this leading international research institution in the field of fishery and aquaculture development in the tropics and subtropics. It is also in agreement with the principle of making the best possible use of scientific data by analyzing them according to the highest methodological standards and to render the results available to the largest possible scientific audience and to potential users in fisheries management and politics.

The present book appears to me as an excellent example of the fruits that trustful international cooperation among scientists can bring forth, even when half of the world has to be bridged in the process. I would therefore, like to congratulate first of all the editors and contributors on their success and thank them for their commitment. I would further like to express my gratitude to Dr. H. Salzwedel, present team-leader of PROCOPA, who wholeheartedly supported this cooperative effort and successfully steered it through some of its crises, and to Dr. W. Schmidt, the project officer of PROCOPA, who helped with essential arrangements from GTZ Headquarters. Particular thanks are due to the management of IMARPE and its Executive Director, Dr. R. Villanueva, for their enthusiastic support and to ICLARM for letting Dr. Pauly contribute a major part of his "research time" through 1986 and 1987.

Although some of the contributions included in this book are highly theoretical, I am confident that its publication represents a great step forward to the understanding of the dynamics of the principal Peruvian marine fishery resource and its management, if only because of the massive amount of data that has been assembled and standardized and of the sheer length of the time series that are now available for detailed study. GTZ is pleased to have been able to contribute to this effort.

Eschborn. June 1987

ICLARM Foreword

DR. IAN R. SMITH
Director General, ICLARM

It is with great pleasure that I have accepted to introduce, on behalf of the International Center for Living Aquatic Resources Management, this book to its readers.

I believe this volume illustrates very well the many facets of ICLARM's concept of management-oriented fishery research conducted by cooperating institutions and more specifically of ICLARM's multidisciplinary emphasis when conducting such investigations.

Three different institutions, based on three different continents, joined in this effort to which scientists from six different countries unselfishly contributed all of their data and much of their time. The disciplines these scientists represent range from physical oceanography and meteorology to fishery biology and economics - with one author actually having worked for almost a decade in the anchoveta fishery. However, it is not only this wide range of skills and talents which has made this book possible. Rather, the crucial factor seems to have been the support which the authors and the editors received from various institutions in Peru, notably from PESCAPERU and IMARPE.

The scientific value of historic data held in the laboratories of developing countries is often unappreciated. This book illustrates the vision and foresight of those who collected these data as well as of those who released them for use by the authors of the various contributions included here.

Three of the key papers included in this book are by staff of the National Marine Fisheries Service of the US Department of Commerce. All of the editors' effort at reaching a comprehensive coverage of the Peruvian ecosystem would have been vain without the massive data sets and in-depth analyses contributed by these authors. On behalf of ICLARM, an institution devoted to research on aquatic resources with institutions in developing countries, I would like to congratulate NMFS for this cost-efficient and well-focused method for transferring data back to where they originated.

This book is the first ICLARM publication dealing exclusively with Latin American resources and I deeply regret that time constraints prevented the editors from preparing Spanish Abstracts and Table and Figure legends, as originally planned. We hope, however, that the opportunity will emerge in due time for a translation of the entire volume into Spanish, which incidentally would allow for an update of the time series in the various contributions, most of which stop in December 1982.

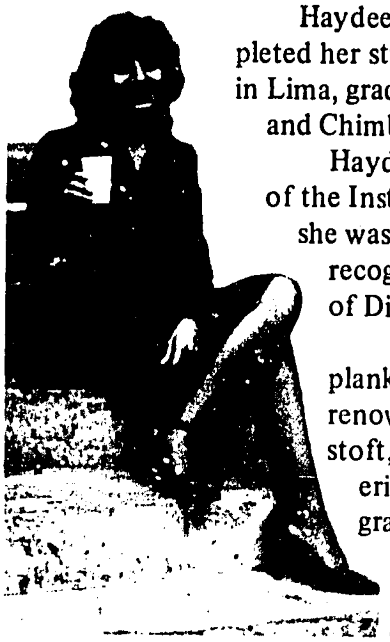
ICLARM is pleased to have had the privilege of cooperating with IMARPE and GTZ, and hope that the volume resulting from this cooperation will be found useful by its readers.

Ian R. Smith

Manila, June 1987

To the Memory of Haydee Santander Bueno

To whom this book is dedicated for her valuable contribution to Ocean Science and for her exceptional human qualities. She passed away on the 25th of March this year in Lima, Peru, being in her peak of scientific production and active involvement in the completion of this book.



Haydee was born in Lima, Peru, in the pleasant district of Brena. She completed her studies in Biological Sciences at the Universidad Mayor de San Marcos in Lima, graduating in 1959 with a thesis on "The Euphausids around Callao and Chimbote and the General Composition of Zooplankton".

Haydee's professional career started in 1961 in the Plankton Department of the Instituto de Recursos Marinos (IREMAR). From 1964 to her last days she was affiliated with the Instituto del Mar del Peru (IMARPE) where, in recognition of her professional achievements, she was advanced to the rank of Director.

Her main field of interest was research on ichthyoplankton and zooplankton having carried out specialization and complementary studies at renowned research centers which include the Fisheries Laboratory, Lowestoft, England; Marine Laboratory, Aberdeen, Scotland; Southwest Fisheries Center, La Jolla, California, USA and Bedford Institute of Oceanography, Halifax, Canada.

She participated as principal researcher of the Zooplankton Component of the Coastal Upwelling Ecosystem Analysis (CUEA) Project, a Peruvian-Canadian project; Cooperative Research of the Anchovy and Its Ecosystem (ICANE); and Peruvian-German Fishery Project (PROCOPA). She was national representative in the planning of the Sardine-Anchovy Recruitment Program (SARP) Project; President of the National Study of the "El Niño" Phenomenon (ENFEN) Multisectoral Committee; and national representative of the Regional Study of the "El Niño" Phenomenon (ERFEN).

Her scientific bibliography is appended. We will miss her.

THE EDITORS

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On the Implementation of Management-Oriented Fishery Research: the Case of the Peruvian Anchoveta*

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Abstract

Some features of previous oceanographic and fishery research in the Peruvian upwelling system are presented and contrasted, with emphasis on the need for biologists to retrieve and standardize historic data and to present and analyze longer time series than commonly done to date.

The genesis and aims of an international, multidisciplinary project between IMARPE, GTZ and ICLARM and aiming at deriving and analyzing monthly time series on the Peruvian current system for the period 1953 to 1982 and beyond are discussed, and the key hypothesis that gives its structure to the present book is presented.

Brief discussions, with copious references, are given of various important species of the Peruvian upwelling ecosystem not discussed in the book of which this contribution forms the introduction.

Introduction

A huge amount of literature exists on the biology and population dynamics of the Peruvian anchoveta *(Engraulis ringens)* (see Table 1). However, this literature differs in an important way from the associated literature on the oceanography of the Peruvian ecosystem: the overwhelming majority of "biological papers" have a very short time scale, usually covering the period of a few months within, or the few years spanning major El Niño events (see e.g. contributions in Arntz et al. 1985).

The reasons for this imbalance are numerous and include objective constraints (assembling and analyzing biological data, say on a monthly scale, over long time series is far more difficult than assembling say temperature measurements (see Tabata 1985) as well as subjective problems, such as those that emerge when biologists working in different laboratories, using different methods, have to share data and ideas.

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* ICLARM Contribution No. 375.

Table 1. Some major source of information on the Peruvian upwelling ecosystem (as of early 1987).

Reference	Type of document/remarks
Garcilaso de la Vega (1609 and 1617)	First historic account of the Inca civilization, as written by the son of an Inca princess and a Spanish conquistador (1539-1616), and including comments on the Incas' efforts to regulate guano exploitation (see Tovar et al., this vol.).
Hutchinson (1950)	Thorough review of guano production and exploitation throughout the world with an account of the biology and physiology of the Peruvian guano birds, and of the guano industry.
Boerema et al. (1965)	as per title (see references).
I Seminario Latino Americano sobre el Oceano Pacifico Oriental (1966), Univ. San Marcos, Lima, Peru, 218 p.	Proceedings of a UNESCO-supported seminar, containing numerous contribution on the Peru current and its resources.
Schaefer (1967), Murphy (1967), Gulland (1968)	Monographs based on data supplied by IMARPE staff.
IMARPE (1970, 1972, 1973, 1974a, 1974b)	Reports of five "Panel of Experts" on the biology and management of the anchoveta, and the economics of the anchoveta fishery.
IIP/IBP (1971)	Contains results of research cruises conducted off Pisco, Peru.
Stevenson and Wicks (1975)	Microfiche bibliography of El Niño and related publications.
Boje and Tomczak (1978)	Proceedings on a symposium on upwelling ecosystems, with four contributions dealing with aspects of the Peru current.
Sharp (1980)	Proceedings of a workshop held in Lima and devoted to the early life history of pelagic species in upwelling systems (Peru and California).
UNESCO (1980)	Proceeding of a Workshop held in 1974(!) in Guyaquil, Equador and including several major reviews.
Dickie and Valdivia (1981)	Compilation of 36 papers either generated as part of a Peruvian-Canadian cooperative research project, or available at the times this was printed. [Some raw data generated by this project are in Doe, 1978].
Glantz and Thompson (1981)	A multiauthored book on upwelling ecosystem, with numerous contributions relevant to Peru and ranging from the prediction of El Niño events to the politics of fishery management and land reform. Includes reprints of older, classical papers, e.g. by R.C. Murphy and G.J. Paulik.
Richards (1981)	Proceedings of a major conference on upwelling ecosystem; includes more than 20 contributions on the Peru Current region.
Sharp and Csirke (1983)	Proceedings of an "Expert consultation" (FAO term for Symposium) "to Examine Changes in Abundance and Species Composition of Neritic Fish Resources", held in San José, Costa Rica, 18-29 April 1983; contains numerous contributions on Peruvian resources.
CPPS (1984)	Proceeding of a Symposium on El Niño, held in Guyaquil, Equador, 12-16 Dec. 1983.
Mariategui et al. (1985)	Indexed bilbiography, with 1,106 entries on El Niño and Peruvian resources.
Arntz et al. (1985)	Proceedings of a Symposium on El Niño and its impact on the marine fauna, held in Arequipa, Peru, Oct. 1983, heavy emphasis on the 1982/83 El Niño. Includes several accounts of benthic animals.
IMARPE *Boletin*	Scientific journal of the Instituto del Mar del Peru; includes crucial informations often missed by non-Peruvian scientists writing on the Peru current and/or the anchoveta.
IMARPE *Informes*	Report series of the Instituto del Mar del Peru; contains crucial information not found elsewhere.
Bol. Cient. de la Cia Adm. del Guano	Scientific journal of an organization previously in charge of guano birds and exploitation; contains numerous papers relevant to anchoveta biology (ser. now defunct.)
Tropical Ocean-Atmosphere Newsletter	Contains many brief, up-to-date articles on the Peru Current area, and discussions of El Niño.

One consequence of this imbalance is that long time series data, to which rigorous multivariate methods could be applied are lacking, and that various hypotheses, advanced decades ago to explain the dynamics of the anchoveta stock of Peru could not be tested and/or refined. Another consequence is that each author, while concentrating on the specific problems(s) she or he is investigating has to "set constant" those variables that are not specifically dealt with, leading to rather old estimates of important anchoveta population statistics being "carried over" from one study to the next.

Underlying these problems, finally, is an enormous waste - or at least underutilization - of information which, while not necessarily being easy to access, does nevertheless exist and which, if properly standardized, could help interpret the behavior of the anchoveta stocks off Peru, and more generally, of stocks of small pelagics throughout the world.

Genesis of the Project Leading to the Present Book

We shall present, in the following paragraphs (based on Pauly et al. 1986) an outline of the genesis of the multidisciplinary project which led to the book presented here, meant to alleviate the situation described above. We shall elaborate on this item more than might appear necessary because we believe that this international effort illustrates a cooperative *modus operandi* that is used far too little in projects with aims similar to ours.

The project emerged out of three, at first unrelated, developments. The first was that the staff of a GTZ project hosted by IMARPE, the Programa de Cooperacion Peruano-Aleman (PROCOPA) was given a mandate to develop, for purposes of fishery management, and in cooperation with their counterparts at IMARPE, a model of the Peruvian ecosystem that would be more realistic and versatile than those of Walsh (1981) or of Kremer and Sutinen (1975). Thus, an attempt was made to involve Dr. E. Ursin, who had earlier worked on a model of the North Sea (Andersen and Ursin 1977) in these efforts (Ursin 1980).

The second development was the 1980 release of the early version of the ELEFAN programs for the estimation of growth, mortality and related statistics from length-frequency data (Pauly and David 1980, 1981; Pauly 1982; Pope et al. 1981), such as have been collected on the Peruvian anchoveta since the 1950s (Clark 1954; Jordan 1959).

The third development, finally, was the identification and refinement, by A. Bakun, R. Parrish and associates at the Pacific Fisheries Environmental Group of NOAA/NMFS (Monterey, California) of a methodology for the analysis of wind data in a context relevant to fisheries in upwelling systems (Bakun 1985; Parrish et al. 1983).

Two of these developments converged in 1981, during the first author's initial visit to IMARPE. A "test run" was undertaken as a consequence of this visit, leading to an analysis of 20 years' worth of monthly anchoveta catch-at-length data using the ELEFAN I and III programs. This provided extremely encouraging results (Pauly and Tsukayama 1983), the three main conclusions from this preliminary analysis being:

i) length-based methods - particularly that described as "VPA III" in Pauly and Tsukayama (1983) and Pauly, Palomares and Gayanilo (this vol.) - appear eminently suited to study the dynamics of anchoveta, and reasonable estimates of monthly recruitment, biomass, fishing mortality and related information can be readily derived from an extremely limited amount of data in addition to catch-at-length data;

ii) the assumption of a constant natural mortality ("M") underlying the preliminary analysis, as well as most fish population models is untenable in the case of the Peruvian anchoveta, and ways must be found to let M vary, e.g., with the biomass of major predators, or by adding anchovetas consumed by predators to those caught by the fishery (see Pauly, Palomares and Gayanilo, this vol.);

iii) the 20-year time series of catch-at-length data used in the preliminary analysis from 1961 to 1979 should be extended backwards to cover the initial phase of the fishery (when biomasses were high and recruitment variability low) and forward in time to cover the period when the anchoveta was (partly) replaced by other small pelagic fishes, and its variability became high.

Item (i) resulted in IMARPE, PROCOPA/GTZ and ICLARM formalizing an agreement to cooperate on a major program of data retrieval and standardization, such that subsequent studies using length-frequency methods, time-series analysis and other methods would become possible.

Item (ii) implied a need to explicitly consider the major predators of anchoveta, of which the guano birds were - at the time (see below) - the only ones we thought were really important.

Estimating the population size and anchoveta consumed by guano birds along the stretch of the Peruvian coast between 4 and 14oS (i.e., such that the "southern stock" of anchoveta is excluded, see Fig. 1) involved performing a planimetric analysis of over 10,000 maps showing

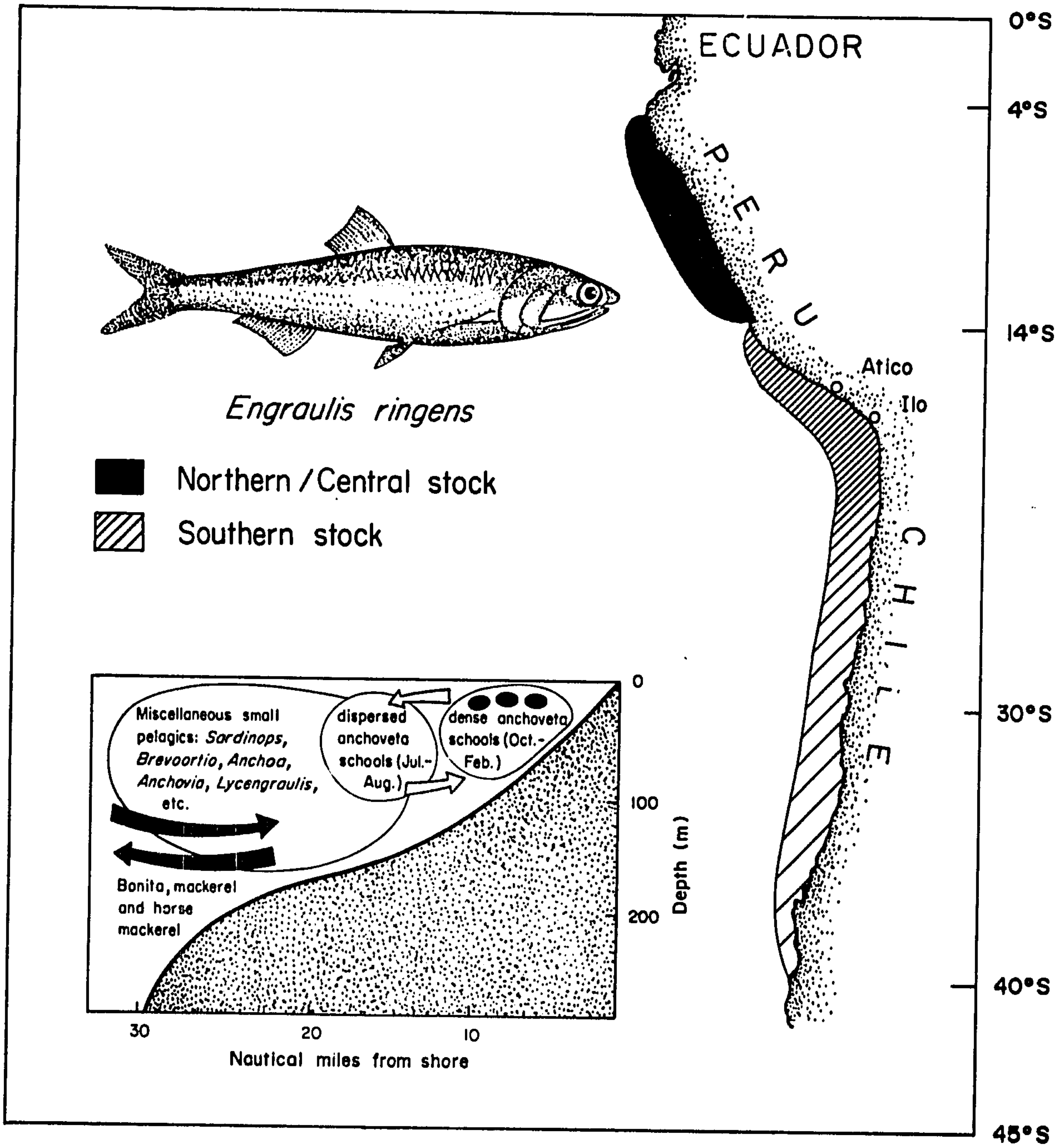

Fig. 1. Distribution of anchoveta stocks along the Eastern Coast of South America. Based on FAO (1981), Jordan (1971), Chirichigno (1974), Brandhorst (1963) and IMARPE (1973).

the distribution of three species of guano birds on 40 guano islands and "points", completed by the guards of the Compania Administradora del Guano and its various successors (see Tovar et al., this vol.). This also involved deriving a model of the predation on anchoveta by the guano birds (see Muck and Pauly, this vol.).

Item (iii) above involved retrieving, from a number of scattered sources, information on the catch and catch size composition of anchoveta for the earlier years of the fishery. This effort brought a surprisingly large amount of material to light (see Tsukayama and Palomares, this vol.), matching previous experiences elsewhere (Ingles and Pauly 1984). These data, as well as data covering the late 1970s and early 1980s indeed allowed for the construction of numerous time series, and showing so few gaps that standard interpolation procedures could be used to obtain uninterrupted series (see, e.g., Pauly, Palomares and Gayanilo, this vol.). This also applied to the time series of oceanographic and meteorological data compiled and analyzed by Brainard and McLain (this vol.), Bakun (this vol.) and Mendo et al. (this vol.).

Identity of the Anchoveta Stock

The Peruvian anchoveta *(Engraulis ringens* Jenyns) belongs to the family Engraulidae (Pisces Clupeomorpha, Clupeoidei). It occurs exclusively along the eastern coast of South America, from 4°30'S off Peru (Jordan 1971) to 42°30'S off Chile (Brandhorst 1963; Mathisen 1979), with heaviest concentration along the coast of northern and central Peru, north (i.e., "downstream") of the strongest upwelling area. At the northern end of their range, anchoveta biomass drops off rapidly, while toward the south, this biomass only tapers off gradually (Fig. 1). 1).

Mapping of anchoveta distribution during "EUREKA" (Villanueva 1975) and other acoustic surveys and during egg surveys suggests the presence during the spawning season of isolated "density centra" (see maps in Santander, this vol.) which may or may not correspond to genetically distinct subgroups or populations. Mathisen (1979), after a thorough review of the then available literature, suggested these "centra" to be genetically distinct populations. However, electrophoretic studies of allelle distribution have not been conducted in anchoveta.

At the gross level however, distinctions can be made straightforwardly between the anchoveta off northern/central Peru, and those from southern Peru/Chile, with anchoveta from southern Peru and Chile having less, coarser gill rakers (Tsukayama 1966) and shorter guts (Rojas 1971), both items suggesting that these fish rely on zooplankton more than their northern counterparts.

IMARPE (1973) wrote that "the results of the recent tagging experiments support the hypothesis expressed in previous reports that the anchoveta resources in the southern area (Atico-Ilo area) are a more or less separate stock".

For the purposes of this, and the other contributions included in this book, we have therefore used 14°S as the limit between the northern/central stock - here reported upon - and the southern Peruvian/Chilean stock of anchoveta (Fig. 1). The strong interactions between the Peruvian and Chilean components of the southern stock of anchoveta would make studies based on isolated "national" data sets of limited usefulness. In fact a detailed investigation of this stock would require a high level of cooperation and data exchange between Peruvian and Chilean scientists and institutions. We hope that such cooperations will materialize in the future, and that the southern stock of anchoveta will become as well documented as the northern/central stock covered in this book.

The Peruvian Anchoveta and the Prediction of Its Recruitment

A research project as comprehensive as the one reported upon in this book cannot be kept on course if a "central hypothesis" is lacking around which the various contributions can be structured.

Our central hypothesis is that the recruitment of the Peruvian anchoveta, "everything else being equal", is determined by a short-frequency burst of wind-driven turbulence, i.e., our central hypothesis corresponds to Lasker's contention that "storms", by dissipating food-rich microlayers in which anchoveta larvae can feed, lead to their starvation and to recruitment failures (Lasker 1978). Given appropriate data, testing this hypothesis is rather straightforward, and indeed, it has been repeatedly and successfully tested off California both for average conditions (Husby and Nelson 1982) and based on time series data (Peterman and Bradford 1987). This hypothesis has also been tested, in the Peru Current area, for average conditions with somewhat equivocal results (see Bakun 1985 for a review of the relevant literature).

What has been lacking to date was a test of this hypothesis using time series data from Peru. For such a test, however, everything else must be at least approximately equal (see above), and the bulk of this book represents an attempt to collect data on those things that have varied, such that they can be explicitly accounted for, and the true effect of wind-induced turbulence isolated from the noise. Thus in a sense, this book is a test of Lasker's hypothesis, probably the most comprehensive test this hypothesis will ever get.

Previous work dealing explicitly with the recruitment of anchoveta include the classic paper of Csirke (1980) who quite conclusively demonstrated that plotting a bivariate stock *vs.* recruitment relationship simply will not do for the Peruvian anchoveta (see Fig. 2), as is indeed also true for any other fish, notwithstanding suggestions to the contrary (e.g., by Shepherd 1982). Also, an attempt exists to deal with anchoveta recruitment in terms of bioenergetics (Ware and Tsukayama 1981).

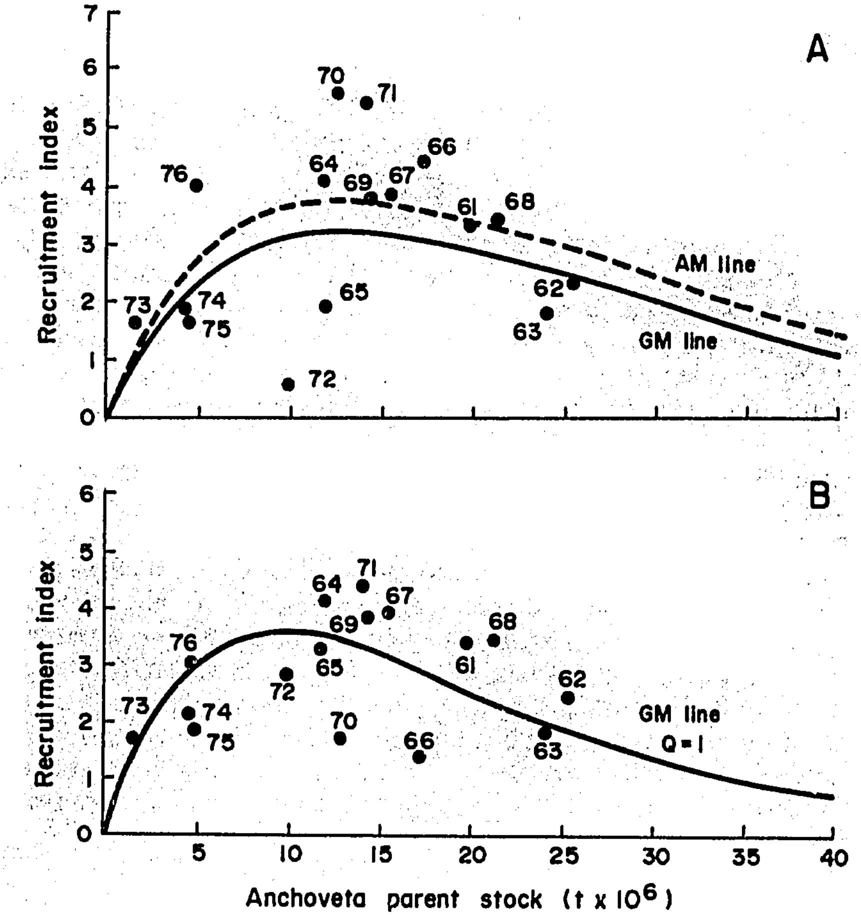

Fig. 2. Stock/recruitment relationships of Peruvian anchovy *(Engraulis ringens)* showing effect of taking an additional variable into consideration. (A) simple Ricker plot, showing rather bad fit and correspondingly low correlation of observed to expected recruitment (GM line, $r = 0.494$). (B) Plot of the residuals of a multivariate relationship involving recruitment, parent stock and concentration index, Q, related to occurrence of El Niño events onto stock recruitment relationship, drawn for an average value of Q. This shows an improved fit with a correlation of observed to expected recruitment of $r = 0.893$ (based on data in Csirke 1980).

An approach to deal with recruitment (R), suggested by Bakun et al. (1982), and following up on the work of Csirke (1980) is to use a model of the form

$$\log (R/S) = a+b_1S+b_2 E_1+b_3 E_2+ \ldots \qquad \ldots 1)$$

where S is the spawning stock and the E_i are environmental variables likely to affect the survival of prerecruits. Bakun et al. (1982) suggests that because data points for such approach are limited (they implied 1 point per year), "the number of explanatory variables must be limited to a minimum", and that "this should be done on rational ground, based on the best available understanding of cause-effect relationships between recruitment and environmental factor".

The problem of data point limitation alluded to by Bakun et al. (1982) has been resolved here at least in part by putting all time series included in this book on a monthly basis (this resolves the problem only in part because other problems, such as seasonal autocorrelation then crop up; see Mendelsohn and Mendo, this vol. and Pauly, this vol.).

On the Time Series and Graphs in This Volume

The criteria applied to decide whether to include a given data set into the present volume were:

i) do the raw data cover reasonably well the period January 1953 to December 1982?, or
ii) does a given data set allow estimation of a "constant" or relationship useful for deriving time series covering 1953 to 1982?

Examples of data sets fulfilling criterion (i) or (ii) are the temperature data in Table 2 and in Bakun (this vol.) and the data on spawning of anchoveta in Pauly and Soriano (this vol.), respectively.

These criteria, on the other hand, led to the nonconsideration of some zooplankton and other time series reported in the literature, which were too short and could not be utilized as input to derived time series.

This approach was needed - at least as far as the major contributions included in this book are concerned - to prevent a large numbers of nonoverlapping time series from being assembled. We feel vindicated in this approach in that:

i) those who contributed to this book made a special effort to "stretch" their data,as far as possible, which now allows simultaneous analysis of a very large number of mutually compatible, uninterrupted time series covering, on a monthly basis, the whole 30-year period from 1953 to 1982;
ii) some readers of this book will feel challenged to match the time series they encounter here with time series of their own; and finally,
iii) a body of background data is now available allowing other authors working with data covering a shorter period to rigorously test whatever hypothesis they might have.

To facilitate further analysis of the data presented in the various contributions included here, we have included throughout the book tables with unaggregated data which readers are welcome to use[a].

The astute reader will notice that this book, despite the restrictive inclusion criteria given above, incorporates more data on the Peruvian upwelling ecosystem than ever published in a single volume. In fact, an attempt was made to make each contribution included here cover the

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[a] The bulk of the data presented in this book is also available as Lotus 1-2-3 files on 5 1/4' diskettes for IBM PC and compatibles; please contact the first author for details.

Table 2. Sea surface temperature off Peru in °C.[a]

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	19.4	21.2	22.6	21.5	19.6	18.0	17.8	17.0	17.2	16.8	17.0	17.6
1954	18.5	19.0	18.4	17.1	16.3	15.4	15.9	14.6	15.0	15.1	15.8	18.2
1955	20.8	19.6	17.8	18.4	17.0	16.8	16.6	15.9	16.3	15.7	16.1	16.8
1956	18.4	19.8	20.2	18.8	18.2	17.8	17.6	17.0	16.6	16.2	16.4	16.2
1957	17.8	22.3	22.1	21.8	22.2	21.2	20.3	18.7	17.7	17.9	17.9	20.6
1958	21.8	22.2	22.0	20.1	18.8	18.2	18.0	17.0	17.0	17.1	17.5	17.0
1959	19.0	21.2	20.6	19.6	18.7	17.8	16.9	16.6	16.8	17.2	17.6	18.6
1960	19.0	19.5	19.2	18.0	17.2	17.1	16.6	16.8	16.7	16.6	16.6	17.6
1961	19.0	20.6	19.3	18.7	18.2	17.3	16.7	16.6	16.4	16.4	16.4	16.8
1962	19.0	19.1	18.1	17.4	17.6	17.0	16.6	16.4	16.6	16.0	16.4	16.5
1963	17.4	18.8	19.4	18.2	18.4	17.9	17.7	17.4	17.3	17.0	17.0	18.0
1964	19.0	19.5	19.2	17.8	16.2	15.6	15.3	15.7	15.8	16.0	16.2	16.2
1965	17.6	19.6	20.4	21.3	20.6	19.5	19.0	18.4	17.6	17.5	17.9	18.6
1966	19.9	20.4	19.2	18.1	17.5	16.8	16.4	16.2	15.6	16.2	16.5	16.8
1967	18.4	19.6	19.1	17.6	16.9	16.2	16.1	15.4	15.4	15.0	15.1	16.4
1968	17.6	17.6	18.5	16.6	16.4	15.5	15.8	16.0	16.4	16.1	16.6	17.1
1969	18.7	19.0	20.4	20.5	21.0	19.5	17.4	17.3	17.2	17.3	17.3	17.8
1970	19.2	19.8	20.0	19.1	18.6	17.8	16.8	16.9	16.9	17.3	17.0	17.2
1971	18.2	19.1	19.6	19.8	18.7	18.0	18.0	18.0	17.4	16.8	17.1	17.2
1972	18.6	20.6	21.8	21.4	21.0	21.4	21.1	20.0	18.9	19.0	19.3	21.4
1973	23.2	23.0	21.3	18.4	17.4	16.6	16.0	15.5	15.7	16.2	17.1	16.4
1974	17.0	18.2	18.6	18.9	18.6	19.1	17.6	16.8	16.1	15.8	16.5	16.3
1975	16.7	18.1	21.1	19.8	18.6	16.9	16.7	16.1	16.0	15.9	15.6	16.4
1976	17.2	21.0	21.3	19.6	19.8	19.9	19.4	19.1	17.6	18.0	18.4	20.2
1977	20.4	20.5	20.6	20.6	19.1	18.2	17.6	17.0	16.6	16.6	17.2	17.8
1978	18.0	20.0	19.9	19.1	17.6	16.5	16.6	15.9	16.2	16.6	17.1	17.3
1979	18.5	18.5	19.2	19.0	18.3	17.3	17.4	17.4	17.0	17.2	17.4	18.3
1980	18.6	18.8	19.4	19.1	18.3	18.0	17.5	16.8	16.6	16.6	16.9	17.6
1981	17.4	18.8	18.5	18.3	18.5	17.6	16.8	16.8	16.2	17.0	16.9	17.0
1982	17.6	18.8	19.1	18.9	19.3	18.6	18.4	17.6	17.5	19.3	21.9	23.7

[a] Mean of values off Talara, Chimbote and Callao and thus referring to the entire Peru coast between 4 and 14°S. Based on data provided by P. Lagos (Instituto Geofisico del Peru, pers. comm.) complemented by data from Zuta and Urquizo (1972).

bulk of the information available on a given topic. Thus for example virtually all bathytermograph casts hitherto taken off Peru have been analyzed by Brainard and McLain (this vol.).

The graphs included in this volume, whether original or redrawn from earlier graphs, have all be done at ICLARM, mainly by Messrs. Mark Anthony Go-Oco and Christopher Bunao, usually on the basis of drafts provided by the senior editor.

As the reader will notice, these often include schematic representation of the animals or processes "meant" by the graphs. This was not done primarily to make the present volume more accessible to nonscientists (although this would be a nice side-effect). Rather, this style was chosen because we believe it is appropriate for scientists to develop, in the course of their research, what Keller (1983) calls "a feeling for the organism" they work on, i.e., to realize their investigations deal with living things and not disembodied entities that manifest themselves as numbers or dots on a graph.

Following Keller (1985) we are thus suggesting "that questions asked about objects with which one feels kinship are likely to be different from questions asked about objects one sees as unalterably alien". The reader will decide whether we have asked the *right* question.

The Mammals of the Peruvian Upwelling Ecosystem

The most comprehensive account of the mammals of the Peru Current - at least as far as their interactions with fish stocks and fisheries are concerned - is that of Northridge (1984). His list of marine mammals from Fishing Area 87 (Southeast Pacific) includes 38 species of cetaceans and pinnipeds. However, his reference to information other than occurrence records and population size estimates (e.g., Aguayo 1975, 1979; Vaz-Ferreira 1979a, 1979b, 1981, 1982), are extremely sparse, almost vanishingly so when only the Peruvian coast is considered.

This scarcity is, however, due to problems with accessing relevant sources since quite a few publications exist which discuss, at least in anecdotal form, actual or potential interactions between Peruvian mammals and fish stocks (Piazza 1959; Vinatera-Jaramillo 1965; Grimwood 1968; Majluf and Trillmich 1981; Trillmich and Majluf 1981; King 1983; Limberger et al. 1983; Majluf 1985; Ramirez and Urquizo 1985; Ramirez 1986 and see references in Muck and Fuentes, this vol.).

Northridge (1984) concluded his review of Area 87 by stating that "there are no documented examples of any effects of competition between marine mammals and fisheries in this area, although the collapse of the anchovy stock could well have affected some species, such as Bryde's whale."

We have consulted Dr. P. Ramirez Advincula, IMARPE's whale biologist, with regard to Bryde's whale *(Balaenoptera edeni)* as a potential anchoveta predator. He informed us that in all the stomach samples he collected at Paita land station over a period spanning 3 decades, only one (1!) ever contained anchoveta. He also asserted that the whales occurring off Peru actually tend to avoid waters in which anchoveta occur, concentrating instead on areas with abundant schools of sardines, mackerels and *Vinciguerria.*

The sperm whale (*Physeter macrocephalus = P. catodon*), similarly, consumes no anchoveta, concentrating instead on squid (Vinatera-Jaramillo 1965), in line with Tomilin (1967) who states that "the distribution of sperm whales is limited by the distribution of cephalopods, on which they feed, and which tend to prefer warmer, more salty waters" (Northridge 1984). Burmeister's porpoise, *Phocaena spinnipinis* appears to be rather abundant off Chile and Peru, with rather high catches reported from the latter country. However, no data are available on its diet off Chile and Peru (Brownell and Praderi 1982).

This leaves only two species, the South American fur seal *Arctocephalus australis* (Zimmerman 1783) and the South American sea lion *Otaria flavescens* (Blainville 1820) as mammal species off Peru that are (a) sufficiently well documented and (b) that could have an impact on the anchoveta resources. The contribution of Muck and Fuentes (this vol.) examines this question.

Coverage of the Fish Feeding on Anchoveta

A crucial element of the time series of anchoveta biomass and derived series presented in this book is that they are based on an approach which explicitly considers some key anchoveta predators.

Thus, large resources were devoted to estimating the guano bird populations in the Peru System (Tovar et al., this vol.) and their anchoveta consumption (Muck and Pauly, this vol.) as well as the population and anchoveta consumption of seals (Muck and Fuentes, this vol.) and bonito (Pauly, Vildoso et al., this vol.).

However, we overlooked, in the first phase of this project the potential impact of the mackerel and horse mackerel which we (erroneously) assumed to be largely limited to the anchoveta prerecruits (i.e., to fish of length under 4 cm). Dr. Peter Muck eventually convinced us that mackerel and horse mackerels most probably have a predatory impact on adult anchoveta far more important than that of birds, bonito and seals especially in later years. Unfortunately the contribution by Muck and Sanchez (this vol.) became available too late to be considered explicitly when deriving Virtual Population Analysis (VPA)-based estimates of anchoveta recruitment and biomass. This is probably the reason why Pauly, Palomares and Gayanilo (this vol.) found M_0 (i.e., the part of natural mortality not explained by the predators explicitly included in their VPA model) to take high values, ranging from 2-4 y^{-1}.

It is obvious from this that future estimates (or re-estimate) of anchoveta biomass should consider mackerels and horse mackerel predation explicitly. Information on the size composition of anchoveta in mackerels and horse mackerels' stomachs, along with other biological data are available which could be used for this purpose.

The role of Peruvian hake *Merluccius gayi peruanus* as a potential anchoveta predator has not been investigated in any of the contribution included in this book, mainly because available time series of population estimates (Espino et al. 1984) do not reach sufficiently far back in time (i.e. do not fulfill criterion (i) above). However, a strong relationship between hake abundance and bottom oxygen concentration (i.e., temperature regime and occurrence of El Niño events) has recently been established (Espino et al. 1985, 1986; Espino and Urquizo 1986) possibly allowing, in combination with more recent population estimates, the construction of time series of inferred hake abundance covering the period from 1953 to the present. Such time series would provide the chronological "backbone" for the hake stomach content data held at IMARPE which suggest that hake preys heavily on anchoveta when its range, normally limited to the north of Peru, is extended southward by the well oxygenated waters typical of El Niño events (M. Espino; H. Fuentes, pers. comm.).

Iteration of Anchoveta Biomasses and Derived Statistics

The astute reader will notice that the interrelationships of the various contributions included here implies an iterative approach.

Thus, in a first iteration, preliminary estimates of anchoveta biomass, available in the literature were used both to estimate the anchoveta consumption by guano birds and seals and to obtain reasonable values of M_0. Then, anchoveta consumption by bird and seals, the estimates of M_0 and other data were used to re-estimate monthly anchoveta biomass for 1953 to 1982, which thus represent the results of a second iteration. The data presented in this book could be used quite straightforwardly for a third iteration, but we have abstained therefrom. We have done so because we believe that the results of the second iteration are good enough to be presented, and to allow others to perform (or to join us in performing) this third iteration, with better data and models than have been assembled here.

We hope that the results presented here on the dynamics of the anchoveta stocks off Peru, and of their upwelling ecosystem wil be found useful for managing this valuable resource.

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Seasonal and Interannual Subsurface Temperature Variability off Peru, 1952 to 1984

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Abstract

Time series of monthly means of subsurface ocean temperature data along the Peru coast are developed for the period 1952 to 1984 for historical studies of anchoveta populations. Monthly mean values of sea surface temperature (SST), depth of the 14°C isotherm, and thickness and heat content of the surface layer were computed from all available subsurface temperature profiles. Means of these four parameters were computed for five areas along the Peru coast from 1 to 17°S, extending approximately 300 km offshore. Intra-annual (seasonal) and interannual variations of the four parameters are described and plotted as contour isograms. Time series of the four parameters are presented for the region from 4 to 14°S, as are monthly means of the Southern Oscillation Index and SST and sea level at Talara and La Punta (Callao), Peru.

Introduction

The coastal waters off the west coast of South America, particularly off Peru, are among the most biologically productive regions of the world's oceans (Ryther et al. 1971). The Peruvian anchoveta *(Engraulis ringens)* once supported the world's largest fishery. The high productivity of the area is a result of coastal upwelling which is an oceanic response to the southeasterly trade winds which cause offshore Ekman divergence, elevating the thermocline and bringing relatively cold, nutrient-rich water to the euphotic zone where the nutrients can be utilized by phytoplankton photosynthesis (Barber et al. 1985). The upwelling ecosystem off Peru is subject to considerable natural variability, with prominent time scales ranging from days to decades. This paper examines two temporal scales of oceanic variability which are likely to affect populations of anchoveta: seasonal (months) and interannual (years). The seasonal or intra-annual variability, being strongly dependent upon the annual solar cycle, is relatively predictable, and therefore likely to promote evolutionary adaptation (Parrish et al. 1983; Bakun, this vol.). The interannual variability, by contrast, has an irregular period which would tend to promote population variations. The dominant form of interannual variability off Peru occurs when the normal seasonal upwelling of nutrients is interrupted by "El Niño" intrusions of relatively warm, clear oceanic waters from the west and north.

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The coastal upwelling off Peru is imbedded within the Peru current system, which consists of several more or less independent currents interacting in a rather complicated manner (Wyrtki 1966). Gunther (1936) first distinguished a poleward countercurrent situated between the northwestward flowing Peru Coastal Current and the northwestward flowing Peru Oceanic Current farther offshore. This intermediate current, the Peru Countercurrent or Gunther Current, is a weak and irregular southward flow along 80°W and is usually observed only as a subsurface current. At the surface it is usually concealed by the wind drift to the northwest and west. It is strongest near 100 m depth, but reaches to about 500 m.

According to Wyrtki (1965, 1966), the Peru Coastal Current flows northwestward along the coast with velocities of 10-15 cm/s. At about 15°S, much of this flow turns westward away from the coast and increases speed to 25-35 cm/s as it joins the South Equatorial Current. Generally, the Peru Coastal Current is strongest from April to September. North of 15°S, the wind drift remains northwestward, but it is shallow and the southward flow of the Peru Undercurrent lies immediately beneath the shallow surface layer. The combined system of the Peru Coastal Current, the westwardwind drift, and the subsurface Peru Countercurrent maintain the upwelling along the coast. North of 15°S, the upwelling is supplied by equatorial subsurface water which is of high salinity and low oxygen content and flows southward in the Peru Countercurrent. The Peru Oceanic Current, which flows in a more westward direction and is slightly stronger than the Peru Coastal Current, seems to have little direct interaction with the more complicated processes closer to the coast.

The mean topography of the thermal structure of the Eastern Tropical Pacific reflects the ocean currents and has been described by Wyrtki (1966). The thermocline is relatively shallow along the coast at depths of 40 to 60 m and slopes downward in the offshore direction to depths of over 200 m about 1,000 km offshore. A region of shallow thermocline extends westward from the coast along the equator out to 130°W and beyond.

The current system off Peru is related to the large-scale oceanic and atmospheric circulations over the entire tropical Pacific. The atmospheric circulation over the region is dominated by the Hadley circulation of rising air over the equatorial region and sinking air over mid-latitudes near 30°N and 30°S. The Hadley circulation creates the high-pressure systems observed over the oceans in these latitudes which are strongest in the summer and weakest in the winter of their respective hemispheres. The meridional Hadley circulation is modified by zonal Walker circulation of rising air over the warm western tropical Pacific (WTP) and sinking air over the cold, upwelled water of the eastern tropical Pacific (ETP). The zonal Walker circulation normally causes heavy rainfall and low pressure over the WTP and sparse rainfall and high pressure over the ETP. The trade winds result from the combination of the Hadley and Walker circulations: the trades blow equatorward from the mid-latitude oceanic highs toward the lower pressure at the equator and westward from the higher pressure over the ETP to the lower presure over the WTP.

The surface wind stress created by the northeast and southeast trade winds drive the warm surface water westward in the North and South Equatorial Currents, respectively. This westward transport of mass and heat depresses the thermal structure and raises the sea level in the WTP. By conservation of mass, the high sea level in the WTP requires a poleward flow of the western boundary currents of the North and South Pacific gyres and eastward flow in the North and South Equatorial Countercurrents and the equatorial Undercurrent or Cromwell Current (within a degree or so of the equator).

The zonal slope of the sea surface downward from the high sea levels in the WTP to the lower sea levels in the ETP establishes a reverse zonal slope of the thermocline upward from the WTP to the shallow thermocline of the ETP. Meyers (1979) showed that near the equator (between 1°N and 1°S), the 14°C isotherm varies from depths of 200 to 250 m in the WTP to depths of 100 to 150 m in the ETP. Off the South American coast, local alongshore winds induce offshore Ekman divergence and the associated upwelling. This upwelling elevates the relatively shallow thermocline, bringing nutrient-rich deep water to the euphotic zone where it supports a high level of biological productivity. In addition, the trade winds cause oceanic divergence or surface transport away from the equator. This divergence forces local upwelling along the equator, which produces a region of shallow thermocline and above normal productivity that extends westward along the equator from the coast.

Interannual variations of the stength of the trade winds cause changes in the ocean circulation and related changes in the upwelling of nutrients off Peru. According to the hypothesis of Wyrtki (1975), El Niño occurs when a weakening or reversal of the trades occurs after a sustained period of anomalously strong trades. The period of stronger than normal winds forces an even greater than normal east to west slope of the sea surface. When the trade winds slacken or reverse, the forcing of the higher than normal sea levels in the WTP is removed. This imbalance generates equatorially-trapped baroclinic disturbances which propagate eastward along the equator in the form of equatorial Kelvin waves (Enfield and Allen 1980). The propagation of these long-period internal waves, and the associated energy, across the entire equatorial Pacific from Indonesia to South America has been observed using an extensive array of sea level monitoring stations (Wyrtki and Nakahara 1984). Upon encountering the South American coast, this energy is observed as a large intrusion of warm water which depresses the normally shallow thermocline and causes a rapid rise in sea level along the coast. As a result, normally arid regions of Peru and Ecuador receive inordinate amounts of rain, with severe flooding occurring during major events.

Interannual variations in the strength of the trade winds are part of a global pattern of surface pressure variation called the Southern Oscillation. The Southern Oscillation is often measured by the difference of atmospheric pressure between weather stations in the ETP and WTP. Quinn (1974) and Quinn and Neal (1983) have used the difference of atmospheric pressure between Easter Island (representative of the Indonesian low) as an index of the Southern Oscillation (SOI, see Table 1). Quinn (1974) demonstrated the strong relationship between anomalously low SOI values and the occurrence of El Niño off the coasts of Peru and Ecuador. A time series of anomaly of the SOI pressure difference shows the major El Niño events of recent decades (Figs. 1 and 2). Note the strong positive SOI presure differences (and implied strong trade winds) during 1954-1956 and 1970-1971. Subsequent sharp declines in the SOI pressure difference in the winters of 1956-1957 and 1971-1972 were followed by El Niño events, as evidenced by the increased SST and sea level at Talara and La Punta. Also, note that the strong 1982-1983 El Niño was not preceded by a period of strong positive SOI, rather, it occurred during a period of predominantly negative SOI which began in 1976.

The formation of El Niño has been modelled numerically by McCreary (1976) who suggested that the anomalous deepening of the density structure observed during El Niño events dissipates by reflection in the form of westward propagating baroclinic Rossby waves and transmission to the north and south along the coast as low-frequency coastally trapped waves and coastal Kelvin waves. Such baroclinic waves can be observed as anomalous deepenings of temperature and salinity surfaces adjacent to the coast and as anomalous rises of sea level at coastal tide stations. Poleward currents along the coast are created in geostrophic response to the anomalous deepening and change in slope of the density surfaces normal to the coast. The currents reverse to equatorward as the anomalous deepening dissipates. To some extent these processes occur each year and anomalous warm years are merely an extreme condition of the normal annual cycle of events (Chavez et al. 1984).

Although the interannual changes associated with El Niño events are dominant, longer period fluctuations also occur. In their 34-year time series of temperature at 100 m along the west coast from British Columbia to Chile, Brainard and McLain (1985) showed a marked warming trend occurring between the early and late 1950s, cooling in the 1960s, and warming again in the mid-1970s and early 1980s (see also Tables 2 and 3). The causes of these long-term temperature trends are unknown, but like the interannual variations, they are related to changes in both the large-scale atmospheric and oceanic circulations. The period of below normal SOI pressure differences during the years 1976-1983 (Fig. 2) is an example. El Niño-like conditions of above normal SST and sea level occurred during much of this period in the northeast Pacific (McLain 1983, and see Fig. 2 and Tables 4 and 5 for monthly sea level data from 1950 to 1974).

Development of historical time series of subsurface temperature conditions off Peru is important for modelling historical changes in fish populations of the area. This paper presents plots and tables of monthly mean values of four parameters computed from subsurface temperature observations for 1952 to 1984 for use in historical studies. These four parameters are SST, depth of the 14°C isotherm, depth to the temperature that is 2.0°C less than the surface temperature (SST-2°C), and heat content from the surface to the SST-2°C isotherm. The depth

Table 1. Southern Oscillation Index (SOI). Monthly mean pressure difference in millibars between Easter Island and Darwin, Australia. Data courtesy of Dr. W. Quinn, Oregon State University.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1948	12.9	11.7	12.3	10.4	9.3	11.6	10.7	11.2	9.3	12.1	9.8	9.3
1949	8.0	12.8	15.0	6.2	7.8	11.9	10.3	9.7	11.7	11.3	13.4	15.1
1950	16.4	17.6	15.0	14.7	9.5	13.8	11.3	9.2	9.1	16.0	17.1	17.6
1951	14.3	14.3	12.9	7.3	4.1	7.8	4.6	5.2	5.4	9.9	13.6	11.8
1952	13.2	11.5	10.8	5.5	8.6	7.0	10.9	8.9	5.8	11.6	12.8	11.3
1953	12.6	9.1	12.1	8.3	6.1	8.4	6.7	5.0	8.2	16.2	12.8	12.8
1954	15.4	15.2	10.6	11.0	10.7	7.1	11.0	8.6	13.8	15.3	14.9	16.3
1955	11.2	18.6	13.9	13.2	10.9	10.6	10.0	11.7	16.2	16.8	13.3	15.1
1956	15.9	15.3	13.6	12.3	12.7	8.0	9.1	10.5	10.7	11.8	10.5	9.8
1957	10.2	10.8	10.0	7.7	3.9	4.1	7.0	8.6	8.6	11.8	9.4	11.5
1958	11.0	13.4	11.3	6.1	3.4	10.3	2.9	10.8	8.6	12.0	13.4	8.5
1959	15.0	11.1	10.1	11.7	5.5	10.0	5.9	11.3	8.5	11.2	13.8	14.5
1960	11.0	12.5	9.4	9.1	8.3	5.4	9.3	9.7	12.5	12.7	12.6	10.5
1961	12.3	14.9	9.5	13.0	4.8	4.4	1.6	4.0	10.0	10.1	11.5	12.0
1962	12.4	11.1	10.6	10.2	10.6	7.5	7.3	11.0	13.0	14.2	10.6	13.2
1963	16.2	13.5	14.9	8.2	5.0	6.0	11.9	7.9	7.5	7.7	12.9	10.6
1964	12.3	13.0	13.0	11.1	6.4	9.9	8.7	11.2	13.1	10.3	9.5	12.8
1965	12.5	12.9	10.1	8.0	4.5	3.2	3.2	6.3	6.7	11.3	8.3	10.2
1966	10.5	13.7	10.4	7.8	3.3	10.4	5.0	10.3	12.0	10.4	11.1	13.8
1967	14.3	15.5	12.7	6.3	9.1	11.6	13.9	11.0	12.5	10.7	11.0	12.5
1968	15.9	12.9	14.8	8.3	7.5	10.8	8.3	6.3	4.8	12.0	10.2	12.7
1969	10.2	14.7	12.7	7.1	6.0	6.3	3.5	8.6	8.2	10.5	15.9	13.1
1970	12.8	12.8	9.8	7.0	12.4	10.2	10.2	10.0	11.9	13.3	16.5	16.8
1971	15.5	16.0	15.2	11.2	14.3	11.1	5.2	12.0	12.7	11.3	14.5	15.1
1972	10.4	11.5	13.4	7.5	.6	.3	5.5	3.2	4.8	8.2	10.2	8.9
1973	12.5	12.7	13.0	3.9	7.6	9.5	8.4	10.7	13.6	13.0	16.2	16.5
1974	16.8	17.1	15.4	9.5	6.1	10.1	9.4	5.3	11.2	13.4	15.7	13.0
1975	11.6	8.6	13.8	8.7	3.8	8.6	8.8	13.4	13.3	14.0	13.6	14.9
1976	14.5	15.0	13.7	6.7	2.4	3.5	3.1	8.2	5.2	7.2	11.0	7.6
1977	10.2	15.0	8.0	5.3	2.3	5.9	11.1	10.0	4.8	7.0	11.5	10.5
1978	13.1	9.7	9.6	6.0	7.8	9.1	7.6	10.7	10.3	6.9	9.1	11.6
1979	11.0	13.1	10.9	4.5	3.7	9.7	2.7	1.1	9.2	10.1	8.3	9.9
1980	13.6	12.2	9.4	8.6	7.4	7.5	6.6	7.3	6.5	12.4	10.3	10.5
1981	16.5	15.0	8.0	7.3	7.6	6.4	8.0	7.4	6.2	9.5	13.6	13.2
1982	14.2	14.4	12.2	4.2	6.3	6.9	2.9	1.5	4.0	6.8	5.3	7.2
1983	3.9	4.3	7.3	7.2	5.8	6.4	4.6	9.0	10.9	10.5	12.4	10.5
1984	9.9	13.6	10.9	5.6	7.0	6.6	8.4	6.5	6.5	10.6	12.5	14.2
1985	13.1	14.2	13.4	12.7	8.3	4.8	5.9	13.0	10.1	****	****	****

of the SST-2°C isotherm indicates the thickness of the mixed layer which provides a measure of the depth of the thermocline and hence, relates to upwelling and availability of nutrients to the euphotic zone. This definition of mixed layer is similar to that used by Robinson and Bauer (1976), except that they chose the depth that is 2°F (1.1°C) less than the SST. The SST-2°C depth was selected for defining the depth of the thermocline from smooth average temperatures because 2°C is larger than the small positive and negative temperature changes near the surface that are present in both the raw data and the analyzed values. Also, a temperature change of 2°C is large enough to reach the large gradients found in the thermocline.

The 14°C isotherm is at depths of 80 to 180 m off Peru and is below the strongest gradients of the thermocline. Variations in the depth of the 14°C isotherm are indicators of large-scale vertical movements of the water column, such as upwelling. Also, Barilotti et al. (1984) related the depth of the 14°C isotherm off San Diego, California, to the depth of the thermocline and hence to the supply of nutrients for kelp growth.

Heat content down to SST-2°C is an indicator of the overall environmental change in the euphotic zone. Combined with wind-derived Ekman transports (Bakun, this vol.; Mendo, this vol.), these vertical temperature parameters can be used to describe the offshore velocity structure which is critical to the reproductive success of the anchoveta (Parrish et al. 1983, and other contributions in this vol.).

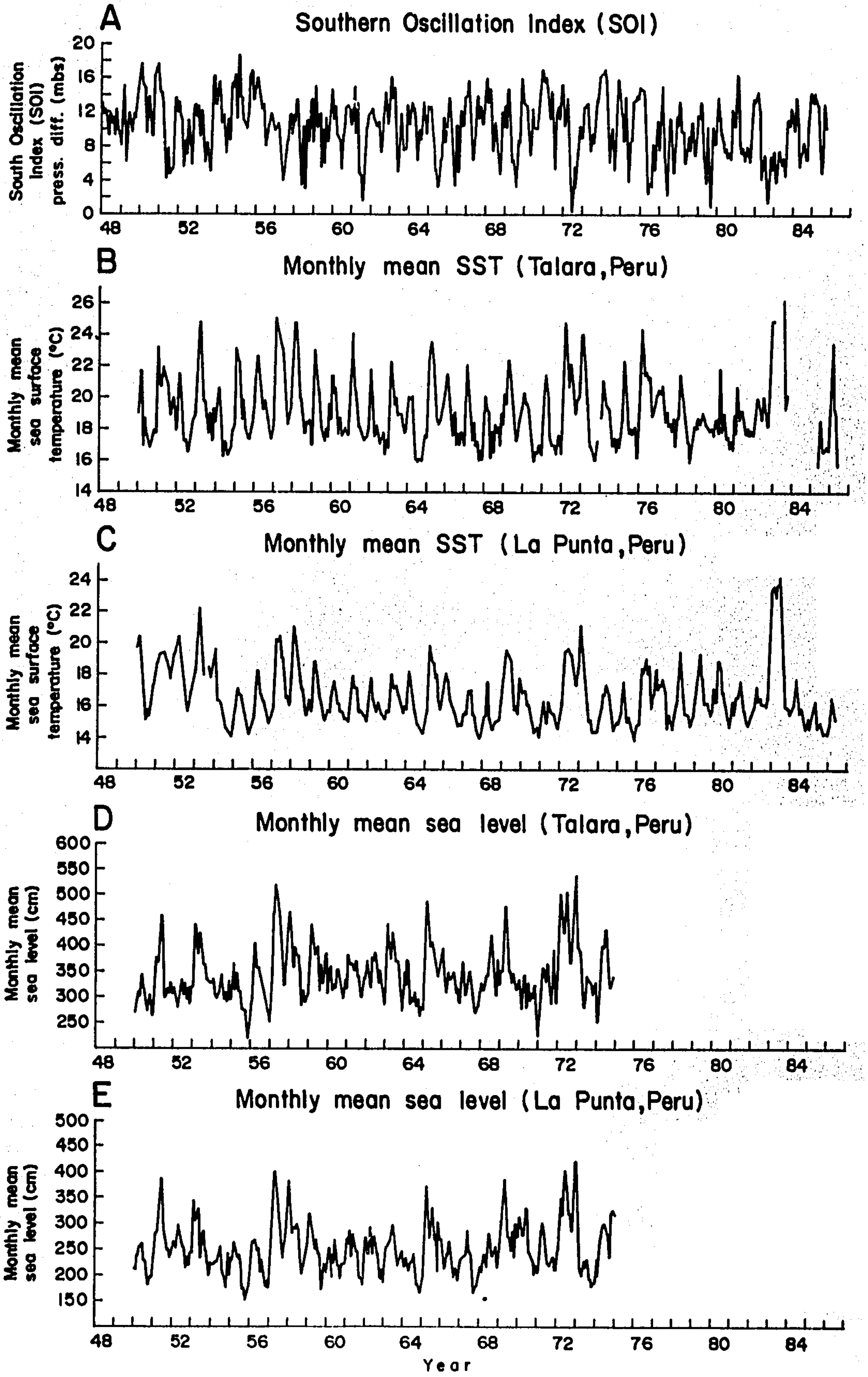


Fig. 1. Time series of monthly means of (A) Southern Oscillation Index (difference of surface barometric pressure in millibars between Easter Island and Darwin, Australia), (B and C) SST in degrees C, and (D and E) sea level in cm at Talara and La Punta, Peru. Values are computed as monthly means of daily observations.

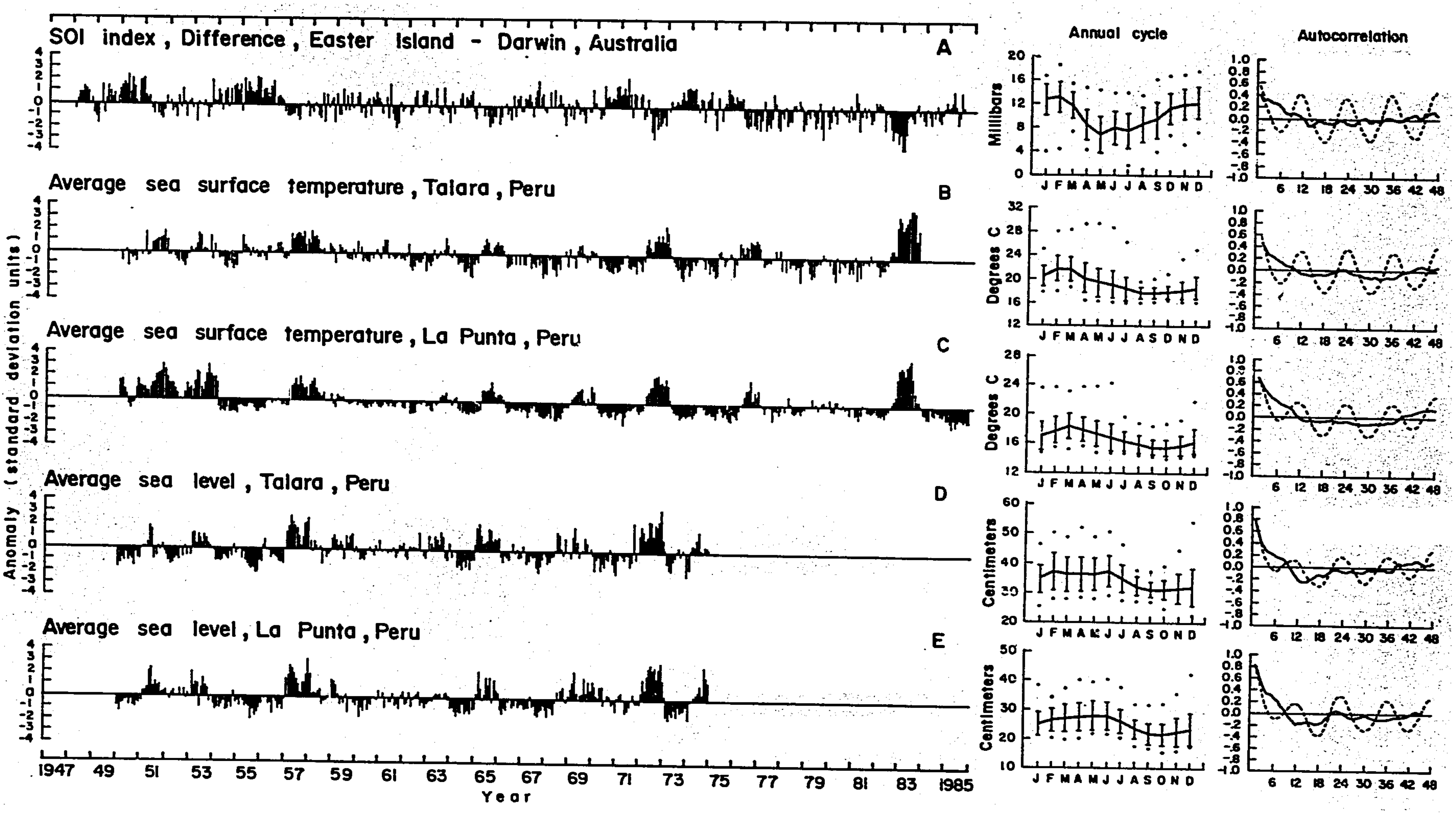


Fig. 2. Annual cycles, autocorrelation functions, and anomalies of monthly means of daily observations at coastal and island stations. Parameters are (A) Southern Oscillation Index, (B and C) SST, and (D and E) sea level at Talara and La Punta, Peru. The annual cycle plot (center) shows the long term (1943-1986) monthly means, between-year standard deviations (bars), and range of interannual variability (dots). The autocorrelation function plot (right) shows the autocorrelation of each original data series (dotted) and the autocorrelation of each anomaly series (solid). The time series of anomalies from 1941-1986 mean (left) are shown in standard deviation units for intercomparison between data series. Based on data in Tables 1-5.

Mean values of the four parameters were computed for each month for the 33-year period from 1952 to 1984 for five areas along the coast from 1 to 17°S (Fig. 3). Each of the given areas spanned 3 degrees of latitude except for the central-most area which spanned 4 degrees. The zonal extent of each area was chosen so that they would extend about the same distance offshore, roughly 300 km. In addition, all data prior to 1952 were combined to form a single composite year. Thus, the resulting fields of monthly means for each parameter for the 5 areas covers 34 years (408 months), for a total of 2,040 cells. The average value for the region from 4 to 14°S was obtained by averaging the values computed for the three central areas. Mean temperature at 25 m depth intervals from the surface to 350 m were also computed for the central area to show vertical variations of temperature with time. The data are plotted as contour isograms of latitude (area) or depth *vs.* month to show both seasonal and interannual variations.

Table 2. Monthly mean sea surface temperature in degrees Celsius at Talara, Peru. Data courtesy of Dr. D. Enfield, Oregon State University.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1950	19.0	21.6	21.7	16.9	18.6	17.6	17.3	16.8	17.6	17.9	17.7	18.1
1951	23.2	20.6	20.9	21.9	21.4	21.1	20.5	18.8	18.9	19.8	19.6	17.9
1952	19.8	21.4	20.6	18.4	17.2	17.3	16.5	16.5	17.1	17.7	18.6	18.8
1953	20.8	23.0	24.8	23.6	19.7	19.7	18.8	17.7	19.0	17.2	19.2	18.4
1954	19.5	20.6	20.4	17.2	16.2	17.1	16.4	16.3	16.7	16.7	17.9	18.2
1955	22.8	22.9	22.4	20.9	18.6	19.7	18.0	17.8	17.3	17.4	18.3	17.9
1956	19.2	22.6	22.5	20.3	19.5	19.3	19.8	18.5	18.1	17.4	17.4	17.9
1957	20.7	25.1	24.3	23.9	23.4	22.8	21.0	19.4	18.3	19.1	19.4	22.1
1958	22.8	24.8	23.8	21.0	19.9	19.7	18.2	17.7	18.4	18.4	18.6	17.0
1959	20.3	23.0	22.4	20.6	19.9	18.1	17.5	17.2	18.0	17.5	19.6	18.6
1960	21.3	20.3	20.6	18.7	17.7	18.7	17.6	17.7	18.0	17.8	17.6	19.6
1961	22.4	24.1	20.7	20.1	18.9	18.1	17.8	17.6	17.3	17.5	17.5	18.1
1962	21.8	19.3	18.7	17.6	18.2	17.5	17.1	17.3	17.8	16.4	17.2	16.8
1963	19.4	22.3	20.8	19.6	19.9	18.9	19.0	19.0	18.4	17.8	17.9	19.2
1964	20.1	19.9	20.1	18.5	16.1	16.0	16.1	16.0	16.0	17.0	17.6	17.5
1965	20.3	22.5	23.3	23.5	22.0	19.8	18.6	18.3	18.5	19.1	19.4	20.2
1966	21.2	21.5	19.4	17.9	17.6	19.1	17.0	17.7	17.0	17.8	17.2	17.1
1967	20.5	22.1	19.4	18.5	17.3	18.4	16.9	17.1	16.1	16.4	16.1	18.1
1968	20.1	19.3	19.1	16.2	17.9	16.6	18.3	17.8	18.1	17.0	19.0	18.4
1969	20.2	19.7	22.4	22.3	21.6	19.7	18.2	17.3	17.5	18.4	18.8	19.2
1970	20.3	19.8	19.6	19.3	18.0	16.8	16.0	16.5	16.5	17.0	16.5	16.5
1971	19.5	20.5	21.5	20.5	17.5	17.0	17.0	17.0	16.5	17.5	17.5	16.5
1972	19.8	23.9	24.8	22.3	20.7	22.2	21.0	19.5	19.0	19.9	20.1	23.3
1973	24.0	23.6	21.9	19.4	17.9	16.9	16.7	16.2	16.0	17.0	17.3	16.0
1974	18.8	21.2	20.4	19.5	19.4	19.1	18.0	16.9	17.4	16.6	17.4	16.9
1975	17.8	18.6	22.4	21.5	19.8	17.8	18.0	17.7	18.1	18.1	16.2	17.7
1976	20.5	24.4	23.6	21.4	21.7	21.2	21.2	19.0	18.9	19.5	20.1	20.3
1977	20.5	20.3	20.8	19.4	18.5	19.1	18.2	18.3	17.9	18.7	16.9	18.7
1978	18.7	21.5	20.1	19.1	18.6	17.3	17.2	15.9	17.3	17.8	18.2	18.1
1979	18.7	18.3	18.7	19.0	18.7	18.3	18.2	18.1	17.9	18.0	17.6	18.5
1980	18.6	17.8	21.8	17.8	19.0	18.4	17.4	17.5	16.8	17.2	16.7	18.9
1981	17.7	20.7	18.6	19.2	19.1	18.7	17.7	18.0	17.6	17.9	17.7	17.7
1982	18.4	19.9	19.9	19.6	18.7	20.0	20.0	18.5	18.2	20.9	23.4	24.9
1983	24.9	27.9	28.3	29.2	29.2	28.5	26.2	19.3	20.1	****	****	****
1984	****	****	****	****	****	****	****	****	****	****	****	****
1985	****	****	****	****	15.7	18.6	17.0	16.6	16.7	16.9	16.7	18.6
1986	20.2	23.5	19.4	18.8	15.7	****	****	****	****	****	****	****

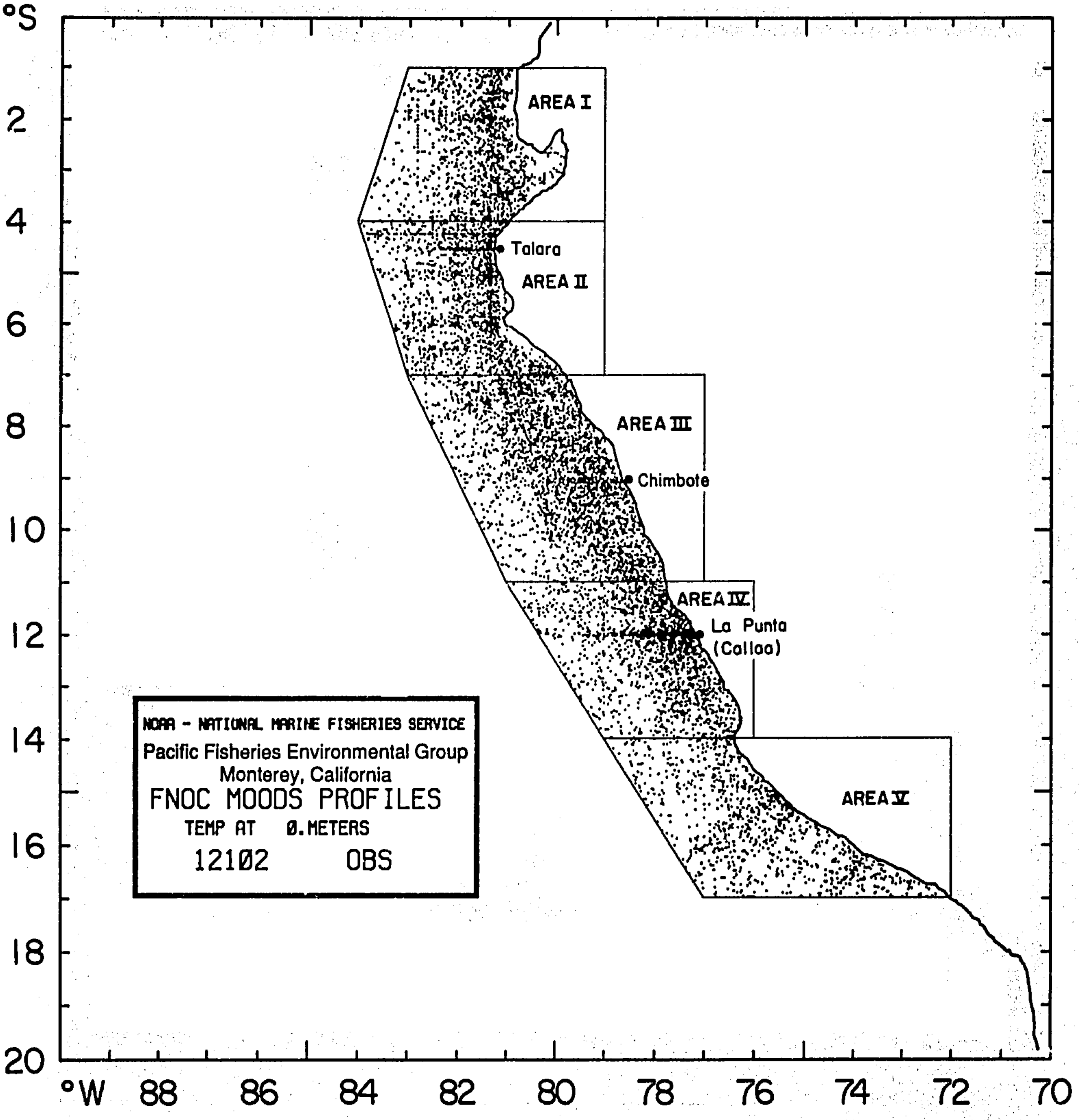


Fig. 3. Locations of five areas along the Peru coast for which subsurface temperature profiles were extracted from the FNOC MOODS and used to perform analyses of surface and subsurface temperature. A total of 12,102 profiles were extracted from the MOODS files for all five areas for SST analyses. Area I is the northernmost area and Area V, the southernmost.

Table 3. Monthly mean sea surface temperature in degrees Celsius at La Punta, Peru. Data courtesy of Dr. D. Enfield, Oregon State University.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1950	19.8	20.4	19.6	18.3	16.3	15.1	15.6	15.4	16.3	17.2	17.2	17.9
1951	18.7	18.9	19.3	19.3	19.4	19.2	18.9	18.5	17.7	18.7	19.2	19.2
1952	19.5	20.0	20.4	19.2	18.1	16.7	16.0	15.7	15.9	16.8	16.9	17.9
1953	18.2	20.3	22.3	21.5	19.0	18.0	****	****	18.4	17.8	18.3	19.2
1954	19.6	16.3	16.4	16.2	15.5	15.2	14.7	14.5	14.4	14.2	14.1	15.2
1955	15.9	16.5	17.1	16.7	16.6	15.9	15.6	15.0	14.4	14.2	14.7	15.1
1956	15.4	17.2	18.2	17.8	16.7	16.5	16.0	15.8	15.3	14.9	15.2	15.5
1957	15.9	19.2	20.2	20.0	20.4	19.1	18.9	17.5	16.5	16.6	16.1	18.3
1958	19.9	21.0	20.0	18.9	18.1	17.3	17.1	15.9	15.5	15.4	16.4	15.7
1959	15.8	18.4	18.8	18.1	17.7	16.5	16.0	15.5	15.2	15.2	15.7	15.6
1960	16.7	17.2	17.6	16.9	16.2	16.1	15.6	15.6	15.4	15.1	15.2	15.0
1961	16.2	17.6	17.9	17.1	17.2	15.9	15.6	15.7	15.5	15.4	15.1	15.3
1962	16.8	17.8	16.5	16.1	15.7	16.3	16.0	15.6	15.5	15.4	15.2	15.7
1963	15.6	16.3	18.1	17.3	17.1	17.3	16.9	16.5	16.2	15.6	15.9	15.8
1964	17.3	18.2	17.3	16.7	15.8	15.4	14.9	14.7	14.6	14.3	14.5	14.9
1965	15.4	16.5	19.9	19.6	18.9	18.6	17.8	18.0	16.4	15.9	16.6	17.4
1966	17.9	18.1	17.6	16.5	16.1	15.9	15.6	15.1	14.8	14.9	14.8	15.4
1967	15.6	15.5	17.0	17.0	17.0	15.5	15.3	14.6	14.3	14.0	14.1	14.6
1968	15.3	15.4	17.6	15.5	14.9	14.6	14.6	15.0	15.1	15.1	15.4	16.4
1969	17.4	18.6	19.5	19.6	19.2	19.1	16.7	15.8	15.9	15.6	17.8	17.8
1970	16.9	17.0	17.0	16.1	16.1	15.6	15.0	14.5	14.4	14.7	14.1	14.8
1971	15.5	16.3	15.1	16.0	16.3	15.8	15.6	15.5	15.3	14.8	14.8	15.3
1972	16.0	17.6	19.5	19.5	19.7	19.4	19.3	18.8	17.9	17.4	18.2	19.0
1973	21.1	20.5	19.0	17.4	16.2	15.1	15.2	14.4	14.4	14.4	14.4	14.8
1974	15.3	15.8	16.8	16.8	17.3	16.9	16.3	15.5	14.7	14.6	15.0	14.9
1975	15.3	15.6	17.2	17.6	16.6	15.1	15.3	14.7	14.2	13.9	14.8	14.9
1976	14.8	16.9	18.4	18.2	18.5	19.0	18.1	18.6	15.9	16.6	16.9	18.3
1977	17.1	17.4	17.3	17.7	17.2	16.6	14.6	15.5	15.0	14.6	15.3	15.6
1978	16.2	17.7	19.5	18.1	16.5	15.6	15.5	15.5	14.8	15.1	15.5	16.2
1979	17.0	17.8	19.4	17.9	17.6	16.2	16.2	16.2	15.8	15.5	15.7	17.2
1980	16.3	16.9	18.9	18.6	17.3	16.7	16.4	15.6	15.3	14.7	15.7	16.3
1981	15.5	16.6	16.5	16.8	17.6	16.7	15.7	15.4	14.9	14.9	15.3	15.5
1982	15.6	16.3	17.3	16.4	16.6	16.2	16.2	16.2	16.0	16.5	19.0	21.7
1983	23.5	23.6	23.0	23.7	23.8	24.2	19.6	17.4	16.0	16.0	15.9	15.5
1984	15.8	16.1	16.7	17.9	16.4	15.6	15.8	15.5	14.8	14.6	15.2	14.7
1985	15.1	15.5	15.5	16.3	14.7	14.7	15.0	14.7	14.3	14.3	14.2	14.3
1986	14.7	16.6	15.9	15.3	15.2	****	****	****	****	****	****	****

Data Acquisition and Processing

Data Sources

The profiles of subsurface temperature for the Peru coastal region were acquired from the US Navy Fleet Numerical Oceanography Center (FNOC) in Monterey, California. The profiles were obtained by merchant, naval and research vessels of many nations using a variety of sampling instruments, including bottle casts, mechanical bathythermographs (MBT), expendable bathythermographs (XBT) and electronic conductivity/temperature/depth profiles (CTD). The capability and accuracy of these instruments vary widely: MBTs, with typical accuracies of 0.3 to 1.0°C, were used until the development of XBTs in the 1960s. Generally, MBTs reached depths of only 100-200 m, whereas the newer XBTs are capable of depths to 450, 700, or even 1,500 m. The accuracy of XBTs are typically 0.1 to 0.4°C. Bottle casts and CTD casts from research vessels are capable of any depth, with typical cast depths to 1,000 or 1,500 m and accuracies of 0.001 to 0.1°C. Profiles from all of these sources are normally mailed to oceanographic data centers and assembled into common data sets. The time lag between observation and final assembly of the data by the data centers may be 5 to 10 years or longer. To reduce this time lag, many of the profiles are manually digitized and transmitted by radio in near

Table 4. Monthly mean sea level (cm) at Talara, Peru. Data courtesy of Dr. D. Enfield, Oregon State University.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1950	267	287	310	301	342	318	310	294	275	303	272	264
1951	344	373	366	386	460	[illegible]	303	301	317	307	328	307
1952	315	302	281	291	312	333	303	325	295	317	285	318
1953	316	442	431	383	425	412	363	358	334	327	326	323
1954	333	305	301	300	310	342	313	297	307	292	329	294
1955	339	363	314	346	310	308	276	274	272	249	219	260
1956	293	383	402	357	356	335	323	306	295	280	263	247
1957	342	455	471	519	487	471	426	357	321	343	420	455
1958	463	410	355	395	381	377	354	285	311	292	298	311
1959	385	442	407	382	394	393	312	358	326	349	380	309
1960	354	354	312	323	317	352	351	329	309	299	333	316
1961	380	365	362	366	351	370	341	330	300	305	336	339
1962	371	336	319	377	369	386	355	327	352	314	295	286
1963	343	442	394	376	425	417	369	369	344	293	275	351
1964	322	373	356	286	299	291	309	282	297	264	279	274
1965	368	486	487	432	397	407	385	379	357	340	367	379
1966	395	342	310	343	336	337	345	344	310	317	291	292
1967	364	367	303	318	347	350	330	282	269	274	285	312
1968	328	313	317	338	344	379	421	369	320	306	374	327
1969	351	343	434	478	411	351	348	330	344	337	317	331
1970	334	278	328	341	281	328	292	307	299	322	273	226
1971	260	333	355	347	331	364	336	289	294	392	289	327
1972	412	501	461	427	436	505	463	367	374	384	445	539
1973	397	386	309	285	281	341	335	330	325	306	330	321
1974	254	284	376	400	396	431	427	333	318	332	341	343

Table 5. Monthly mean sea level (cm) at La Punta, Peru. Data courtesy of Dr. D. Enfield, Oregon State University.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1950	212	212	239	246	258	261	228	225	185	181	197	197
1951	232	279	285	305	378	388	289	269	247	251	236	247
1952	265	265	254	284	296	275	256	251	215	234	218	244
1953	245	343	308	325	328	232	286	283	249	239	199	224
1954	221	220	226	226	242	256	212	200	195	178	239	202
1955	234	232	263	254	235	241	223	174	177	152	161	178
1956	222	264	262	269	246	252	204	229	202	178	190	175
1957	240	325	355	400	393	371	319	267	233	259	281	332
1958	383	341	280	291	290	297	283	216	202	207	229	245
1959	309	317	317	286	249	270	240	240	171	211	220	207
1960	223	253	196	237	223	266	219	221	195	219	219	223
1961	272	261	285	236	280	258	245	245	193	195	181	244
1962	270	241	248	290	241	273	268	244	236	193	208	188
1963	228	251	260	264	285	294	269	247	218	230	245	243
1964	217	234	222	208	224	221	241	196	181	178	165	182
1965	214	281	373	314	273	291	329	270	282	207	300	269
1966	270	227	213	239	233	264	257	212	198	214	193	207
1967	231	233	236	240	287	248	240	195	166	177	182	205
1968	216	207	240	240	221	267	282	237	245	254	220	222
1969	262	296	337	387	306	277	274	250	285	237	300	272
1970	312	309	283	278	331	328	246	236	231	226	205	218
1971	211	270	288	302	279	226	224	219	220	234	212	215
1972	237	287	350	317	381	402	379	318	319	287	354	421
1973	316	276	212	201	227	217	229	193	198	179	186	187
1974	230	202	268	276	295	301	290	275	236	322	325	319

real-time as BATHY messages for support of real-time ocean analyses. BATHY messages, although more timely, require additional editing to correct digitizing and transmission errors. With improved digital data acquisition and satellite data transmission systems, the time lags and transmission errors are being reduced.

Subsurface temperature profiles from many available sources have been assembled by FNOC in the Master Oceanographic Observations Data Set (MOODS). MOODS is in a compact binary format and contains almost 5 million subsurface temperature profiles globally. The MOODS file is by no means a complete file of all ocean temperature profiles that have even been made; rather, it is only that subset which have been made available to FNOC and merged into the file. Probably many additional profiles exist and if obtainable, could be used to improve analyses of historical conditions. At present, MOODS occupies 12 reels of magnetic tape and is sorted in the sequence: month, 1 degree square of latitude and longitude, year, day and hour. For compactness, many of the temperature profiles are stored at significant or inflection points so that the original data can be recreated by linear interpolation between inflection points.

The distribution of the profiles in time and space is critical for making consistent time series of subsurface temperature. A total for all years of only 12,102 profiles were available in the MOODS file for the five areas along the Peru coast (Fig. 3). Temperature profiles off Peru are almost nonexistent in the MOODS file for the years prior to 1955 but are more abundant for the years from the late 1950s to the early 1970s. Lags in data assimilation have reduced the amount of data in MOODS since the mid-to-late 1970s, with most of the recent data being acquired via BATHY messages. Profiles taken prior to 1952 have been included in the analysis by combination into the single composite year, labelled "1951" in the plots and tables. Inclusion of early profiles in the analysis is useful to help establish the edition scheme and to improve the long-term means.

In addition to an insufficient quantity of profiles over the 33-year analysis period, many of the available profiles are very "patchy" in their distribution. A cell in the data fields having 100 or more observations is often surrounded by many cells with no observations. This inhomogeneity of the data fields reflects the fact that relatively large numbers of temperature profiles are taken during short, localized research expeditions.

The subsurface temperature profiles in the MOODS file suffer from many types of errors. Teague et al. (1985) have described some of the errors based on samples of the data for the North Atlantic. Many of the profiles have erroneous spikes and tails which require editing, whereby the profiles are truncated to retain the portion of the profile above the erroneous data. About 1 to 5% of the profiles are from incorrect positions or times, as evidenced by reports from land areas. No attempt was made in this analysis to correct for position and time errors of the profiles as this would have required resorting the profiles into original cruise sequences and tracking each ship individually.

Because of the errors in profiles and more importantly insufficient distribution of observations in time and space, a complicated scheme was necessary to compute reasonable monthly mean values. Thus, the MOODS profiles were edited, monthly means were computed, and then the means were interpolated to fill gaps in coverage.

Editing Scheme for Subsurface Temperature Profiles

The first stage of editing the profiles was a gross error check requiring all reported temperatures to be in the range of -2.0 to +38.0°C and all depths to be nonnegative and increase sequentially. No two temperatures were allowed from the same reported depth; in such cases (which are rare), the depth of the second reported temperature was increased by an arbitrary value of 1 m. In order to eliminate gross error spikes, the size of allowable temperature changes between successive reported depth levels was limited between +2.0 and -12.0°C. When data were rejected by these edits, the profile was truncated at the depth of failure and the remaining upper portion of the profile was retained.

The second stage of profile editing checked for unusually strong positive and negative vertical temperature gradients to further reduce unreal spikes and vertical gradients. In the surface layer and thermocline, where the water temperatures were greater than 6.0°C, the vertical temperature gradients were required to be in the range of -2.0 to +0.5oC per meter of depth. For reported temperatures less than 6.0oC, the allowable gradients were tightened to -0.5 to +0.1oC/m. As for the first stage editing, when gradients exceeding these limits were encountered, the profiles were truncated and the remaining, upper portions of the profiles were retained.

The third stage of editing was a check against the mean and standard deviations of a running series of 10 values of a temperature editing parameter. For SST, depths of the 14oC and SST-2oC isotherms and heat content, the computed parameter itself was used as the editing parameter. For the vertical temperature series, the temperature at 100 m was interpolated from each profile and used as the editing parameter. The running series was started with the first 10 profiles for each month and 1 degree square of latitude and longitude. (Because the data were sorted in the sequence: month, 1 degree square, year, day and hour, the first 10 profiles in a one degree square were often from years earlier than 1952 and thus errors in the first 10 profiles did not cause serious contamination of the 1952-1984 time series). After acceptance of the first 10 profiles, the mean and standard deviation of the running series of 10 editing values were computed and used to check the next profile. A new profile was accepted if the editing parameter computed from it was within a specified tolerance of the mean of the previous 10 values, where the tolerance was arbitrarily defined to be 1.3 times the standard deviation of the previous 10 values. Each new accepted value was then added to the series and the oldest value in the series deleted. Use of the running series of 10 values allowed the editing mean to move up or down with warm and cold periods defined by the data themselves. Similarly, the scheme allowed the editing tolerance range to widen as the data became more variable (in periods of climatic change or in areas near oceanic boundaries) and to narrow as the data became less variable (during more stable periods or in areas far from oceanic boundaries).

Computation of Individual Monthly Mean Values

After editing the temperature profiles as described above, values of the four parameters (SST, depth of the 14oC isotherm, depth of the SST-2oC isotherm, and heat content down to the SST-2oC isotherm were computed for each profile. Individual monthly means of the four parameters were computed for each cell (5 areas x 408 months) for the years 1951 to 1984. The resulting monthly mean fields were very sparse, having mean values in only about 37% of the 2,040 total cells.

Temperatures at 25 m depth intervals from the surface to 350 m were computed from each profile to display vertical variations of temperature versus time in each of the five areas. The data were processed as differences between the surface temperature and the temperature at each 25 m depth interval because of the effect of varying maximum depths of the profiles. Direct computation of mean temperatures from profiles of varying maximum depth can cause unrealistic subsurface temperature gradients (Robinson and Bauer 1976).

After computation of the individual monthly mean values, the 12 long-term monthly means and 12 between-year standard deviations were computed for each area (or depth for the vertical plots). Here, long-term mean is defined as the mean of all the individual monthly means, e.g., the January long-term mean is the mean of all individual January monthly means. The between-year standard deviation (bysd) is the standard deviation of the individual monthly means computed by month to show the interannual variability. The monthly anomalies were then computed as the differences between the individual monthly means and the appropriate long-term monthly mean, e.g., the January 1952 anomaly is the individual monthly mean for January 1952 minus the January long-term mean.

In some cases, no profiles were available in a month during any year for an area (or depth). In these cases, it was not possible to compute a long-term monthly mean. Such gaps in the long-term mean field were filled using a 5 x 5 matrix interpolation which used information from surrounding long-term means. Empty cells were filled with averages of surrounding mean values, weighing proportionately to the square root of the number of years of data represented by the mean and inversely to the square of the distance (in grid lengths) away from the cell.

The fields of individual monthly mean values were rather noisy, particularly those computed from small numbers of profiles which are considered less reliable than those based on relatively large numbers of profiles. To reduce the errors associated with limited numbers of profiles, the individual monthly means were adjusted toward the long-term mean for each month, i.e., means based on only a single profile were set to the average of the mean and the long-term mean for that month, while means based on two or three profiles were weighed proportionately less toward the long-term mean.

Monthly anomalies were computed as the difference of the adjusted individual and long-term monthly means. To partially fill the gaps in the anomaly field between data values, the same 5 x 5 matrix interpolation scheme was used as for the long-term means, weighing proportionately with the square root of the number of profiles represented by the mean and inversely with the square of the distance away from the cell. In regions that were 3 or more cells away from mean values, no interpolation of the anomaly was made. Use of this interpolation scheme increased coverage of the field from about 37% to about 91%. Use of a 5 x 5 matrix interpolator was reasonable as autocorrelation functions (not shown) of the individual monthly means were computed and had magnitudes greater than 0.4 for lags of at least two months in time and at least three areas (9 degrees of latitude) along the coast in space. The correlations are in agreement with Enfield and Allen (1980) who showed similar strong coastwise coherence of sea level and SST along the coast of North and South America from Alaska to Chile.

After adjustment and interpolation of the anomaly field, the fields of individual monthly means were recomputed. Gaps in the coverage were partially filled by the addition of the interpolated anomaly field and the long-term mean field. Use of the anomaly fields to interpolate the monthly mean fields for filling gaps in coverage is based on the assumption that the anomaly fields are smoother in time and space than the monthly means. This assumption is justified because of the large seasonal changes that are observed in the monthly means but relatively smoother changes in the anomalies (see, e.g., Fig. 2, autocorrelation functions).

Spatially Averaged Monthly Means for the 4 to 14oS Region

Monthly anomalies for the three central areas were further averaged to make time series of monthly mean anomalies for the entire region from 4 to 14oS. The averaged monthly anomalies were then added to the appropriate averaged long-term means to obtain time series for the four computed parameters by month for the region 4-14oS. Plots and tables of the time series values are presented along with the total combined number of observations for the three central areas. Values are only given if observed or interpolated mean values were available for all three areas. This requirement reduced the coverage of the time series to about 90% of the 408 possible months. For cases where anomaly values were not available for each of the three areas for any particular month, asterisks are printed in the tables and values are not plotted.

Results and Discussion

Each of the parameters (SOI, SST, sea level, depth of the 14oC isotherm, depth of the SST-2oC isotherm, vertical structure of subsurface temperature and heat content from the surface to the SST-2oC isotherm) is presented separately. The data are displayed in a variety of formats to emphasize the seasonal and interannual scales of variability, both horizontally along the coast and vertically through the water column. For each of the parameters, tables and plots of spatially-averaged (for the region from 4-14oS) monthly means are presented. Plots of the long-term annual cycle, between-year standard deviation, monthly anomaly in standard deviation units, and autocorrelation functions of the anomalies for each of the parameters are presented to describe seasonal and interannual variability. Also, time-latitude and time-depth contour plots of profile data are presented to show horizontal and vertical variations of subsurface temperature.

Southern Oscillation Index

Time series of the monthly mean Southern Oscillation Index (Fig. 1A, Table 1) and anomaly of SOI (Fig. 2A) show the buildups and subsequent declines of pressure differences associated with the onset of El Niño, as described earlier. Major buildups and declines occurred in 1949-1952, 1954-1958, 1970-1972 and 1975-1977. The most recent decline in 1982-1983, associated with that strong El Niño, followed a long period (1976-1981) of relatively weak negative pressure difference. There was also a sharp decline in 1979 associated with a weak coastal warming event in that year. Perhaps the 1979 event would have been more notable (more comparable to other moderate or weak El Niños) if it had not occurred during an already warm period.

The SOI has a relatively strong annual cycle (Figs. 1 and 2) which varies from a peak difference of about 13 mbs in February, indicating strongest trade winds in late austral summer to a low of about 7 mbs in May, indicating weakest trade winds in late austral fall. The interannual variability of SOI is relatively constant throughout the year as indicated by the similar values of between-year range and standard deviation. The SOI is moderately persistent in time with an autocorrelation of anomaly of about 0.4 at one month lag. From 12 to 36 months lag, the autocorrelation of the anomaly remains very close to zero, then becomes weakly positive at lags of 36-48 months. This suggests that the period of important interannual changes in the SOI is greater than 3 years, in agreement with the frequently reported period for El Niño of 3-7 years.

Sea Surface Temperature

Time series of monthly mean SST (Figs. 1B and 1C, Tables 2 and 3) and anomaly of SST (Figs. 2B and 2C) at Talara and La Punta (Callao) and spatially-averaged SST for the region from 4-14°S (Table 6, Figs. 4A, 5A) show significant seasonal and interannual variability of SST. Both the shore station and spatially-averaged SST data show the major El Niño and anti-El Niño events. Positive anomalies occurred in the years 1953, 1957-1958, 1965, 1972-1973, 1976-1977, 1979 and 1982-1983. Each of the figures also show longer period interannual variations: cool conditions in the early 1950s, warm conditions in the late 1950s, moderately cool conditions throughout the 1960s and early 1970s (except the 1965 and 1972-1973 El Niños), and finally a long-term warming during 1976-1983. Comparison between the two shore stations, Talara in the north and La Punta in the south, shows the northerly station to have more low-amplitude, high frequency variability than the southerly station. This difference is assumed to be caused by the more complicated equatorial ocean dynamics occurring in the northern region.

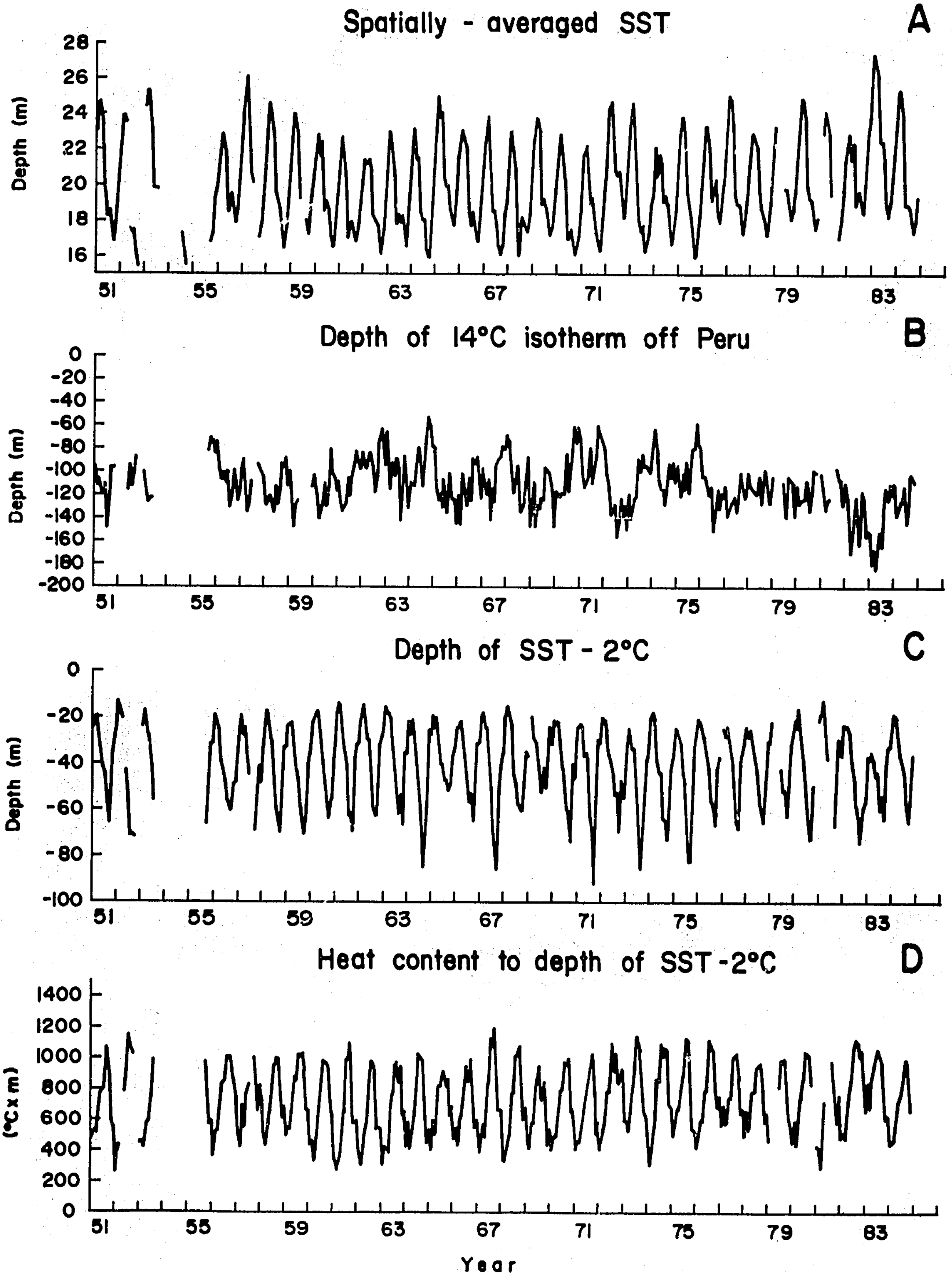
Along the coast, the El Niño events of 1953, 1957-1958, 1965, 1969, 1972-1973, 1976-1977 and 1982-1983 (Rasmusson 1984) are seen as tongues of warm SST, extending variable distances southward (Fig. 6). A moderate warming occurred in 1979-1980, in agreement with the below normal SOI that year. The extreme magnitude (large region of SST > 28°C), duration, and coastwise coherence of the 1982-1983 event distinguish it as the most significant warm feature of this series. The poorly documented 1953 El Niño shows a surprisingly strong surface manifestation of warm water. The 1954-1956 cold event is only weakly evident, probably due to sparse data. With the exception of the 1982-1983 warm event, each of the warm surface events are shown to be preceded by a period of anomalously cool SST.

The annual cycles of SST at the two shore stations (Figs. 2B and 2C) and for the spatially-averaged region (Fig. 7A) vary from highs during the austral fall to lows during the austral spring. The amplitude of the annual variation of SST is greatest nearer to the equator and the complex dynamics associated with the interaction of equatorially-trapped waves with the eastern boundary (Fig. 6). The spatially-averaged long-term means (Fig. 7A) show high SST (>23.5°C) from January through March or April, when warm water intrudes from the north, followed by a rapid transition to lower temperatures in April with the onset of upwelling along the central and southern portions of the coast. SSTs of 17-19°C occur during the upwelling regime from May to October along the coast, except for the northernmost area where upwelling is weak.

Along the coast, the annual cycle is strong, varying between upwelling and nonupwelling regimes for the central and southern areas and the weak seasonal variation for the northern area.

Table 6. Monthly mean surface temperature (C) for the region 4-14° off Peru. These means are averages of the monthly means for the three Central areas, computed from subsurface temperature profiles. The corresponding number of profiles used in computing each mean is printed (in brackets) to the right of the mean. Means based on zero profiles are computed from interpolated values. Asterisks indicate months in which neither observed nor interpolated means were available in all three areas.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1951	23.0 (1)	24.3 (1)	24.5 (129)	23.5 (0)	19.5 (0)	18.2 (2)	18.5 (36)	17.6 (6)	16.8 (0)	17.6 (0)	19.2 (0)	21.0 (0)
1952	22.8 (35)	23.9 (0)	23.6 (0)	**** (0)	17.5 (0)	17.3 (0)	17.4 (129)	16.2 (0)	15.4 (0)	**** (0)	**** (0)	**** (0)
1953	24.4 (0)	25.2 (0)	25.1 (49)	23.1 (93)	19.8 (23)	19.8 (0)	19.7 (0)	**** (0)	**** (0)	**** (0)	**** (0)	**** (0)
1954	**** (0)	**** (0)	**** (0)	**** (0)	**** (0)	**** (0)	17.3 (0)	16.3 (2)	15.5 (0)	**** (0)	**** (0)	**** (0)
1955	**** (0)	**** (0)	**** (0)	**** (0)	**** (0)	**** (0)	**** (0)	**** (0)	16.8 (0)	17.2 (0)	19.3 (51)	19.7 (95)
1956	21.0 (5)	22.5 (0)	22.8 (0)	22.0 (31)	18.5 (0)	18.4 (0)	19.5 (0)	18.5 (0)	17.8 (31)	18.3 (0)	19.9 (13)	21.5 (0)
1957	23.9 (0)	24.8 (1)	26.1 (33)	23.3 (25)	20.6 (0)	20.1 (0)	**** (0)	**** (0)	17.0 (0)	17.6 (0)	18.8 (15)	21.3 (6)
1958	23.1 (75)	24.5 (10)	24.1 (66)	22.8 (8)	19.6 (4)	19.0 (0)	18.6 (7)	17.2 (0)	16.4 (74)	17.1 (0)	18.6 (5)	21.0 (160)
1959	22.7 (0)	23.9 (0)	23.8 (32)	22.6 (0)	19.2 (0)	**** (0)	**** (0)	18.0 (0)	17.2 (0)	17.9 (4)	19.4 (0)	20.5 (0)
1960	21.4 (0)	22.8 (4)	21.6 (13)	22.3 (51)	18.5 (4)	19.0 (0)	18.7 (0)	17.3 (0)	16.5 (14)	16.8 (97)	18.1 (41)	20.1 (0)
1961	21.5 (0)	22.7 (79)	21.5 (63)	20.2 (60)	17.0 (0)	17.9 (14)	17.7 (9)	17.0 (156)	16.8 (29)	17.5 (8)	19.0 (1)	20.1 (0)
1962	21.4 (93)	21.2 (89)	21.4 (24)	20.8 (98)	18.3 (94)	18.1 (37)	17.7 (47)	16.9 (0)	16.1 (0)	16.9 (18)	17.8 (274)	20.1 (61)
1963	21.6 (33)	22.9 (178)	22.2 (55)	20.7 (69)	17.8 (0)	18.3 (0)	17.9 (55)	18.2 (142)	17.6 (46)	16.6 (155)	18.8 (44)	19.9 (72)
1964	21.7 (0)	23.1 (10)	21.5 (38)	21.5 (0)	18.5 (42)	18.0 (65)	18.0 (3)	16.4 (47)	15.9 (49)	16.0 (8)	18.6 (175)	20.6 (2)
1965	22.6 (0)	24.9 (10)	23.8 (1)	24.1 (43)	20.4 (0)	19.9 (0)	19.9 (31)	18.6 (66)	18.0 (49)	17.7 (26)	19.4 (135)	21.5 (15)
1966	22.2 (0)	23.0 (80)	22.5 (57)	22.0 (17)	18.5 (50)	17.7 (9)	18.5 (0)	17.5 (5)	16.8 (148)	16.9 (2)	18.7 (28)	20.0 (49)
1967	21.8 (0)	22.7 (116)	23.8 (15)	21.4 (5)	18.5 (45)	18.6 (2)	17.8 (2)	16.6 (95)	16.1 (69)	16.5 (0)	18.3 (28)	18.9 (48)
1968	21.3 (0)	22.9 (97)	22.2 (0)	20.8 (2)	16.1 (55)	16.0 (0)	18.1 (0)	18.0 (0)	17.6 (86)	17.4 (38)	18.1 (12)	20.3 (71)
1969	22.4 (46)	23.3 (20)	23.7 (8)	23.0 (2)	18.9 (0)	19.2 (8)	18.7 (53)	17.8 (36)	17.2 (159)	17.5 (0)	18.9 (62)	20.2 (19)
1970	21.9 (0)	22.8 (0)	21.4 (0)	20.3 (0)	17.1 (8)	17.0 (33)	17.5 (0)	16.8 (0)	16.1 (63)	16.7 (94)	17.0 (100)	18.3 (32)
1971	20.6 (0)	21.8 (0)	22.2 (0)	20.3 (5)	18.9 (23)	19.3 (19)	18.4 (0)	17.2 (151)	16.5 (43)	16.3 (11)	18.4 (109)	19.6 (62)
1972	22.4 (1)	24.3 (19)	24.7 (68)	23.3 (68)	20.8 (14)	20.5 (1)	20.7 (31)	19.5 (0)	18.2 (0)	18.2 (20)	20.6 (139)	22.1 (4)
1973	23.7 (0)	24.6 (16)	22.6 (89)	20.6 (6)	18.1 (2)	17.4 (0)	17.8 (6)	16.3 (33)	16.5 (25)	17.1 (1)	18.9 (0)	19.3 (0)
1974	22.2 (2)	20.5 (28)	21.7 (38)	21.2 (5)	19.0 (4)	19.4 (34)	18.9 (3)	17.7 (6)	16.7 (0)	17.4 (3)	18.6 (65)	20.5 (0)
1975	22.5 (6)	23.7 (2)	23.8 (53)	22.5 (29)	19.6 (37)	18.8 (1)	18.1 (0)	16.8 (133)	15.9 (0)	16.3 (0)	17.6 (13)	20.0 (17)
1976	21.6 (0)	23.3 (0)	23.3 (4)	22.0 (21)	19.1 (0)	19.8 (0)	20.3 (25)	18.3 (26)	17.9 (0)	19.2 (16)	20.2 (0)	21.6 (27)
1977	23.6 (0)	25.0 (26)	24.7 (0)	23.5 (1)	19.5 (0)	19.0 (9)	18.9 (0)	17.6 (13)	17.3 (0)	18.4 (11)	19.0 (11)	20.8 (0)
1978	22.0 (0)	22.9 (0)	22.6 (5)	22.1 (0)	19.7 (1)	18.7 (0)	18.3 (9)	17.4 (0)	17.2 (0)	18.3 (0)	19.9 (19)	21.5 (0)
1979	23.3 (0)	**** (0)	**** (0)	**** (0)	**** (0)	19.8 (0)	19.8 (0)	18.8 (28)	18.1 (0)	18.5 (0)	19.5 (0)	21.1 (8)
1980	23.4 (0)	24.9 (4)	24.7 (11)	23.7 (0)	20.0 (0)	19.3 (0)	19.3 (0)	18.4 (12)	17.6 (0)	18.2 (0)	**** (0)	**** (0)
1981	23.0 (0)	24.1 (0)	23.6 (21)	2.8 (0)	19.5 (0)	**** (0)	**** (0)	**** (0)	17.1 (0)	17.8 (0)	19.2 (34)	21.4 (19)
1982	22.4 (0)	22.8 (1)	21.5 (29)	22.4 (21)	18.9 (0)	19.6 (0)	19.6 (0)	18.6 (19)	18.5 (0)	20.5 (0)	22.6 (34)	23.4 (6)
1983	26.0 (0)	27.4 (17)	26.5 (1)	26.0 (31)	22.5 (0)	22.4 (30)	21.5 (18)	19.0 (2)	18.3 (0)	19.1 (11)	20.4 (0)	22.2 (0)
1984	24.1 (0)	25.3 (12)	25.0 (0)	23.7 (0)	19.0 (0)	19.0 (0)	18.8 (11)	18.2 (12)	17.4 (0)	17.9 (0)	19.4 (7)	**** (0)



Spatially - averaged SST

A

Depth of 14°C isotherm off Peru

B

Depth of SST - 2°C

C

Heat content to depth of SST-2°C

D

Fig. 4. Time series of spatially-averaged monthly means for the region 4 to 14°S as computed from profiles of subsurface temperature. Parameters are (A) SST, (B) depth to 14°C isotherm, (C) depth to SST-2°C isotherm, and (D) heat content from the surface down to SST-2°C.

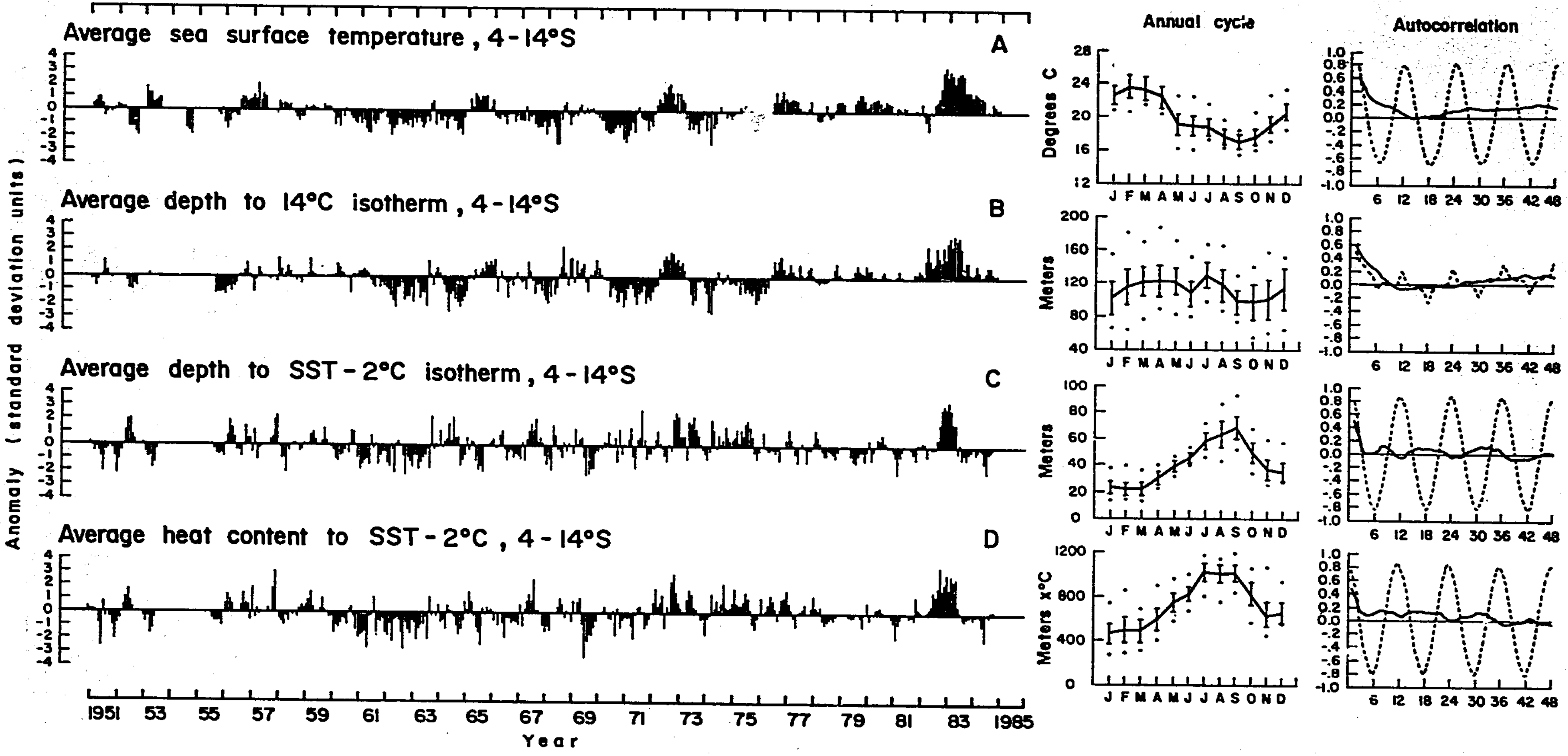


Fig. 5. Annual cycles, autocorrelation functions, and anomalies of (A) SST, (B) depth of the 14°C isotherm, (C) depth of SST-2°C isotherm, and (D) heat content from the surface down to SST-2°C isotherm off Peru from 1952 to 1984. Data shown for "1951" are a composite of data for all years prior to 1952.

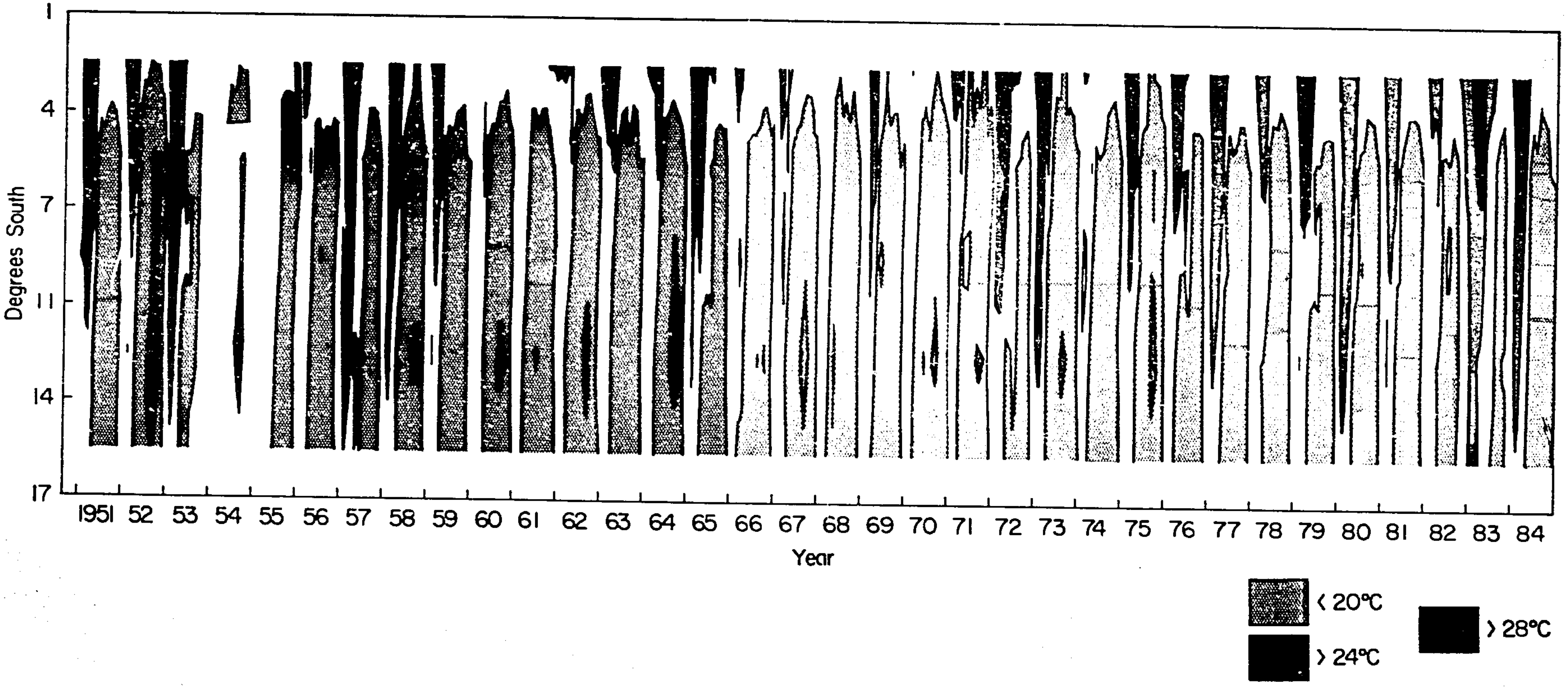


Fig. 6. Time-latitude contour plot of monthly mean SST for the 5 areas off Peru. Data shown for "1951" are a composite of data for all years prior to 1952. Tongues of water greater than 24°C penetrate a variable distance southward along the coast during January to March from year to year and are indicators of El Niño. Water of greater than 28°C intruded southward in early 1983. Low temperature tongues, associated with upwelling, extend northward.

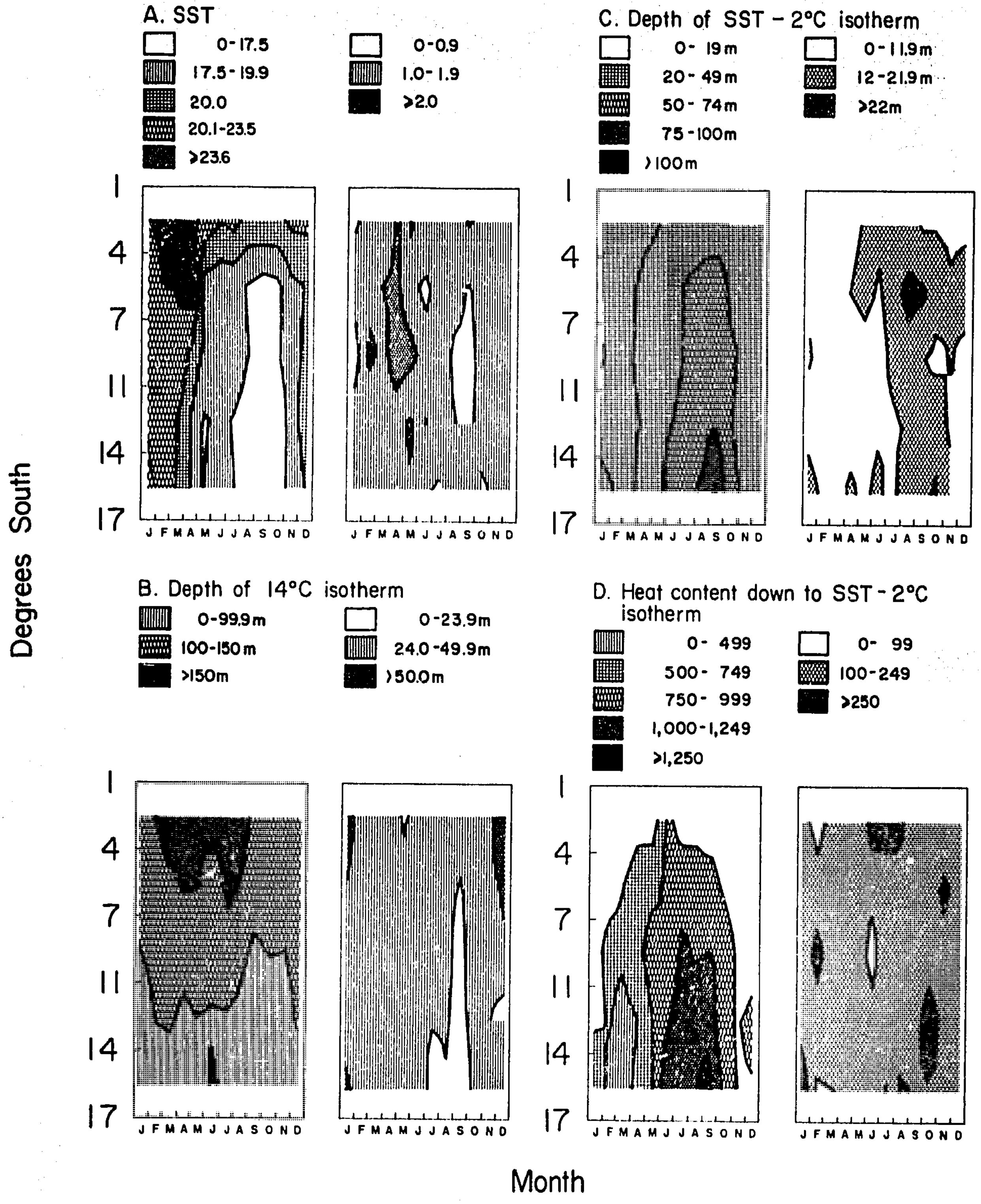


Fig. 7. Time-latitude contour plots of annual cycles and between-year standard deviations of (A) SST, (B) depth of 14°C isotherm, (C) depth of SST-2°C isotherm, and (D) heat content down to SST-2°C isotherm for 5 areas along the Peru coast. The long-term mean annual cycles are shown in the left-hand plots. When no profiles were available for a month in any year, the long-term mean was interpolated. The between-year standard deviations are shown in the right-hand boxes.

The time-latitude between-year standard deviation plot (Fig. 7A, left-hand plot) shows the highest interannual variability to occur during the fall transition from the warm current regime to the upwelling regime, particularly in area 2 which is between the strong upwelling to the south and the weak upwelling to the north. The interannual variability of SST is lowest during peak upwelling.

The autocorrelation function of the anomaly of the spatially-averaged SST (Fig. 5A) is moderately persistent with a lag one value of about 0.6. After 18 months' lag, the autocorrelation function begins to rise, peaking again at a lag of about 44 months. Anomaly of SST at the two shore stations has autocorrelation functions with moderately strong persistence at lags one and two, negative correlation between lags of 12 and 36 months, and weakly positive correlation after a lag of about 40 months (see Figs. 2B, 2C). This pattern is similar to that described for SOI.

Vertical Structure of Subsurface Temperature, 0-350 m

The interannual variability of subsurface temperature for the central area (Area III) off Peru (Fig. 8) shows monthly variations of isotherm depths from the surface to 350 m for the period 1952 to 1984. A similar plot of the anomaly field was used for the analysis (but not shown because anomalies must be carefully analyzed to avoid misinterpretation of events caused by slight phase shifts). Interestingly, the 12, 14 and 16°C isotherms show a general long-term depression of the thermal structure for the period 1976-1984, in agreement with the changes in SOI and SST discussed previously and with other reports of a large-scale coastal warming during the period.

Shorter duration depressions of the isotherms are observed for the 1957-1958, 1965-1966, 1969, 1972-1973, 1976-1977, 1979-1980 and 1982-1983 El Niño warming events. The magnitude and vertical extent of these isotherm depressions varies noticeably between different events. Each of these El Niño events is characterized by moderate to strong surface warming. The anomaly field (not shown) has double peaks for most of these warming events, as has been reported by others for many El Niño events (e.g., Cane 1983; Reinecker and Mooers 1986). The 1957-1958 El Niño appears to be of shallower extent but of longer duration than most of the other events, lasting for about 3 years. The 1965-1966 El Niño had intense surface warming (down to 150 m) which began in January 1965 and lasted until about July, followed by a second, weaker warming which peaked in about December. There was also a weak isotherm depression between 275 and 350 m. The 1969 El Niño had a weak signal from the surface down to about 300 m. The 1972-1973 El Niño was similar in vertical extent and duration to the 1965 event, except the second peak was less defined. The 1976-1977 event was moderately strong at all depths from the surface down to 350 m. The 1979-1980 event had a weak depression at all depths. During the 1982-1983 El Niño, a strong depression of 50 to 80 m was observed at all depths. For this event, it is interesting to note that the 12 and 14°C isotherms were depressed 5-6 months prior to the depressions of the surface layer isotherms. It is yet to be determined whether this relates to the idea of downward and poleward propagating coastally trapped waves (McCreary 1976).

The annual cycles of subsurface temperatures for the five areas along the coast are shown by vertical contour plots of the long-term monthly means (Fig. 9). The areas are arranged from north to south from left to right across the page. The strongest vertical temperature gradients are in the upper 75 m, indicating a relatively shallow mean thermocline. The isotherms display a relatively linear slope upwards with increasing latitude (southward) along the coast, as would be expected. The 12 and 14°C isotherms shoal from mean depths of about 285 m and 170 m for Area I, near the equator, to mean depths of 205 m and 90 m for Area V, in the south. Similarly, the SST varies between 21 and 24°C for the northern area and between 16 to 21°C for the southern area. Each of these plots show a strong annual cycle having relatively warm temperatures during the austral summer, with annual highs occurring in February and March, and cooler temperature during the austral winter, with annual lows occurring in September. This pattern of the annual cycle becomes less apparent with increasing depth, where the 12, 14 and 16°C isotherms have an interesting double peak.

The interannual variability of subsurface temperature off Peru is shown by vertical contour plots of the between-year standard deviation (bysd, see Fig. 10) for the long-term monthly means

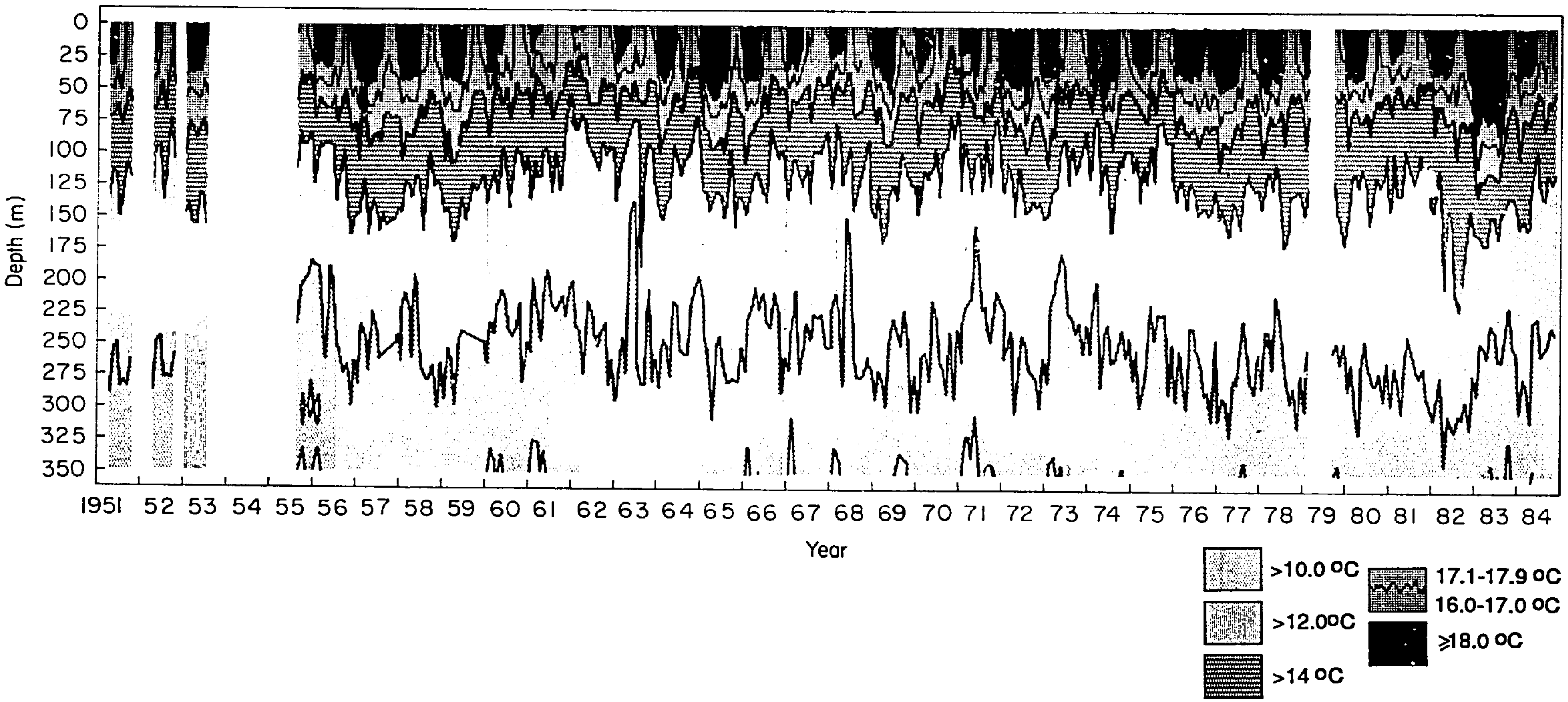


Fig. 8. Time-depth contour plot of monthly mean subsurface temperature off Peru from 1952 to 1984. Data are computed at 25 m depth intervals from 0 to 350 m from subsurface temperature profiles for central area (Area III). Values shown for "1951" are a composite of data for all years prior to 1952. Note the depression of the 12°C and 14°C isotherms from the early to mid-1970s to a maximum depth in 1982.

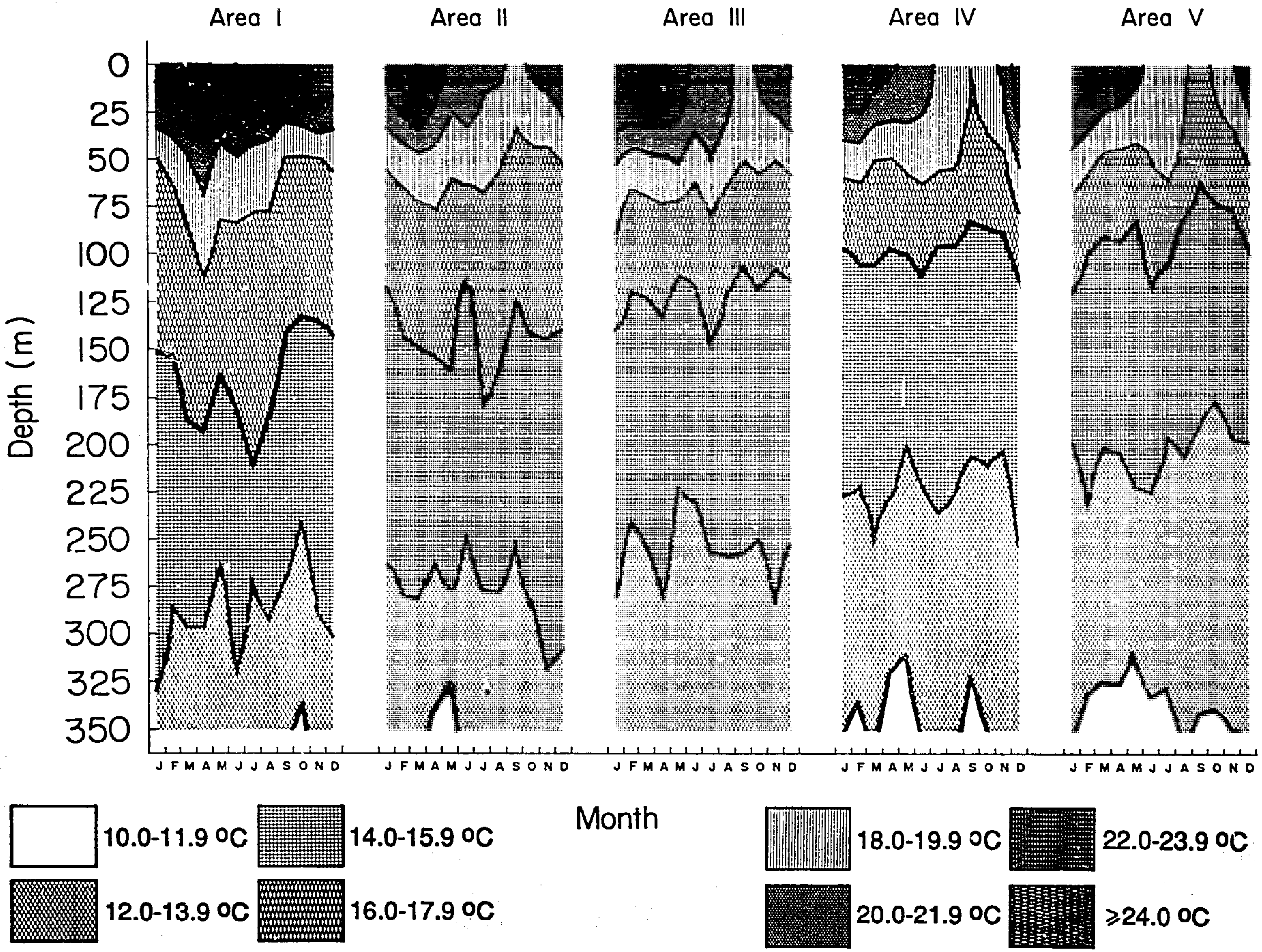


Fig. 9. Annual cycles of subsurface temperature vertically from 0 to 350 m for 5 areas along the Peru coast. Note the progressive rise of the isotherms from north (Area I on the left) to south (Area V on the right). For example, the 14°C isotherm rises from depths of 250-325 m in the north to depths of 75-125 m in the south.

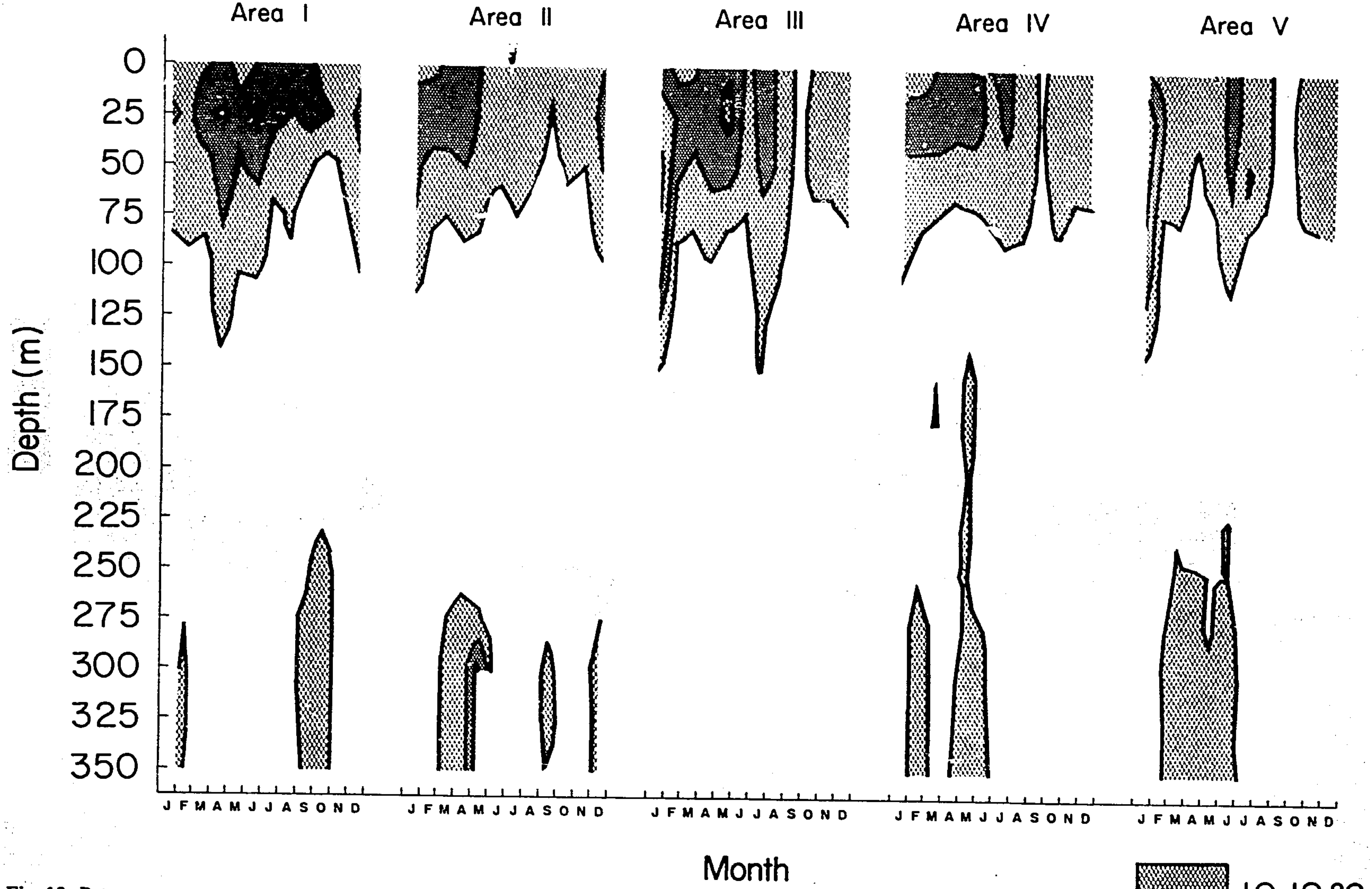


Fig. 10. Between-year standard deviation of subsurface temperature vertically from 0 to 350 m for the 5 areas along the Peru coast. The highest interannual variability occurs in the upper 100 m during the relaxed upwelling period (December to June).

just discussed. The highest variability is found in the upper 50 m, as would be expected for the thermocline. Seasonally, this upper layer variability appears to be highest (bysd = 2.7-3.0oC) from March through July and lowest (bysd = 0.7-1.2oC) in September. With a few exceptions, the interannual variability is consistently low (bysd = 0.2-0.9oC) below 100 m in each of the 5 areas.

Depth of the 14oC Isotherm

Unlike the previous section which described time variations of the thermal structure vertically for a single area and the long-term annual cycle of the slope of the thermal structure for the five areas along the coast, this section examines temporal and spatial variations of the depth of the 14oC isotherm in greater detail. The time series of monthly mean depth of the 14oC isotherm (Fig. 11, Table 7) shows considerable seasonal and interannual variability. The 14oC isotherm deepened during each of the warming events, with the most striking example occurring during the 1982-1983 El Niño. The anomaly of the depth of the 14oC isotherm (Fig. 5B) shows persistent deep or shallow anomalies lasting several years. The 14oC isotherm deepened in 1976 and remained anomalously deep throughout the rest of the record.

The annual cycle of the depth of the 14oC isotherm (Fig. 7B) differs from the annual cycles of each of the other parameters in that it displays a double peak. Seasonally, the depth of the 14oC isotherm for the region from 4 to 14oS has maximum depths in April and July and minimum depths in June and September. This double peak exists for each of the five areas (Fig. 9), although the months of occurrence differ slightly.

The 14oC isotherm is relatively deep in the north and shallow in the south (Figs. 9 and 11). The annual long-term mean depths of the 14oC isotherm for Areas I through V are 152, 135, 109, 90, and 78 m, respectively. The transition from depth to shallow depths is usually rapid, typically occurring in 1-2 months. The interannual variability of the depth of the 14oC isotherm is highest in December and January for the three northern areas (between-year standard deviations greater than 50 m), associated with the intrusion of the warm water. The interannual variability is lowest during peak upwelling in September.

Along the coast, the depth of the 14oC isotherm (Fig. 11) provides an indication of the coastwise interannual variability of the thermocline depth and the effect of coastal upwelling on the thermal structure. The 14oC isotherm deepened moderately during the years 1957-1958, 1965, 1969, 1976-1977 and 1979-1980 and strongly during the 1972-1973 and 1982-1983 El Niños. This plot shows the 1982-1983 El Niño to be the largest event of the record, both in magnitude and duration. The 14oC isotherm remained below 200 m for most of the period from February 1982 through July 1983 for the northern two areas. Likewise, the 14oC isotherm remained significantly deeper than normal during this period for the southern three areas. Both plots show the 1957-1958, 1965, 1969, 1972-1973 and 1976-1977 El Niños were preceded by cold period having shallow depths of the 14oC isotherm. The 1979-1980 and 1982-1983 warm events, by contrast, occurred during the long-term coastal warming from 1976 to 1984.

The 1979-1980 warming, which was not included in Rasmusson's (1984) list of El Niños, had moderate signals for each of the three parameters thus far discussed. Norton et al. (1984) described a strong surface warming in 1979-80 in the California current system which attenuated rapidly with depth, seemingly unrelated to tropical warming.

Wyrtki (1975) pointed out that El Niño conditions off the coast of Peru were not caused by a local weakening of the upwelling favorable winds, as had been previously hypothesized. He showed that not only did the upwelling favorable winds not weaken but also appeared to have strengthened during El Niño events. Using Bakun's (this vol.) time series of wind stress, turbulent mixing index, and offshore Ekman velocity and transport, we now strengthen Wyrtki's argument and show that each of the major El Niño events of the past three decades occurred during periods of anomalously strong southeast trades and offshore Ekman transport. One would expect intense offshore transport to be associated with intense coastal upwelling and shallow thermocline. However, comparison of the time series of offshore transport with depth of the 14oC isotherm indicates the opposite. Periods of strongest offshore transport correspond to periods of deepest depth of the 14oC isotherm. The 1957-1958, 1965, 1972-1973 and 1982-1983

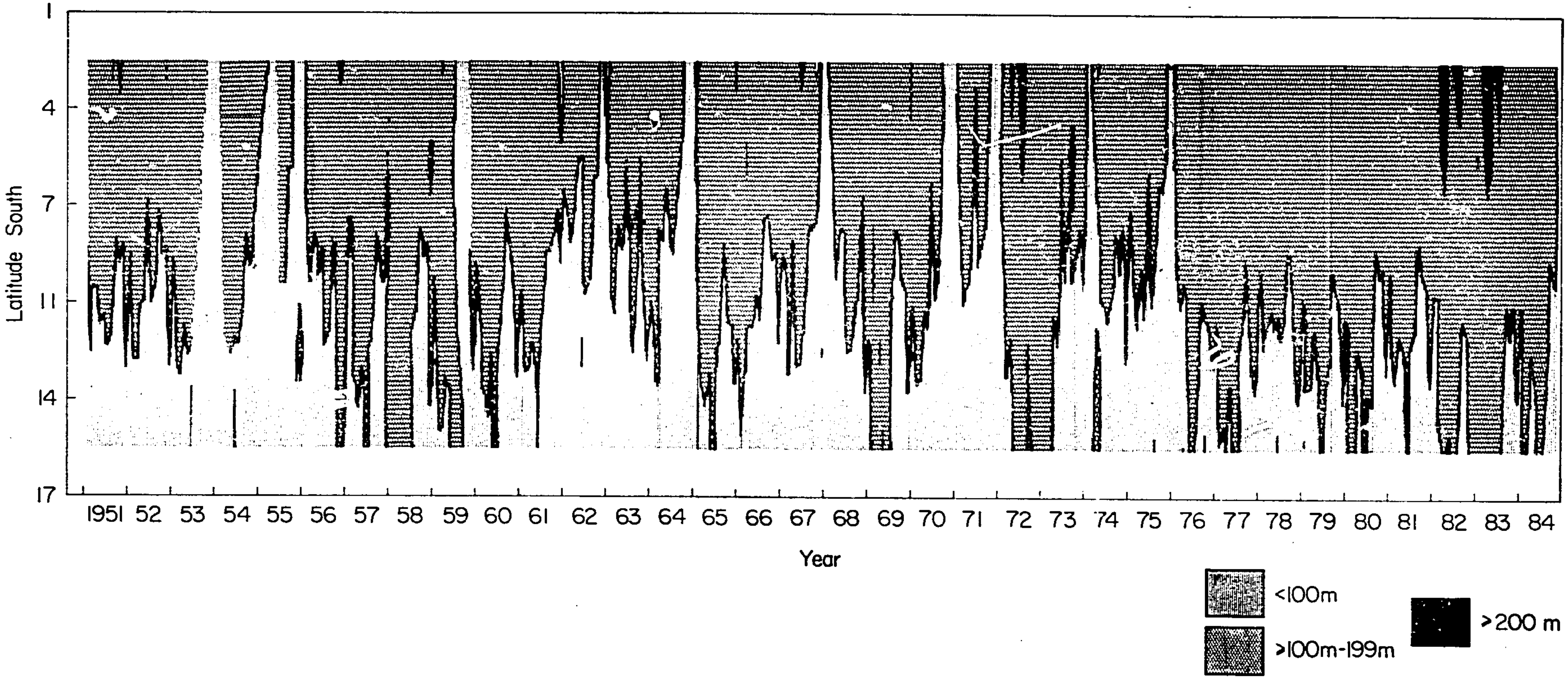


Fig. 11. Time-latitude contour plot of monthly mean depth of the 14°C isotherm for 5 areas along the coast off Peru. Data shown for "1951" are a composite of data for all years prior to 1952. The 14°C isotherm is generally shallower than 100 m in the south and deeper than 100 m in the north. The isotherm was occasionally deeper than 200 m in the northernmost areas (e.g., 1967, 1972, 1982 and 1983). Note the large region in the north during 1976-1984 when the 14°C isotherm was consistently deeper than 100 m.

Table 7. Monthly mean depth of the 14°C isotherm (m) for the region 4-14°S off Peru. These means are averages of the monthly means for the three central areas, computed from subsurface temperature profiles. The corresponding number of profiles used in computing each mean is printed (in brackets) to the right of the mean. Means based on zero profiles are computed from interpolated values. Asterisks indicate months in which neither observed nor interpolated means were available in all three areas.

Year	Jan		Feb		Mar		Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec	
1951	96	(1)	112	(1)	108	(2)	116	(0)	121	(0)	110	(0)	149	(17)	126	(7)	96	(0)	96	(0)	****	(0)	****	(0)
1952	****	(0)	****	(0)	****	(0)	****	(0)	116	(0)	94	(0)	113	(144)	106	(0)	87	(0)	****	(0)	****	(0)	****	(0)
1953	101	(0)	115	(0)	127	(1)	123	(0)	123	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)
1954	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)
1955	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	81	(0)	73	(0)	73	(69)	85	(104)
1956	75	(5)	97	(0)	108	(0)	102	(47)	110	(0)	100	(0)	131	(0)	121	(0)	99	(30)	108	(0)	126	(5)	119	(0)
1957	98	(0)	90	(3)	118	(43)	135	(10)	127	(0)	108	(0)	****	(0)	****	(0)	94	(0)	98	(0)	102	(5)	105	(2)
1958	129	(41)	128	(9)	121	(65)	127	(6)	136	(2)	113	(0)	129	(1)	118	(0)	94	(51)	96	(0)	89	(5)	112	(173)
1959	101	(0)	120	(0)	148	(5)	129	(0)	125	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	113	(0)
1960	103	(0)	118	(3)	140	(32)	137	(75)	128	(3)	111	(0)	130	(0)	116	(0)	81	(7)	102	(94)	105	(33)	117	(0)
1961	109	(0)	126	(55)	134	(60)	131	(15)	127	(0)	105	(12)	121	(14)	104	(124)	96	(24)	82	(8)	91	(0)	98	(0)
1962	85	(63)	96	(77)	97	(24)	88	(90)	86	(101)	96	(20)	118	(35)	110	(0)	75	(0)	68	(20)	67	(284)	95	(54)
1963	66	(88)	113	(99)	115	(40)	93	(30)	104	(0)	90	(0)	96	(60)	143	(49)	101	(3)	86	(61)	110	(14)	132	(18)
1964	109	(0)	112	(11)	113	(13)	101	(0)	81	(51)	89	(99)	113	(2)	86	(59)	73	(61)	54	(9)	60	(180)	79	(0)
1965	80	(0)	114	(0)	125	(0)	119	(34)	132	(1)	109	(0)	136	(26)	130	(53)	103	(34)	123	(21)	124	(85)	145	(18)
1966	121	(0)	145	(47)	103	(42)	122	(32)	130	(44)	106	(21)	125	(0)	89	(5)	94	(135)	87	(2)	100	(29)	123	(41)
1967	99	(0)	109	(130)	120	(11)	107	(5)	142	(52)	114	(9)	126	(2)	95	(113)	90	(63)	88	(1)	79	(31)	81	(55)
1968	70	(0)	75	(114)	96	(1)	119	(7)	102	(32)	96	(0)	134	(0)	134	(0)	128	(57)	107	(32)	88	(9)	148	(37)
1969	130	(12)	109	(15)	148	(7)	130	(2)	134	(2)	123	(14)	125	(48)	97	(31)	101	(117)	102	(0)	113	(23)	148	(8)
1970	117	(0)	121	(0)	122	(0)	119	(0)	120	(1)	87	(26)	118	(0)	101	(0)	74	(67)	62	(95)	76	(125)	63	(47)
1971	71	(0)	100	(0)	114	(0)	109	(4)	101	(22)	79	(15)	111	(0)	98	(170)	90	(47)	60	(11)	69	(112)	74	(60)
1972	31	(1)	102	(20)	113	(49)	138	(59)	130	(17)	128	(0)	157	(25)	147	(15)	124	(0)	139	(22)	130	(87)	150	(2)
1973	121	(0)	141	(11)	134	(77)	124	(14)	121	(3)	90	(0)	100	(9)	86	(36)	95	(24)	94	(0)	99	(0)	101	(0)
1974	80	(2)	64	(24)	75	(40)	107	(7)	115	(7)	115	(15)	129	(5)	112	(5)	94	(0)	105	(3)	93	(57)	109	(0)
1975	95	(8)	105	(2)	121	(53)	102	(35)	116	(63)	92	(1)	118	(0)	99	(134)	81	(0)	80	(0)	59	(17)	76	(16)
1976	81	(0)	104	(0)	104	(6)	111	(11)	121	(0)	113	(0)	151	(21)	132	(14)	115	(0)	133	(23)	120	(0)	123	(12)
1977	113	(0)	139	(24)	133	(0)	128	(0)	127	(0)	123	(2)	135	(0)	120	(14)	101	(0)	114	(11)	122	(8)	121	(0)
1978	102	(0)	113	(1)	116	(5)	119	(0)	119	(2)	105	(0)	128	(1)	117	(0)	99	(0)	111	(0)	128	(20)	124	(0)
1979	106	(0)	***	(0)	***	(0)	***	(0)	***	(0)	110	(0)	139	(0)	138	(25)	105	(0)	108	(0)	110	(0)	139	(3)
1980	113	(0)	129	(4)	125	(14)	125	(0)	124	(0)	108	(0)	135	(0)	128	(11)	99	(0)	101	(0)	***	(0)	***	(0)
1981	102	(0)	119	(0)	133	(19)	126	(0)	124	(0)	***	(0)	***	(0)	***	(0)	97	(0)	105	(0)	109	(33)	129	(17)
1982	110	(0)	118	(5)	149	(29)	171	(19)	146	(0)	121	(0)	149	(0)	164	(14)	119	(0)	125	(0)	156	(12)	151	(1)
1983	154	(10)	180	(16)	168	(6)	185	(85)	169	(7)	151	(73)	166	(68)	134	(9)	114	(0)	125	(13)	110	(0)	120	(0)
1984	111	(0)	138	(18)	132	(0)	126	(0)	125	(0)	114	(0)	145	(14)	136	(10)	103	(0)	104	(0)	109	(7)	****	(0)

El Niño periods of anomalously deep thermocline occurred during the four highest peaks of offshore Ekman transport. Thus, the thermocline deepens sharply during periods when local wind forcing should produce anomalously shallow thermocline.

Depth of the SST-2°C Isotherm

The depth of the SST-2°C isotherm is an indicator of the thickness of the surface mixed layer, i.e., the depth to the top of the thermocline. The time series of monthly mean depth of the SST-2°C isotherm (Fig. 4C, Table 8) show that variations in the depth of this isotherm occur over both seasonal and interannual time scales. Although anomalies (Fig. 5C) occurred during the major El Niño events, the interannual variations of the depth of the SST-2°C isotherm are less closely correlated with El Niño events than were the other parameters discussed. Rather, the dominant interannual variations appear to occur over longer time scales. The SST-2°C isotherm was anomalously shallow throughout most of the 1960s, anomalously deep from 1970 to 1976, near the long-term mean annual cycle from 1976 until 1982 and deep during the 1982-1983 El Niño.

The annual cycle of the depth of the SST-2°C isotherm (Fig. 7C) is strong, varying from a minimum depth of 20-25 m from January through March (austral summer) to a maximum depth of 60-70 m from July through September (austral winter). This annual cycle corresponds well with Bakun's (this vol.) seasonal wind mixing index and surface wind stress calculations, further establishing the depth of the SST-2°C isotherm as a reasonable measure of the mixed layer depth. Thus, the annual cycle of the depth of the SST-2°C isotherm fluctuates with the upwelling cycle, being deep during the upwelling season and shallow during the nonupwelling season. Upwelling elevates the thermal structure in response to offshore transport of the surface water. The elevated thermal structure combined with increased turbulent mixing during the upwelling season apparently force the observed deepening of the SST-2°C isotherm.

The between-year standard deviation and range between extrema vary between lows of about 5 and 20 m, respectively, in May and June to highs of about 20 and 40 m, respectively, in August and September (Fig. 7C). There is an inverse correlation between SST and depth of the SST-2°C isotherm. The autocorrelation function of the depth of the SST-2°C isotherm indicates weak persistence (Fig. 5C). This suggests that the mixed layer changes due to local rather than large-scale processes, which makes sense because it is primarily an indicator of the thickness of the wind forced mixed layer (or local upper layer stratification due to heat budget considerations).

Along the coast, the depth of the SST-2°C isotherm slopes from a shallow annual mean depth in the north (Area I) of 31 m to a relatively deep annual mean depth in the south (Area V) of 50 m. The maximum coastwise between-year standard deviation occurs in August in Area II, which is located between the weak upwelling area to the north and the strong upwelling areas to the south, reflecting interannual variations in the northerly extent of the upwelling.

Heat Content from the Surface to the SST-2°C Isotherm

The heat content from the surface down to the SST-2°C isotherm (Fig. 4D) is computed as the vertically averaged mean temperature down to the SST-2°C isotherm multiplied by that depth. Since the magnitudes of depth variations (in meters) are significantly greater than for temperature variations (in degrees Celsius), the computed heat contents are dominated more by depth than temperature. Thus, heat content is low (300 to 500°C x m) during nonupwelling periods when the surface layer is warm but the SST-2°C isotherm is very shallow. Conversely, heat content is high(>1,000°C x m) during the upwelling regime when the surface layer is cool but the SST-2°C isotherm is deep. Time series of monthly mean heat content (Fig. 4D, Table 9) and anomaly of heat content (Fig. 5D) reveal interannual variations almost identical to those described for the depth to the SST-2°C isotherm.

The annual cycle of heat content has characteristics similar to the annual cycle described for depth to the SST-2°C isotherm (Fig. 7D). The long-term mean values vary from about 500 mC

Table 8. Monthly mean depth of the SST-2°C isotherm (m) for the region 4-14°S off Peru. These means are averages of the monthly means for the three central areas, computed from subsurface temperature profiles. The corresponding number of profiles used in computing each mean (in brackets) is printed to the right of the mean. Means based on zero profiles are computed from interpolated values. Asterisks indicate months in which neither observed nor interpolated means were available in all three areas.

Year	Jan		Feb		Mar		Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec	
1951	24	(1)	22	(1)	20	(195)	29	(0)	37	(0)	42	(0)	45	(34)	59	(6)	66	(0)	49	(0)	35	(0)	29	(0)
1952	13	(37)	17	(0)	20	(0)	**	(0)	43	(0)	53	(0)	71	(143)	71	(0)	72	(0)	**	(0)	**	(0)	**	(0)
1953	24	(0)	20	(0)	18	(62)	26	(145)	32	(24)	40	(0)	56	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)
1954	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)
1955	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	66	(0)	45	(0)	32	(70)	31	(114)
1956	19	(5)	23	(0)	26	(0)	39	(47)	44	(0)	48	(0)	56	(0)	60	(0)	61	(31)	50	(0)	48	(15)	39	(0)
1957	26	(0)	20	(3)	28	(50)	25	(33)	38	(0)	45	(0)	**	(0)	**	(0)	69	(0)	53	(0)	42	(16)	48	(10)
1958	34	(78)	22	(16)	18	(90)	26	(8)	31	(4)	44	(0)	58	(4)	65	(0)	70	(54)	50	(0)	34	(5)	33	(174)
1959	24	(0)	23	(0)	23	(36)	34	(3)	43	(1)	47	(0)	58	(0)	64	(0)	71	(0)	60	(4)	40	(0)	36	(0)
1960	23	(0)	21	(7)	18	(47)	25	(107)	36	(4)	43	(0)	56	(0)	63	(0)	64	(10)	59	(92)	45	(49)	36	(0)
1961	19	(0)	14	(113)	16	(97)	25	(55)	35	(0)	40	(14)	63	(10)	62	(137)	70	(27)	39	(6)	32	(1)	32	(0)
1962	21	(102)	16	(130)	15	(35)	29	(100)	31	(107)	46	(36)	60	(27)	63	(0)	62	(0)	33	(20)	31	(273)	27	(58)
1963	16	(94)	19	(184)	19	(55)	22	(73)	34	(0)	42	(0)	54	(61)	62	(118)	54	(29)	67	(76)	36	(44)	36	(61)
1964	23	(0)	28	(13)	22	(47)	32	(0)	41	(54)	52	(95)	61	(3)	85	(37)	74	(40)	55	(7)	26	(182)	28	(2)
1965	20	(0)	25	(10)	21	(1)	32	(87)	40	(1)	41	(0)	47	(35)	48	(69)	52	(43)	50	(24)	37	(139)	35	(29)
1966	25	(0)	25	(96)	22	(65)	30	(34)	42	(69)	50	(25)	57	(0)	53	(4)	65	(130)	47	(0)	31	(29)	31	(50)
1967	20	(0)	18	(147)	24	(16)	25	(11)	41	(65)	50	(9)	69	(2)	76	(103)	86	(54)	52	(1)	42	(32)	37	(62)
1968	20	(0)	16	(120)	18	(1)	22	(7)	45	(41)	49	(0)	57	(0)	60	(0)	61	(73)	52	(36)	35	(11)	37	(73)
1969	**	(17)	20	(23)	29	(8)	31	(2)	41	(3)	48	(20)	53	(58)	42	(34)	51	(149)	37	(0)	25	(59)	32	(19)
1970	22	(0)	23	(0)	22	(0)	32	(0)	40	(3)	50	(25)	60	(0)	65	(0)	74	(55)	41	(91)	47	(129)	31	(50)
1971	24	(0)	23	(0)	25	(0)	37	(12)	36	(28)	39	(23)	62	(0)	70	(172)	92	(46)	54	(8)	30	(118)	32	(58)
1972	21	(1)	22	(26)	25	(96)	36	(90)	40	(35)	45	(2)	54	(53)	53	(17)	70	(0)	48	(31)	53	(148)	53	(21)
1973	34	(6)	26	(15)	26	(114)	34	(25)	35	(3)	53	(0)	70	(11)	86	(38)	80	(25)	57	(0)	39	(0)	34	(0)
1974	21	(2)	18	(37)	21	(45)	40	(12)	44	(7)	45	(31)	64	(5)	65	(5)	73	(0)	62	(3)	43	(68)	38	(0)
1975	26	(8)	26	(2)	29	(56)	32	(45)	44	(64)	49	(1)	70	(0)	83	(141)	82	(0)	56	(0)	34	(15)	29	(19)
1976	22	(0)	23	(0)	28	(6)	30	(17)	38	(0)	44	(0)	57	(42)	59	(27)	67	(0)	42	(26)	38	(0)	**	(17)
1977	26	(0)	29	(27)	25	(0)	31	(0)	37	(0)	41	(11)	59	(0)	66	(14)	68	(0)	41	(13)	36	(9)	34	(0)
1978	25	(0)	29	(1)	26	(5)	32	(0)	38	(2)	43	(0)	54	(4)	61	(0)	66	(0)	46	(0)	31	(21)	33	(0)
1979	23	(0)	**	(0)	**	(0)	**	(0)	**	(0)	43	(0)	52	(0)	52	(29)	63	(0)	47	(0)	35	(0)	28	(8)
1980	22	(0)	25	(4)	18	(17)	29	(0)	39	(0)	48	(0)	62	(0)	73	(13)	72	(0)	51	(0)	**	(0)	**	(0)
1981	22	(0)	19	(0)	13	(21)	27	(0)	38	(0)	**	(0)	**	(0)	**	(0)	67	(0)	46	(0)	30	(36)	37	(19)
1982	24	(0)	24	(5)	24	(36)	27	(24)	39	(0)	45	(0)	58	(0)	63	(23)	74	(0)	64	(0)	59	(81)	57	(21)
1983	37	(14)	39	(32)	36	(6)	39	(99)	46	(7)	44	(99)	60	(80)	55	(11)	64	(0)	43	(13)	34	(0)	33	(0)
1984	23	(0)	20	(18)	21	(0)	30	(0)	38	(0)	41	(0)	46	(15)	59	(14)	66	(0)	49	(0)	37	(7)	**	(0)

Table 9. Monthly mean heat content from the surface down to the SST-20°C isotherm (°C x m) for the region 4-14°S off Peru. These means are averages of the monthly means for the three central areas, computed from subsurface temperature profiles. The corresponding number of profiles used in computing each mean (in brackets) is printed to the right of the mean. Means based on zero profile are computed from interpolated values. Asterisks indicate months in which neither observed nor interpolated means were available in all three areas.

Year	Jan		Feb		Mar		Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec	
1951	491	(1)	524	(1)	506	(188)	609	(0)	748	(0)	772	(0)	801	(31)	1,063	(3)	984	(0)	837	(0)	596	(0)	553	(0)
1952	270	(37)	401	(0)	440	(0)	***	(0)	789	(0)	895	(0)	1,154	(122)	1,069	(0)	1,036	(0)	***	(0)	***	(0)	***	(0)
1953	458	(0)	465	(0)	419	(59)	558	(137)	613	(24)	748	(0)	984	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)
1954	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)
1955	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	974	(0)	763	(0)	568	(59)	594	(113)
1956	371	(5)	495	(0)	552	(0)	728	(44)	832	(0)	865	(0)	1,011	(0)	1,000	(0)	1,039	(30)	886	(0)	809	(14)	730	(0)
1957	514	(0)	436	(3)	683	(45)	560	(33)	771	(0)	822	(0)	***	(0)	***	(0)	1,012	(0)	864	(0)	664	(14)	831	(5)
1958	737	(64)	515	(15)	441	(83)	527	(8)	670	(2)	813	(0)	967	(2)	1,003	(0)	1,001	(40)	834	(0)	610	(4)	689	(171)
1959	510	(0)	549	(0)	548	(35)	697	(3)	876	(1)	856	(0)	1,020	(0)	1,012	(0)	1,031	(0)	937	(3)	673	(0)	664	(0)
1960	436	(0)	472	(6)	336	(42)	496	(101)	659	(4)	780	(0)	984	(0)	975	(0)	947	(9)	850	(83)	698	(42)	632	(0)
1961	341	(0)	280	(109)	318	(94)	429	(52)	632	(0)	664	(14)	998	(8)	994	(126)	1,101	(25)	652	(6)	577	(1)	593	(0)
1962	425	(102)	326	(129)	309	(35)	507	(100)	570	(98)	797	(32)	985	(24)	963	(0)	895	(0)	558	(17)	555	(246)	541	(58)
1963	314	(87)	435	(183)	413	(55)	391	(72)	650	(0)	774	(0)	946	(59)	980	(107)	857	(28)	952	(71)	625	(42)	663	(59)
1964	440	(0)	578	(12)	419	(46)	542	(0)	652	(42)	861	(81)	1,034	(3)	1,015	(26)	990	(33)	734	(3)	452	(179)	541	(2)
1965	409	(0)	600	(9)	509	(1)	752	(76)	822	(0)	816	(0)	924	(30)	890	(57)	827	(43)	864	(24)	641	(121)	697	(27)
1966	475	(0)	535	(96)	434	(60)	599	(33)	673	(59)	828	(24)	953	(0)	857	(3)	988	(114)	794	(0)	560	(27)	602	(50)
1967	400	(0)	404	(142)	558	(15)	496	(9)	774	(65)	881	(8)	1,132	(2)	1,079	(79)	1,197	(43)	845	(1)	673	(31)	670	(62)
1968	380	(0)	340	(199)	385	(1)	463	(4)	753	(40)	827	(0)	1,023	(0)	1,040	(0)	1,097	(67)	897	(33)	611	(11)	678	(65)
1969	458	(46)	431	(21)	588	(6)	602	(2)	824	(3)	898	(19)	950	(53)	748	(26)	851	(145)	669	(0)	447	(58)	555	(14)
1970	415	(0)	498	(0)	490	(0)	604	(0)	797	(2)	834	(23)	992	(0)	974	(0)	1,024	(38)	665	(72)	693	(112)	557	(49)
1971	421	(0)	474	(0)	459	(0)	568	(10)	672	(25)	711	(20)	1,014	(0)	1,039	(141)	1,053	(39)	844	(8)	522	(116)	582	(52)
1972	427	(1)	504	(25)	573	(85)	780	(76)	799	(30)	880	(2)	1,130	(45)	921	(17)	1,054	(0)	842	(27)	922	(108)	930	(8)
1973	605	(4)	599	(13)	539	(109)	613	(25)	762	(1)	893	(0)	1,167	(10)	1,117	(23)	1,045	(19)	864	(0)	656	(0)	618	(0)
1974	435	(2)	317	(36)	452	(44)	582	(10)	875	(7)	856	(23)	1,100	(5)	1,024	(5)	1,070	(0)	1,049	(3)	711	(64)	698	(0)
1975	504	(6)	592	(2)	684	(55)	677	(42)	806	(55)	868	(1)	1,095	(0)	1,131	(115)	1,102	(0)	864	(0)	557	(15)	548	(18)
1976	431	(0)	514	(0)	612	(6)	596	(17)	771	(0)	872	(0)	1,127	(38)	1,083	(25)	1,045	(0)	786	(23)	688	(0)	760	(30)
1977	570	(0)	707	(26)	579	(0)	626	(0)	734	(0)	771	(11)	1,019	(0)	1,021	(9)	1,037	(0)	906	(11)	653	(9)	674	(0)
1978	501	(0)	658	(1)	542	(5)	627	(0)	797	(2)	799	(0)	949	(4)	960	(0)	979	(0)	809	(0)	592	(21)	648	(0)
1979	470	(0)	***	(0)	***	(0)	***	(0)	***	(0)	818	(0)	999	(0)	988	(26)	1,009	(0)	828	(0)	623	(0)	564	(8)
1980	462	(0)	605	(4)	447	(17)	593	(0)	759	(0)	849	(0)	1,051	(0)	1,040	(11)	1,027	(0)	838	(0)	***	(0)	***	(0)
1981	438	(0)	430	(0)	303	(21)	519	(0)	727	(0)	***	(0)	***	(0)	***	(0)	993	(0)	815	(0)	594	(35)	776	(19)
1982	494	(0)	525	(5)	488	(35)	596	(24)	768	(0)	854	(0)	1,070	(0)	1,135	(23)	1,117	(0)	1,022	(0)	1,056	(32)	832	(7)
1983	663	(6)	849	(14)	688	(1)	883	(63)	957	(3)	988	(59)	1,067	(50)	1,017	(8)	982	(0)	782	(13)	617	(0)	641	(0)
1984	456	(0)	464	(16)	476	(0)	590	(0)	735	(0)	777	(0)	855	(11)	1,006	(12)	997	(0)	848	(0)	680	(7)	***	(0)

from January through March to about 1,000 °Cm from July through September. The between-year standard deviation varies from about 100 °Cm in June to about 200 °Cm in November and February. The range between extrema varies from 200 to 600 °Cm. The autocorrelation function of heat content is 0.5 at lag one and decreases rapidly thereafter, indicating weak persistence with time (Fig. 5D). Along the coast, the long-term monthly means of heat content generally slope downward to the south. For instance, the long-term annual mean heat contents for Area I in the north and Area V in the south are 582 °Cm and 843 °Cm, respectively. This alongshore variation is a consequence of the deepening of the mixed layer in response to upwelling, which is stronger in the south. The interannual variability of the heat content is highest in areas and months around the edges of the upwelling regime.

Sea Level

Sea level represents a vertical integral of the thermohaline structure over the entire water column. Integrating over the water column has the effect of combining many subsurface processes into a single parameter. Frequently, this combining of factors provides an invaluable indication of large-scale oceanic change. Monthly means and anomalies of sea level at Talara and La Punta (Figs. 1D, 1E and 2D, 2E, Tables 4 and 5) show seasonal and interannual variability similar to that described for SST. Sea level at both coastal stations was variable during the early 1950s, moderately low during the mid-1950s, moderately high for the 1957-1959 El Niño episode, slightly below normal for most of the 1960s (except the 1965 and 1969 warm events when it was above normal), very high during the 1972-1973 El Niño, and variable until 1974.

The annual cycle of sea level is characterized by relatively high levels from February through June and low levels from August through December. The interannual variability is generally high from December through June and low from August through September. Bigg and Gill (1986) showed that the long period response of sea level off Peru separates into a remotely forced component mainly due to zonal winds along the equator to the west, and a locally driven component where sea level slopes to balance the alongshore wind. Their examination of the annual component of sea level indicates that the locally forced component dominates, whereas the remotely forced component plays a major role at semiannual and interannual periods.

Summary and Implications

All of the time series presented show considerable seasonal and interannual variability. Each series had a strong annual cycle, dominated by seasonal shifts from an intensified upwelling regime from May to October to a relaxed upwelling regime in which warm water intrudes from the north from January through March. Contrary to this single peak pattern observed for SOI, SST, sea level, depth to the SST-2°C isotherm, and heat content, deep isotherms, represented by the depth of the 14°C isotherm, had double peaks in their annual cycles. Along the Peru coast, the seasonal variability increased from north to south, with lowest variability associated with weaker upwelling in the north than in the south.

Interannual variations of most of the series were similar, being dominated by remotely-forced El Niño signals. Contrary to this pattern, however, interannual variations of the depth to the SST-2°C isotherm and heat content down to this isotherm were only weakly correlated to El Niño signals. Interannual variations of these two parameters appear to occur at longer periods. Weaker persistence suggests that these two parameters may be dominated by local rather than large-scale processes, such as local wind or heating events. The parameters which were correlated to El Niño signals showed that coastal waters off Peru (4-14°S) were generally cool in the early 1950s, moderately warm during 1957-1959, near normal during 1960-1965, warm in 1965, near normal during 1966-1968, warm in 1969, cool in 1970 and 1971, very warm in 1972, cool during 1973-1975, warm during 1976-1981, extremely warm in 1982-1983 and variable in 1984. La Punta SST was below normal in 1984-1985, but the 14°C isotherm was still depressed.

The warm events described by the above interannual variations represent a general deepening of the thermal structure along the coast as indicated by a depression of the 14°C isotherm. Such depressions cause a change in the slope of the thermal structure normal to the coast and a tendency to increase transport of warm water and associated organisms poleward along the coast. Furthermore, deepening the thermal structure would reduce the biological productivity of the surface waters by reducing the ability of upwelling favorable winds to upwell nutrient-rich water. These depressions of the thermal structure have been shown to occur even during periods of maximum offshore transport, which normally correspond to maximum upwelling and availability of nutrients.

The effects of interannual variability of subsurface temperature on Peruvian anchoveta populations are difficult to access. If one assumed that some combination of factors associated with warming and depression of the thermal structure is detrimental to anchoveta recruitment and/or growth, a scenario of events based on the subsurface variability presented here may be as follows. Heavy fishing pressure in the late 1960s and early 1970s combined with the strong El Niño of 1972, which had a deeply depressed thermal structure, caused a collapse of the anchoveta population. The stock then recovered slightly in 1974-1976 (Avaria 1985) following cool water conditions (upwelling) of 1973-1975 as described by the depression of the 14°C isotherm. However, this slight recovery was subject to continued strong fishing pressure. The moderate 1976-1977 El Niño and the warm, depressed conditions thereafter, especially during the 1982-1983 El Niño, have prevented good recruitment, resulting in very low anchoveta populations. A reversal to cooler conditions since 1983 may be associated with a modest recent recovery of the population. Clearly, the actual ecosystem of the Peruvian anchoveta is much more complicated than this simple scenario suggests. This scenario does, however, illustrate the potential value of multiple environmental time series such as presented in this volume.

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Monthly Variability in the Ocean Habitat off Peru as Deduced from Maritime Observations, 1953 to 1984

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BAKUN, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations,1953 to 1984, p. 46-74. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

Monthly time series, generated from summaries of maritime reports from the region off Peru, are presented for the period 1953 to 1984. These include sea surface temperature, cloud cover, atmospheric pressure, "wind-cubed" index of rate of addition of turbulent mixing energy to the ocean by the wind, wind stress components, solar radiation, long-wave back radiation, evaporative heat loss and net atmosphere-ocean heat exchange. All series are found to undergo interrelated nonseasonal variations at multiyear periods. El Niño episodes are characterized by intense turbulent mixing of the ocean by the wind, intense offshore-directed Ekman transport and by low net heat gain to the ocean through the sea surface. Effects of constant versus variable transfer coefficient formulations on the bulk aerodynamic flux estimates are discussed. Certain comments on the utilization of these data in analysis of biological effects are offered.

Introduction

By international convention, weather observations are recorded routinely on a various types of ships operating at sea. These maritime reports remain the primary source of information on large-scale variability in the marine environment. Even with the increasing development of satellite observation systems, analysis of time series of decadal length and longer must continue to depend heavily on these maritime reports for some time to come. Observations of wind speed and direction, air and sea temperature, atmospheric pressure, humidity and cloud cover included in these reports provide a basis for estimating a number of environmental variables pertinent to the study of variations in ocean climate and of effects of these variations on the associated communities of marine organisms. In this paper, the historical files of these observations are summarized to yield monthly estimates of properties and processes at the sea surface within the extremely productive upwelling ecosystem off central and northern Peru. The 32-year period treated encompasses several dramatic El Niño events and the spectacular rise, collapse, and indications of a recent rebound, of the largest exploited fish population that has ever existed, the Peruvian anchoveta.

Although remarkably rich both in biological productivity and in climatic scale ocean variability, the area off Peru is rather poor in maritime data density. Thus the region presents a particular challenge to the methodologies employed here. The area is very sparsely sampled in comparison to the corresponding eastern ocean boundary ecosystems of the northern hemisphere, with most of the reports coming from a narrow coastal shipping lane lying within about 200 km of the coast (Parrish et al. 1983). Maritime reports are subject to a variety of measurement and transmission errors, of which improper positioning is perhaps the most troublesome, sometimes introducing very large errors in all derived quantities (e.g., when a wrong hemisphere, etc., may be indicated). And it is difficult to establish effective procedures for rejecting erroneous reports without also suppressing indications of real variations, particularly in the area off Peru which is perhaps uniquely subject to drastic and abrupt natural environmental perturbations. For example, early indications of the 1982-1983 El Niño event went unnoticed by meteorological agencies in Europe and North America, because the reports which clearly indicated an event of unprecedented intensity were so far from the norm that they are rejected as erroneous by the automated data editing procedures (Siegel 1983). In addition, even when no actual errors are involved, irregular distribution of the reports in both time and space may introduce biases and nonhomogeneities into time series constructed from these data.

Tests of the precision of the methodology on interyear time scales, involving subsamplings of the much richer data distributions off the Iberian Peninsula in the northeast Atlantic Ocean, have indicated benefits to be gained by utilizing rather large areal samples, i.e., of the order of 10 degrees of latitude and longitude in extent, with the increase in report frequency overriding increases in sampling variance resulting from incorporation of additional spatial variability (Bakun, unpublished data). These same tests have indicated that the use of the ordinary 'standard error of the mean' provides a useful guide to the precision of monthly estimates, even though the underlying processes may be very highly variable on much smaller temporal and spatial scales than those used for data summarization. For the time series presented herein, reports available within an area extending some 10 degrees of latitude along the Peru coast and about 4 degrees of longitude offshore (Fig. 1), between Talara and a point just to the south of Pisco, were

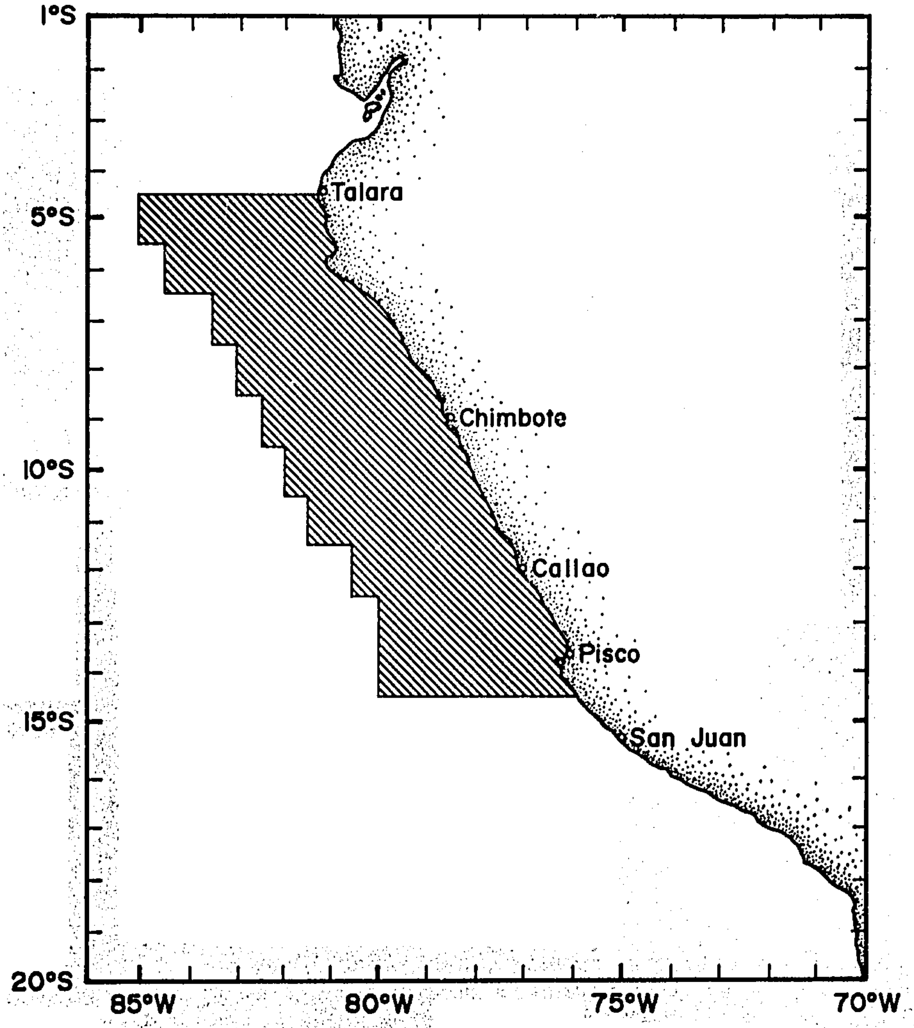

Fig. 1. Summary area. Maritime reports from within the area indicated by diagonal hatching were used for assembling monthly samples.

composited together. These composite samples are assumed to characterize temporal variability, at least in the relative sense, in conditions affecting the neritic fish habitat along that stretch of coastline which appears to have some degree of natural unity both in terms of environmental processes and biological community (Santander 1980; Parrish et al. 1983). The rather ragged offshore edge of the summary region was chosen to facilitate initial extraction of the reports from the data archive files. Consistent features of spatial variability tend to be much less intense in offshore areas of coastal upwelling regions than in coastal areas; thus no substantial effect of the irregularity of shape of the offshore boundary is expected. Also all the monthly summaries are treated identically in terms of areal selection and so time series homogeneity is preserved. In any case, report density is extremely low at the outer edge of the summary area.

Assembly of Data Series

Impossible or highly improbable values occur occasionally in the maritime report files, due to keypunch errors, etc. In the data record format, temperature values between -99.9 and 99.9°C are possible. Initial efforts to construct the data series resulted in rather large standard errors for certain of the monthly values due to incorporation of improbable data. For this reason, only values falling between the limits 11 to 31°C were accepted as valid observations of air temperature, sea surface temperature, or 'wet bulb' air temperature, for this region. (Note that the lower bound on the wet bulb temperature caused only 16 reports, no more than a single report in any one month, to be rejected). Wind speeds of up to 199 knots (102 m/sec) are possible in the record format. Erroneously high wind speeds have a particularly serious effect since wind speed is squared in the stress computation and cubed in the wind mixing index formulation. Reports of wind greater than 45 knots (23 m/sec) occurred within the summary region less than ten times in the entire 32-year record and were in no case corroborated by neighboring (in either space or time) data. Thus wind reports exceeding this value were excluded in preparing these time series. The data record format limited wind direction to values between 0 and 360 degrees, cloud cover observations to the range 0 to 100% of sky obscured, and barometric pressure to values between 890 and 1,070 millibars.

In assembling the monthly data samples, if any one of the reported values of sea surface temperature, barometric pressure, wind speed, or wind direction, were missing or unacceptable the entire report was excluded from the summaries. These four observed properties are sufficient to produce time series of sea surface temperature (Table 2), atmospheric pressure (Table 4), wind stress components (Tables 5 and 6), and wind mixing index (Table 7). The numbers of reports having acceptable observations of these four items are entered as the first of the three numbers shown for each month in Table 1. In addition, if a valid cloud cover observation was available the report was also incorporated in the cloud cover series (Table 3); numbers of reports including acceptable observations of these five items are entered as the second number of each monthly set in Table 1. Finally, if acceptable values of both air (dry bulb) temperature and either wet bulb or dew point temperature were included, the report was also used for construction of time series of atmosphere-ocean heat exchange components (Tables 8 to 11). Numbers of available reports containing acceptable observations of all seven properties required to construct all the time series presented in this paper are shown as the third number under each month in Table 1. All computations of derived quantities were performed on each individual report prior to any summarization process. A simple mean was taken as an estimate of the central tendency of each monthly sample. Computed standard errors of these mean values are displayed within the parentheses following each monthly value presented in the various data tables. An approximate 95% confidence interval estimate can thus be generated by multiplying the indicated standard error by the factor 1.96, and adding and subtracting the result from the monthly mean value (point estimate) to yield the upper and lower limits of the interval.

A small percentage of the reports contain wind observations in which the direction is noted as "variable"; i.e., no direction could be assigned. This properly occurs only when the wind speed is very low. In these cases the wind speed is used, as reported, in the calculations where it enters as a scalar quantity, i.e., in the calculations of wind mixing index, evaporative heat loss and conductive heat loss. In the computation of surface wind stress, wind enters as a vector quantity and directionality is crucial. Accordingly, for the surface wind stress calculations, variable winds are treated as calms. Because the wind speed enters the calculation as a "square", low wind values act essential as zeros in their effect on the monthly means, and so treating these weak variable wind observations as calms has no substantial effect. Also, the net effect of a stress from one direction is cancelled by an equal stress from the opposite direction, and so treating variable-directional stress as equivalent to calm conditions makes physical sense.

Sea Surface Wind Stress

Sea surface stress was estimated according to:

$$(\tau_x, \tau_y) = \rho_a C_D (|\vec{W}_{10}| U_{10}, |\vec{W}_{10}| V_{10}) \qquad \ldots 1)$$

where τ_x and τ_y are components of stress directed onshore and alongshore, respectively; a characteristic onshore direction of 62 degrees and an alongshore direction of 332 degrees (from true north) was assigned to the entire summary area. ρ_a is the density of air, considered constant at 1.22 kg/m^3. C_D is a dimensionless drag coefficient. $|\vec{W}_{10}|$ is the wind speed at 10 m height. U_{10} is the onshore-directed component of wind velocity; V_{10} is the alongshore-directed (positive equatorward) component. For the data series presented in the tables, C_D was considered to be a constant equal to 0.0013. The use of this constant drag coefficient has been a somewhat standard practice in climatological studies of upwelling regions (Bakun et al. 1974; Nelson 1977; Parrish et al. 1983). However, it is recognized that the value of the drag coefficient is actually a variable which depends on the nature of atmospheric turbulence near the sea surface. Thus a dependence on both atmospheric stability and wind magnitude near the sea surface is indicated; the stability effect is particularly important in reducing air-sea transfers in upwelling regions due to the stable atmospheric boundary layer formed over cool upwelled surface water. No clear consensus as to the proper formulation of these dependencies is presently available. However, a reasonable variable drag coefficient formulation has been chosen and has been applied to these data for evaluation of possible differences from results based on the constant drag coefficient formulation. In this case we follow the method of Nelson (1977) for incorporation of the atmospheric stability effect, which is based on a bulk Richardson number parameterization (Deardorff 1968). We incorporate a dependence on wind speed according to the recommendations of Large and Pond (1981) who find a linear increase in the drag coefficient at wind speeds greater than 11 m/sec.

Offshore Ekman Transport

In their climatological study of seasonality and geography of anchovy and sardine reproductive habitats within eastern ocean boundary upwelling systems, Parrish et al. (1983) found a pattern of minimization of both wind-driven offshore surface flow (Ekman transport) and of wind-induced turbulence in the spawning habits of these fishes. They therefore suggest the likelihood of important effects of both processes on reproductive success. Offshore Ekman transport at a given latitude is proportional to the alongshore stress, being simply the product of the alongshore stress and the reciprocal of the local Coriolis parameter. Ekman transport (Ekman 1905) provides an acceptable description of ocean surface transport directly driven by surface wind stress at periods which are long compared to the half-pendulum day; the half-pendulum day is 2.9 actual days in length at 10° latitude but increases to infinity at the equator. Obviously, the Ekman transport description cannot be applied directly at the equator. Here we assume the Ekman transport description to be adequate for the effect of wind stress variations affecting the summary area as a whole on the monthly time scale; thus we simply divide the monthly alongshore wind stress by a characteristic value of the Coriolis parameter (we choose the local value at 10°S, i.e., 0.0000253/sec, to characterize offshore Ekman transport in response to large-scale, long period wind variations over the anchoveta reproductive habitat; this choice will affect the average magnitude but not the time series properties of the resulting indicator series, which will be identical to those of the alongshore stress series).

Wind Mixing Index

The rate at which the wind imparts mechanical energy to the ocean to produce turbulent mixing of the upper water column is roughly proportional to the third power, or "cube", of the wind speed (Elsberry and Garwood 1978). A "wind mixing index", which is simply the mean of the cube of the observed wind speeds in each monthly sample (Table 7) is presented as a guide to longer period variability in this particular process. However, it is to be noted that these series may not reflect energetic shorter-term variability which may be more crucial to reproductive success of anchovies (Husby and Nelson 1982). The hypothetical basis for interest in this process in relation to anchoveta reproductive success is Lasker's (1978) suggestion that first-feeding success of anchovy larvae may be dependent upon availability of fine scale food particle concentrations which may be dispersed by wind-driven turbulent mixing events. These occur at atmospheric storm event scales which are much shorter than one month. Furthermore, it is not the exact magnitude of mixing that is crucial according to this hypothesis, but rather the existence of time-space "survival windows" within which the rate of addition of turbulence by the wind does not reach a level that homogenizes the food particle distributions (Bakun and Parrish 1980). The wind speed level at which this occurs and the minimum required duration of the window for substantial survival to result are unclear and undoubtedly are variable functions of other factors such as water column stability, the particular food particle organism's growth rate, behavior, motility, etc. In any case, the maritime reports occur irregularly in time and space and so are not amenable to indicating durations of periods characterized by specific conditions, even if we were able to specify the required nature of the conditions. This would require utilization of a time-and-space continuous meteorological analysis procedure (Bakun 1986) which might be ineffective due to the low maritime report density in the region and particularly seaward of the region. The use of shore station data, despite interference from local topographic influences, etc., might be the best available option for indicating short time scale wind variability over the ocean habitat off Peru (see Mendo et al., this vol.).

Solar Radiation

Net incoming solar radiation, Q_S, absorbed by the ocean was estimated according to the formula:

$$Q_S = (1 - \alpha)\, Q_0\, (1 - 0.62C + 0.0019h) \qquad \ldots 2)$$

where α is the fraction of incoming radiation reflected from the sea surface, Q_0 is the sum of the direct and diffuse radiation reaching the ground under a cloudless sky, C is the observed total cloud amount in tenths of sky covered and h is the noon solar altitude. For each maritime report, the total daily direct solar radiation reaching the ground under cloudless conditions was extracted from the Smithsonian Meteorological Tables (List 1949) as a function of the date and latitude of the report, using a 4 x 4 element curvilinear interpolation on the table entries via Bessel's central difference formula and assuming the atmospheric transmission coefficient of 0.7 recommended by Seckel and Beaudry (1973). The diffuse solar radiation was estimated according to List's recommendations as follows. The solar radiation reaching the top of the atmosphere was extracted from the appropriate table. This value was decreased by 9% to allow for water vapor absorption and 2% for ozone absorption. The result is subtracted from the value previously determined for the direct radiation reaching the ground to yield the energy scattered out of the solar beam. This is reduced by 50% (to reflect the fact that half is diffused upward and therefore only half is diffused downward) to yield the total diffuse solar radiation reaching the ground. The total daily direct and diffuse radiation values corresponding to each report are then summed to yield Q_S. The remainder of the computation follows the procedures adopted by Nelson and Husby (1983). The linear cloud correction in Equation (2) is as suggested by Reed (1977), and Reed's recommendation that no correction be made for cloud amounts less than 0.25 of total sky was followed. Sea surface albedo was extracted from Payne's (1972) tables, following Nelson and Husby's (1983) algorithm which consists of entering the tables with the 0.7 atmospheric transmission coefficient reduced by a factor equal to the linear cloud correction applied in Equation (2) and the mean daily solar altitude. The possible error in the net radiation estimate introduced by using the mean daily solar altitude to indicate albedo, rather than an integration over the entire day of entries at short time intervals with instantaneous solar altitudes, is estimated to be of the order of 1%.

Radiative Heat Loss

Effective back radiation is the difference between the outgoing long-wave radiation from the sea surface, which depends on the 4th power of the absolute temperature of the sea surface, and the incoming long-wave radiation from the sky, which depends on the water vapor content of the atmosphere and on the nature of the cloud cover. Here we follow exactly the computational scheme of Nelson and Husby (1983) who used the modified Brunt equation (Brunt 1932) with the empirical constants of Budyko (1956) and the linear cloud correction formula of Reed (1976) to compute the effective back radiation (radiative heat loss), Q_B:

$$Q_B = 5.50 \times 10^{-8}\,(T_S + 273.16)^4\,(0.39 - 0.05e_a^{1/2})\,(1 - 0.9C) \qquad \ldots 3)$$

The vapor pressure of the air, e_a, was computed according to the formula provided in the Smithsonian Meteorological Tables (List 1949) using the observed barometric pressure, and "dry bulb" and "wet bulb" air temperatures. For reports that were without an acceptable wet bulb temperature but included an acceptable dew point temperature, the vapor pressure was computed as the saturation vapor pressure at the dew point temperature using an integrated form of the Clausius-Clapeyron equation (Murray 1967).

Evaporative and Conductive Heat Losses

In estimating evaporative heat loss (latent heat transfer) and conductive heat loss (sensible heat transfer), the procedures of Nelson and Husby (1983) are again followed closely, except for a modification of the wind speed dependence in their variable transfer coefficient formulations as indicated below. The bulk aerodynamic formula for turbulent fluxes of latent and sensible heat across the air-sea interface in a neutrally stable atmospheric boundary layer (Kraus 1972) can be expressed as

$$Q_E = \rho_a L C_E (q_0 - q_{10})\,|\vec{W}_{10}| \qquad \ldots 4)$$

$$Q_C = \rho_a c_p C_H\,(T_3 - T_a)\,|\vec{W}_{10}| \qquad \ldots 5)$$

where ρ_a and $|\vec{W}_{10}|$ are as in Equation (1), with ρ_a assigned the same constant value (1.22 kg/m^3) as in the stress computation. L is the latent heat of vaporization, assigned a constant value of 2.45 x 10^6 J/kg (585.3 cal/gm). c_p is the specific heat of air, assigned a constant value of 1,000 J/kg/^{o}C (0.239 cal/g/^{o}C). The empirical exchange coefficients, C_E and C_H, were assigned constant values of 0.0013 in the construction of the time series presented in Tables 10 and 11. In addition, time series based on variable transfer coefficient formulations incorporating dependencies on atmospheric stability and on wind speed were also assembled for comparison. These formulations are again those chosen by Nelson and Husby (1983) which incorporate the atmospheric stability effect according to a bulk Richardson number parameterization (Deardorff 1968); however, Nelson and Husby's wind speed dependencies were in this case modified according to the recommendations of Large and Pond (1982) who suggest an increase in C_E and C_H which is proportional to the square root of the wind speed. The specific humidities of the air in contact with the sea surface, q_0, and at 10 m or deck level, q_{10}, were computed according to

$$q \approx E\frac{e}{P} \qquad \ldots 6)$$

where E is the known ratio (a constant equal to 0.622) of the molecular weight of water vapor to the net molecular weight of dry air, *e* is the vapor pressure and P is the barometic pressure. For this calculation the variation in P is negligible and so a constant value of 101,325 pascals (1,013.25 mb) was assigned. The calculation of *e* at 10 m, or deck level, is as indicated for the radiative heat loss calculation (Equation 3). To calculate *e* at the sea surface, the saturation vapor pressure over pure water was computed from a formula given by Murray (1967), and reduced by 2% to account for the effect of salinity (Miyake 1952).

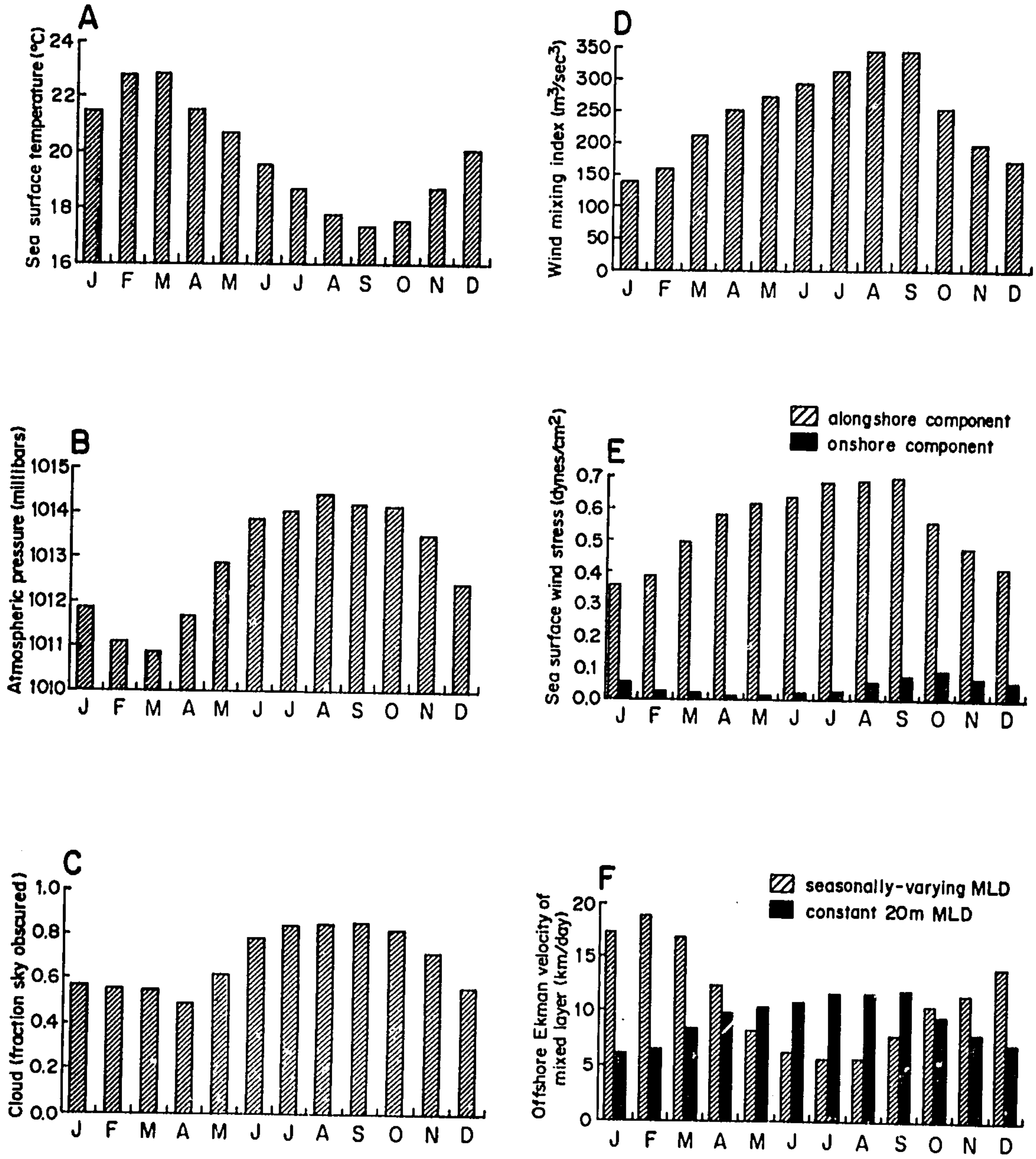

Fig. 2. Seasonal cycles. 32-yr mean monthly values.

The Seasonal Cycles

The idea of regular seasonal cycles for the coupled ocean-atmosphere system off Peru is to some degree illusory in view of the predominant influence of interyear variability in the region. However, the seasonal variation is the most cyclic and predictable of the large components of variability. It is therefore the component of variation which is most likely to be reflected in biological adaptations. Accordingly, a summary of the long-term mean monthly values of the various series (Figs. 2 and 3) serves as a useful starting point for discussion.

Being situated within the tropical band, the region experiences two passages of the sun each year; the sun is directly overhead in October and again in February-March. Also, since the earth's meteorological equator is displaced to the north of the geographical equator, the region is dominated by southern hemisphere atmospheric dynamics; thus austral winter dominates the seasonality of transfers of momentum and mechanical energy from atmosphere to ocean.

The 32-year mean monthly sea surface temperature (Fig. 2A) is at a maximum in March, coinciding with the second period of vertical sun which marks the culmination of the extended austral summer period of relatively high sun. The temperature falls to a minimum in August. The atmospheric pressure (Fig. 2B) tends to be directly out of phase, being at a minimum in the austral summer and at a maximum in the winter season. Cloudiness (Fig. 2C) lags the atmospheric pressure variation by about one month. On average less than 50% of the sky is obscured by clouds in April; this increases to greater than 85% in September.

The strength of the wind exhibits a typical southern hemisphere seasonality, being strongest in austral winter and weakest in summer. Thus the 32-year mean monthly values of the index of rate of addition of turbulent mixing energy to the water column (Fig. 2D) reach a maximum in August-September and a minimum in January. The fact that the seasonal spawning peak of anchoveta is centered within this August-September turbulent mixing maximum would indicate non-adaptation of reproductive strategy for minimization of turbulent mixing effects. This is not in accordance with the general pattern suggested by Parrish et al. (1983) as generally characterizing seasonality and geography of spawning of eastern ocean boundary anchovy populations. Although no claim is made for conclusiveness, the inference would seem to be that Lasker's (1978) hypothesis is not, at least in most years, the major factor affecting anchoveta reproductive success off Peru. Note that the level of turbulent mixing index intensity off Peru is low compared to other anchovy reproductive habitats, even at its seasonal maximum.

The alongshore component of wind stress on the sea surface is consistently equatorward; in no case in the 32-year series (Table 5) did any monthly wind mean stress value deviate from this predominently alongshore and equatorward tendency in the transfer of momentum from atmosphere to ocean. The long-term mean values of alongshore stress (Fig. 2E) follow the same seasonal pattern as the turbulent mixing index, reaching a maximum in September and a minimum in January. The 32-year mean monthly values of the onshore component of stress are small compared to those of the alongshore component, but are positive (onshore-directed) at all seasons.

Surface Ekman transport, being proportional to the alongshore stress but directed perpendicularly to the left of the stress, is thus directed offshore, with a seasonal maximum again corresponding to the seasonal spawning peak of anchoveta. This "anomaly" to the pattern of apparent minimization of offshore transport in spawning strategies of engraulids puzzled Bakun and Parrish (1982). However, Parrish et al. (1983) showed that the seasonal variation in mixed layer depth off Peru proceeds in phase with that of transport, in response to the seasonalities in turbulent mixing (Fig. 2C) and surface cooling (Fig. 2A), but has greater relative amplitude. The result is that drifting organisms which are distributed through the upper mixed layer would experience a faster net offshore drift in the thinner surface mixed layer of austral summer than in the deeper mixed layer of winter, even though the winter transport (by volume) is much larger. This is illustrated in Fig. 2F, which shows calculations of mean monthly offshore Ekman velocity of the mixed layer performed in two different ways (based on the 32-year mean monthly values of the data presented in Table 5). Firstly, the monthly estimates of offshore Ekman transport are divided by the composite mean (20 m) of the mixed layer depth values given for 2-month segments of the seasonal cycle by Parrish et al. (1983). Secondly, the same monthly estimates of offshore Ekman transport are divided by monthly mixed layer depth estimates produced by curvilinear interpolation of the 2-month seasonal segments. The effect of variable mixed layer depth on the net offshore velocity is apparent, and suggestive of adaptation of spawning seasonality for avoidance of offshore loss of larvae (for additional discussion of this aspect, see Bakun 1985). The effect of the choice of a constant or variable drag coefficient formulation in the stress computation (Equation 1) on the seasonal signal is indicated in Fig. 3A. The 32-year mean monthly Ekman transport values based on the variable coefficient formulation follow a seasonal progression which is very similar to those based on the constant coefficient formulation (i.e., presented in Table 5); however they are slightly smaller in magnitude, reflecting the effect of stability in the atmospheric boundary layer which is stabilized as the onshore-directed airflow is cooled from below while traversing the coastal upwelling zone.

Solar radiation entering the ocean (Q_S) is at a maximum during the February overhead passage of the sun (Fig. 3B). This is due to substantially reduced cloud cover relative to the November solar passage. Solar radiation is at a minimum in July, when solar altitude has just passed its June minimum, and cloudiness is approaching its winter maximum.

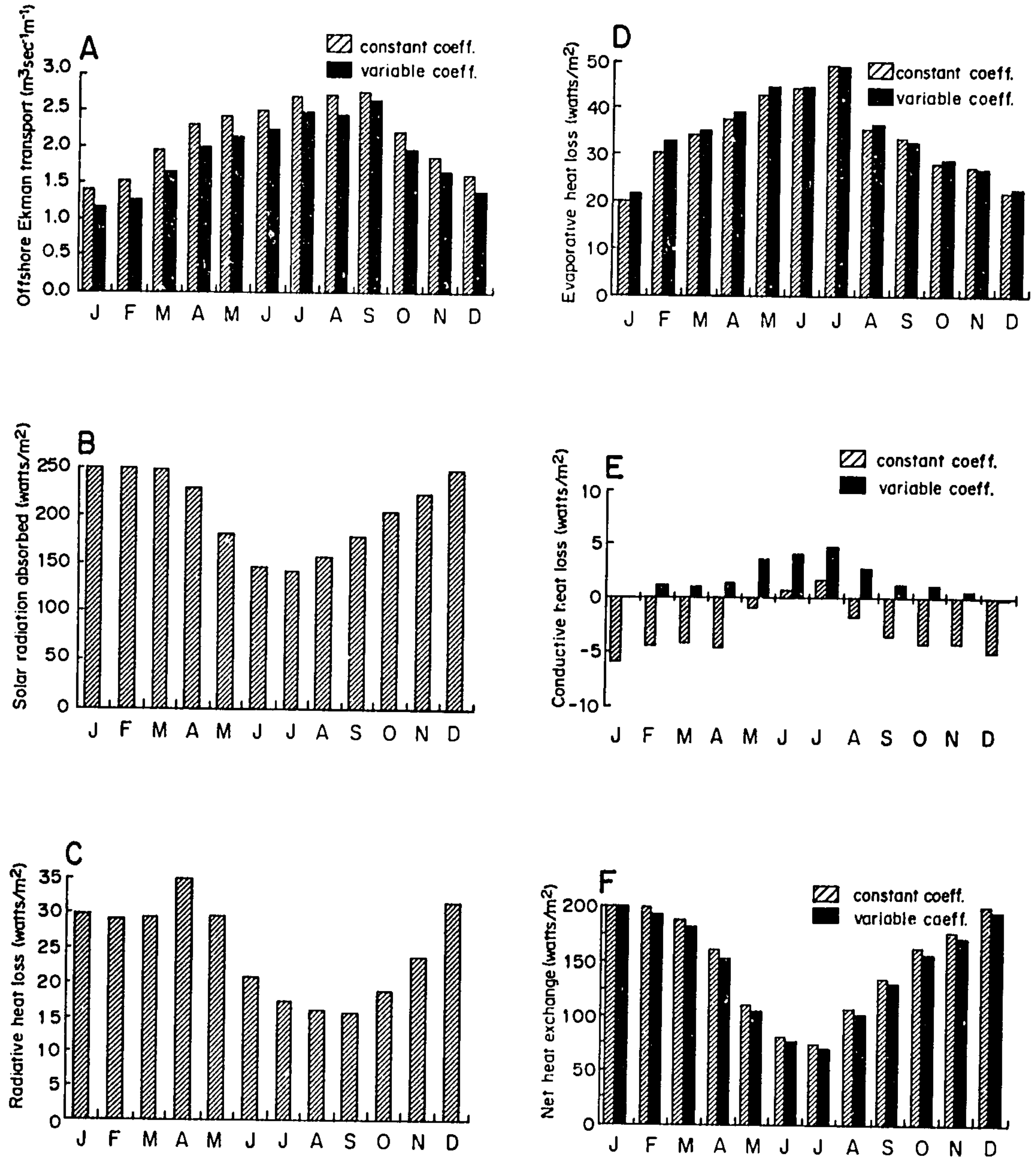

Fig. 3. Seasonal cycles. 32-yr mean monthly values. (Note that the SI-standard heat flux units, watts per square meter, may be converted to calories per square centimeter per day by multiplying by the factor 2.604)

Heat loss from the sea surface via long-wave radiation (Q_B) is only a small fraction of the short-wave radiation absorbed reflecting the area's location within the tropical band (Fig. 3C). Radiative heat loss is at a seasonal maximum during April, corresponding to the minimum in cloudiness, and at a minimum in September, corresponding to the cloudiness maximum.

Heat loss from the ocean via evaporation at the sea surface (Q_E) is at a maximum during austral winter and at a minimum during summer (Fig. 3D). The choice of constant or variable transfer coefficient has only a slight effect, with the results of the variable coefficient formulation appearing to increase very slightly in magnitude relative to those of the constant coefficient formulation toward the summer and fall seasons.

Heat loss via conduction (Q_C) is very small compared to the other heat exchange components (Fig. 3E). This is fortunate because the choice of transfer coefficient formulation completely changes the seasonal pattern. With the constant coefficient formulation, conductive heat loss is mostly negative, indicating heating of the ocean surface by contact with the atmosphere. This reflects the common situation of cool upwelling-affected surface waters being in contact with a generally warmer atmosphere. However, the strong stability of the atmosphere boundary layer inherent in this situation inhibits conductive heat transfer according to the variable transfer coefficient formulation. Thus the less common situation where the air is cooler than the water dominates the sensible heat transfer according to the variable coefficent formulation, with the result that conductive heat loss is indicated as being positive in all the 32-year composite monthly means except the summer months of January and February.

The 32-year monthly means of the time series of atmosphere-ocean heat exchange (Q_N), which represent the resultant differences between the amount of solar radiation absorbed by the ocean and the sum of the heat losses due to long-wave radiation, evaporation and conduction, indicate substantial heat gain by the ocean throughout the year (Fig. 3F). As expected, the average heat gain is greatest in austral summer, reaching values of the order of 200 watts/m^2 (413 cal cm^{-2} day^{-1}) in January, and least in winter, falling to about 70 watts/m^2 (144 cal cm^{-2} day^{-1}) in July. The constant coefficient formulations yield slightly greater numerical values of net heat exchange than do the variable coefficient formulations, mainly due to the differences in the respective indications of the conductive heat loss component discussed in the previous paragraph; however the respective seasonal progressions are very similar.

Interyear Variations

If cyclical seasonal effects are those most likely to be adapted for and incorporated in life cycle strategies of organisms, major nonseasonal variations are those most likely to cause disruptions in life cycle processes and therefore to be reflected in population variations. Very short-scale nonseasonal variations are not well resolved in these monthly composites of irregularly distributed maritime reports. However, when shorter period variability is smoothed and the cyclic seasonal effects are suppressed, nonseasonal variations of longer than annual period, which represent substantial perturbations of the environmental "normalcy" to which reproductive strategies or other life cycle strategies should have become tuned, are clearly manifested. For the purposes of this discussion, a simple 12-month running mean filter is chosen to suppress seasonalities and smooth the higher frequencies.

Problems (negative side lobes, wavelength-dependent phase shifts, etc.) with such equally-weighted moving average filters are well known (Anon. 1966). However, in this case the alternatives also present problems. We particularly wish to suppress the seasonal cycle, and so weighting the filter elements to suppress side lobes at other frequencies while increasing leakage of the seasonal frequency, is not desirable. Smoothed monthly series of anomalies from long-term monthly means (e.g., Quinn et al. 1978; McLain et al. 1985) have the property that the filtering is "nonlocal", i.e., that any value is dependent on other values in the same calendar month in temporally "distant" parts of the time series. Thus, for example, an intense warming (e.g., El Niño) occurring within a generally cool climatic period appears as a much less intense anomaly than a warming of similar magnitude within a warm period; also, the degree of indicated intensity changes whenever the length of the series used for determination of the long-term mean changes. More importantly, if the amplitude (or shape, phase, etc.) of the seasonal variation is undergoing nonseasonal variation, taking anomalies introduces spurious seasonal-scale variations into the filtered series. A "local" seasonal filter that avoids some of these problems can be based on 12th-differences, e.g., the result of subtracting from each monthly value the value for the same calendar month in the previous year, but the result is thereby transformed to annual rates of change of a property rather than the property itself, which complicates a descriptive discussion. However, the use of 12th-difference transforms is worth considering for empirical modelling efforts. For the purposes of this discussion, the simple 12-month running mean provides a "local" seasonal filter/smoother which will be familiar to many readers and adequate for a descriptive treatment.

The filtered sea surface temperature series (Fig. 4A) illustrates well the major El Niño warm events of the period: 1957-1958, 1965, 1969, 1972-1973, 1976 and 1982-1983. Generally elevated temperatures in the period between the 1976 and 1983 events are also apparent. Also apparent is the extended cold period of the mid-1950s; the indication of rise in temperature from this cold period to the peak of the 1957-1983 El Niño is comparable in total magnitude to that of the rise of the 1982-83 El Niño from the much warmer climatic base temperature level of the late 1970s.

Major features in the filtered cloud cover series (Fig. 4B) are visibly related to those in the temperature series, but not in any simple, consistent manner. Cloud cover minima often appear to coincide with the relaxation of El Niño events. An extraordinarily low degree of cloudings appears to have coincided with the return to normal sea temperatures in 1984. Another sharp cloud cover minimum coincided with the leveling off of the temperature decline following the 1957-1958 event. Likewise cloud cover maxima often appear to coincide with rapid drops of temperature into cool periods. Atmospheric pressure variations (Fig. 4C) are obviously highly inversely correlated, at these low frequencies, with those of sea surface temperature.

It is not surprising, in view of the dynamic linkage of wind to horizontal gradient of atmospheric pressure, that wind variations would be related to those of atmospheric pressure. The relation of the "wind-cubed" index of rate of addition of turbulent mixing energy to the ocean by the wind (Fig. 4D) to El Niño periods is striking. El Niño events are evidently strong wind-mixing events which, according to Lasker's (1978) scenario, would correspond to periods of high probability of starvation for first-feeding anchoveta larvae. The period during and immediately following the 1972 El Niño appears to have been characterized by an extended period of highly turbulent upper water column conditions. The period during and following the 1982-1983 event appears to have been similarly turbulent, except for a 2-month "window" of relaxed turbulent mixing index during December 1983 and January 1984 (somewhat masked by the smoothing in Fig. 4C, but evident in the unsmoothed monthly values in Table 7).

The magnitude of alongshore (equatorward) wind stress also increases during El Niño events (Fig. 4E), in agreement with Wyrtki's (1975) conclusions which were based on a summary area displaced somewhat southward along the coast (10-20°S, 70-80°W) from the one used here (Fig. 1). Thus in addition to potential increases in larval starvation due to increased destruction of food particle strata by turbulent mixing, an increase in potential offshore loss of larvae from the favorable coastal habitat is also indicated. The onshore component of surface wind stress is relatively small and consistently positive (onshore-directed) in the filtered series.

In the previous section, the effect of seasonally-varying mixed layer depth on the offshore Ekman velocity of particles which are continually mixed through the upper mixed layer was discussed (i.e., in reference to Fig. 2F). To investigate the effect on interyear time scales, filtered time series of offshore Ekman velocity were calculated as in that section, i.e., (i) assuming a constant MLD of 20 m and (ii) assuming a seasonally varying MLD derived from the values given by Parrish et al. (1983). The result indicates that, at least for the MLD values chosen, the effect of seasonally-varying mixed layer depth is such as to substantially increase on average the rate of offshore movement of passive particles in the mixed layer. If the effective mixed layer depth is increased during El Niño, as would be expected both from the effect of the propagating baroclinic wave in deepening the surface layer and also from the enhanced wind induced turbulent mixing, the effect would be to counteract the increased rate of offshore movement indicated from the Ekman transport calculations.

The effect of the choice of constant or variable drag coefficient formulation in the stress computation (Equation 1) is illustrated in Fig. 4G, where the alongshore stress variation is

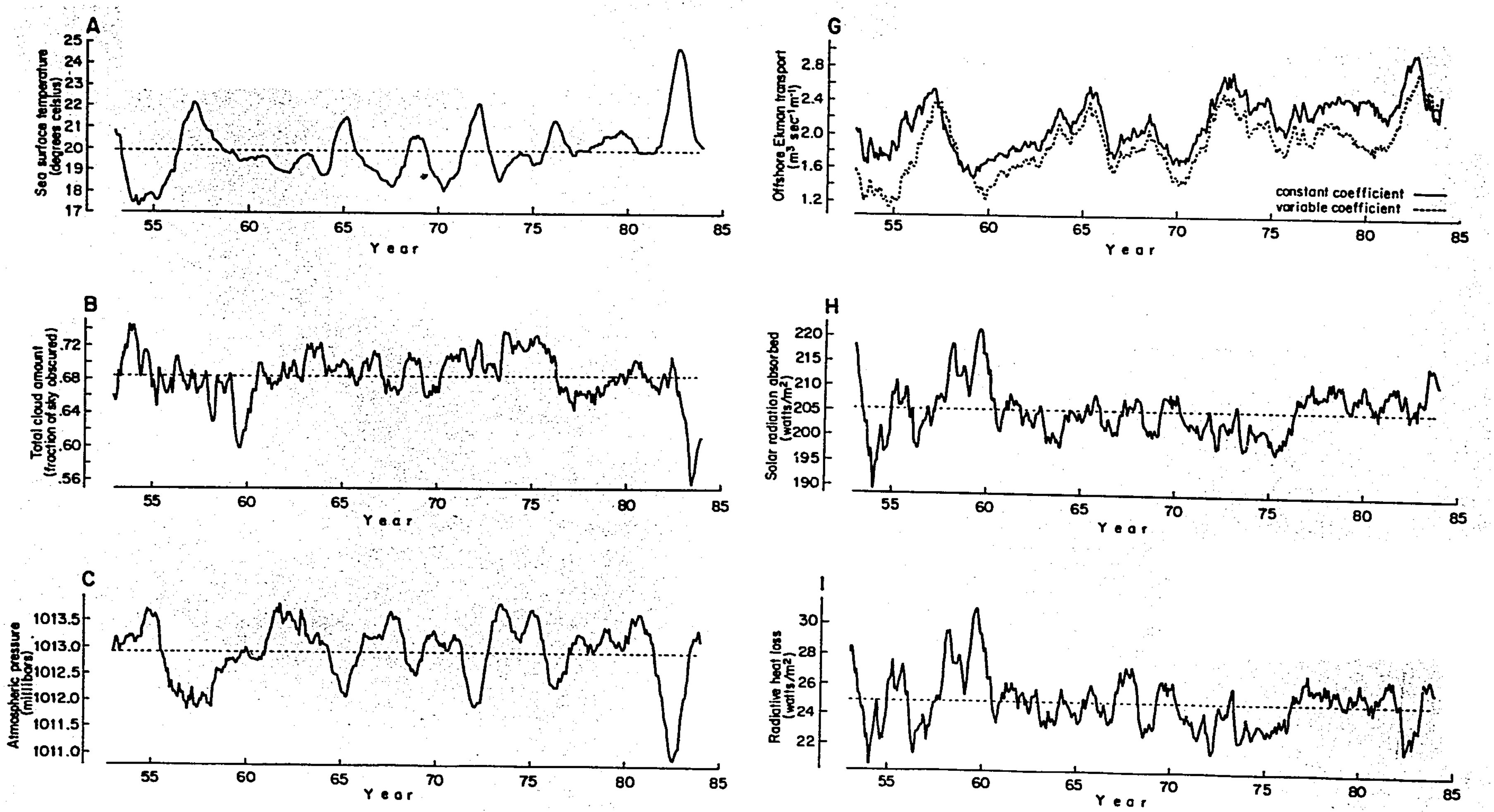

Fig. 4. Low-frequency nonseasonal variations, 12-month running means of monthly time series values. (Note that the SI-standard heat flux units, watts per square meter, may be converted to calories per square centimeter per day by multiplying by the factor 2.064.)

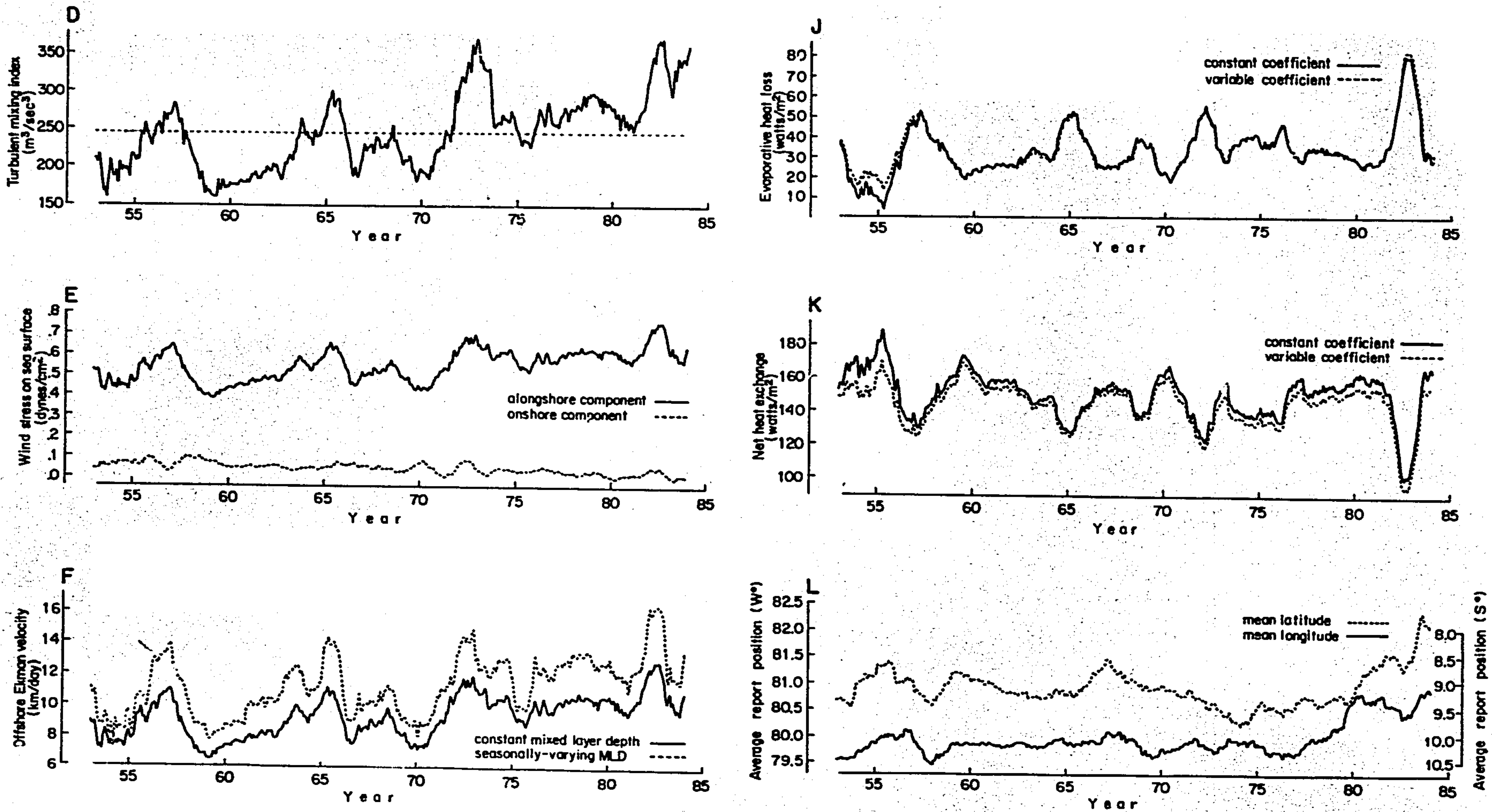

Fig. 4. Continued. Low-frequency nonseasonal variations, 12-month running means of monthly time series values. (Note that the SI-standard heat flux units, watts per square meter, may be converted to calories per square centimeter per day by multiplying by the factor 2.064.)

plotted in terms of its directly proportional transform, offshore Ekman transport. The variable coefficient formulation produces generally lower estimates of stress due to the influence of the stability of the lower atmospheric boundary layer over upwelling-affected surface waters. However the differences essentially disappear during the period of relaxation of the intense El Niños of 1957-1958 and 1982-1983. A possible explanation is the tendency for a less stable atmosphere in contact with the ocean surface due to residual warmth which would linger longer in the ocean than in the atmosphere due to the much greater heat storage capacity of water compared to that of air.

The filtered series of estimates of absorption of solar radiation by the ocean (Q_S) exhibits some interesting patterns (Fig. 4H). Since the variables that control the solar radiation estimate (Equation 2) derived from a maritime report at any given latitude are calendar date and cloud cover, it is not surprising that maxima in Fig. 4H often correspond to minima in Fig. 4B, and vice versa. However there are discernible differences between the two series that result from the interaction of the cloud cover variations with the seasonal changes in solar height in the solar radiation time series. An impressive feature in the solar radiation series is the early large-amplitude alternation consisting of deep minimum of solar radiation entering the ocean corresponding to the early part of the intense 1954-1955 cold period, followed by a sharp, highly erratic rise to a high peak in early 1960. In addition, the entire period of the 1960s and the first half of the 1970s appears to have been characterized by low absorption of solar radiation relative to the more recent period since 1976.

The long-wave radiative heat loss (Q_B) tends to be an order of magnitude smaller than the short-wave absorption, but varies very similarly (Fig. 4I). This similarity is perhaps explainable in the similar dependence of both types of estimate on cloud cover, with the sea surface temperature dependence in the long-wave radiation estimate (Equation 3) being related seasonally to the solar height dependence in the solar radiation estimate (Equation 2). There may also be some actual causal effect of the long period variations in solar radiation on the sea temperature dependence in the long-wave radiation estimate.

The filtered series of evaporative heat loss (Q_E) delineates the various El Niño episodes and the 1954-1955 cold period, in a very similar fashion to the sea surface temperature series (Fig. 4J). The long-term variation in vapor pressure difference between the sea surface and the overlying atmosphere (Equation 4) is apparently very closely linked to that of sea surface temperature. As discussed above, the wind speed dependence is also a strong function of these climate scale events. The effect of choice of constant or variable transfer coefficient apparently makes very little difference, except during the mid-1950s cold period, where increased stability of the air over the cold ocean apparently inhibited the turbulent exchange of latent heat according to the variable coefficient formulation.

The net ocean-atmosphere heat exchange series (Q_N) indicates long-term variations in net ocean heat gain such that minima are associated with El Niño episodes and maxima with cold periods. The variations appear to be controlled to a substantial extent by the evaporative heat loss (Fig. 4J). This is so because the variations in heat gain by absorption of short-wave solar radiation (Fig.4H) are partially offset by the highly correlated variations in long-wave radiative heat loss (Fig. 4I). The net effect of the choice of variable or constant transfer coefficient formulations in the evaporative and conductive components is a slight general lowering of the magnitude of net heat gain in the variable coefficient case. This difference is due primarily to the stability effect on the conductive heat loss term, as discussed in the previous section in reference to Fig. 2E, where the average change in the mean net value of this component, approximately 5 watts/m^2, corresponds in general to the approximate difference between the curves in Fig. 4K, except in the mid-1950s where stability effects on the evaporative heat loss term are appreciable.

In order to check for long-period variations in the distribution of observations within the summary area (Fig. 1), filtered series of the monthly averages of the respective latitudinal and longitudinal locations of reports were prepared (Fig. 4L). Since the coastline is oriented somewhat northwest to southeast, variations in the two curves which tend to parallel each other in the figure, will tend to yield a resultant displacement in the alongshore direction. More serious with respect to the long-term homogeneity of the monthly series herein presented are variations in Fig. 4L where the curves are changing in the opposite sense, i.e., where the net displacement of the mean position of reports is in the onshore-offshore direction; these situations are

Table 1. Numbers of observations in monthly samples used to construct time series. For each month the first number refers to observations used in constructing the values in Tables 2,4,5,6 & 7 (sea temperature, atmospheric pressure, wind stress components, and "wind cubed" index; the 2nd number refers to observations used in constructing the values in Table 4 (cloud cover); the 3rd number refers to observations used for values in Tables 8,9,10 & 11 (heat exchange components).

	Jan			*Feb*			*Mar*			*Apr*			*May*			*Jun*		
1953	21	19	19	29	29	29	22	22	19	23	23	10	33	33	33	16	16	6
1954	61	57	40	19	19	17	21	21	21	59	59	53	42	39	39	36	34	24
1955	24	22	20	35	35	29	16	15	12	9	9	5	24	24	13	35	35	30
1956	41	38	15	17	15	15	16	16	3	39	39	21	22	22	16	20	20	7
1957	32	32	32	25	24	15	98	98	47	38	38	29	25	25	21	53	52	33
1958	153	153	106	74	73	44	69	69	34	84	84	28	67	66	44	110	107	52
1959	128	125	51	162	162	49	143	138	37	115	112	37	97	96	21	67	67	43
1960	98	95	42	148	146	110	166	166	105	151	146	101	171	164	135	85	82	59
1961	148	147	127	124	124	90	115	111	94	183	180	150	89	86	66	130	128	104
1962	185	183	127	149	148	134	163	162	142	157	155	122	114	111	105	177	177	147
1963	78	76	71	103	102	102	182	181	167	180	177	170	157	156	149	185	185	185
1964	129	129	98	138	137	135	82	81	81	76	76	76	45	45	45	52	52	52
1965	59	59	58	75	71	70	137	137	137	99	99	96	139	136	136	139	139	138
1966	107	107	107	82	82	82	113	112	111	106	106	106	117	113	110	137	137	137
1967	111	109	102	60	52	52	80	80	78	147	144	144	75	74	74	66	66	66
1968	76	76	76	128	127	127	108	108	108	139	137	137	91	87	87	111	109	108
1969	67	67	67	87	84	84	134	131	131	91	91	91	56	56	56	102	102	102
1970	90	87	82	57	57	53	103	100	90	51	51	48	99	98	92	208	206	200
1971	103	101	93	81	77	75	89	89	89	53	53	52	44	44	44	22	22	21
1972	109	108	104	54	52	51	49	49	47	85	85	85	81	81	81	56	56	56
1973	55	54	40	44	44	39	89	89	89	50	50	48	58	58	56	57	54	47
1974	84	78	78	63	63	58	113	109	100	57	54	54	119	118	117	73	72	72
1975	59	57	56	73	72	69	140	140	140	99	92	90	140	138	136	116	115	114
1976	70	69	68	20	19	19	76	73	71	59	59	55	71	71	70	49	44	40
1977	51	51	51	109	106	105	79	79	73	101	99	94	93	88	87	70	70	69
1978	57	56	56	65	65	62	71	69	67	92	92	88	71	71	71	41	40	35
1979	97	96	89	58	57	51	105	104	98	85	85	77	83	80	74	48	45	34
1980	96	93	80	106	105	93	125	123	102	75	70	54	151	146	119	246	201	98
1981	116	113	85	90	89	82	139	137	124	108	103	95	115	108	79	128	124	108
1982	91	89	82	90	90	80	152	146	139	100	98	88	103	98	80	54	54	41
1983	68	64	54	126	126	116	94	91	86	76	72	61	93	92	83	61	61	55
1984	90	75	26	99	80	39	90	59	14	75	41	16	58	39	6	56	49	29
	Jul			*Aug*			*Sep*			*Oct*			*Nov*			*Dec*		
1953	10	10	9	39	35	26	29	28	25	18	18	11	24	24	18	19	18	11
1954	40	39	38	14	14	10	27	26	22	44	43	37	30	30	6	18	18	9
1955	17	17	12	37	36	21	35	35	6	45	44	34	27	27	20	13	13	5
1956	45	45	36	21	21	21	29	29	21	41	40	29	63	61	20	24	24	6
1957	27	27	11	24	24	21	64	64	38	112	110	65	100	99	53	115	115	86
1958	51	51	27	159	159	83	96	93	44	113	108	47	115	110	63	58	43	26
1959	100	100	57	103	101	39	85	81	42	74	74	21	110	110	55	114	114	85
1960	169	168	147	114	111	67	142	142	94	75	75	46	63	63	23	82	81	59
1961	108	107	82	155	155	142	153	151	141	128	127	80	197	197	192	135	133	118
1962	213	212	193	168	168	159	81	81	75	129	125	125	173	172	152	91	88	79
1963	120	120	120	70	70	70	110	110	101	70	70	70	61	61	58	56	56	53
1964	90	88	87	71	65	64	94	94	88	129	127	121	62	61	58	105	104	102
1965	92	92	92	119	117	115	99	99	98	67	67	67	177	176	176	111	111	106
1966	116	112	112	122	118	118	185	182	182	131	125	125	89	89	88	123	123	123
1967	89	87	87	67	67	67	84	84	84	76	71	71	73	73	73	99	97	97
1968	58	58	58	82	81	81	59	59	56	111	109	108	118	118	118	66	65	65
1969	70	70	70	86	84	84	108	97	92	102	102	97	137	137	127	101	101	96
1970	75	74	74	66	65	65	91	90	90	50	50	50	127	125	124	68	68	67
1971	43	43	42	58	58	54	28	28	23	51	51	47	78	78	78	34	31	30
1972	35	32	30	60	58	54	32	32	29	81	74	74	31	28	26	51	51	48
1973	81	75	74	105	92	88	89	84	82	55	54	50	100	98	98	71	71	70
1974	102	101	101	90	89	89	67	66	66	53	52	50	78	78	77	44	44	44
1975	67	66	65	53	48	47	70	68	68	70	65	60	68	68	67	88	88	88
1976	74	74	72	21	21	18	88	87	86	76	76	73	46	44	44	58	57	57
1977	55	54	53	55	51	51	73	70	68	106	104	104	183	166	163	67	59	[illegible]
1978	37	33	30	55	51	50	73	72	67	53	49	49	99	79	76	87	87	85
1979	80	75	63	117	108	90	116	109	82	84	77	53	77	75	59	39	35	26
1980	281	233	53	207	182	90	148	131	94	129	118	89	80	74	61	70	66	47
1981	169	161	78	174	159	63	122	111	92	127	115	97	174	155	142	154	147	127
1982	78	74	68	78	70	66	71	62	55	106	102	81	132	124	113	93	89	51
1983	124	121	84	145	116	46	70	48	19	156	150	90	73	73	24	96	90	32
1984	104	90	41	112	95	65	87	69	8	75	54	25	62	40	14	77	61	35

Table 2. Sea surface temperature in degrees Celsius. The standard error of the mean appears within parentheses to the right of the mean temperature value.

	Jan	*Feb*	*Mar*	*Apr*	*May*	*Jun*
1953	21.14(.50)	23.08(.64)	24.63(.51)	24.78(.49)	22.79(.37)	20.52(.46)
1954	18.55(.33)	22.86(.46)	22.01(.42)	16.36(.29)	17.86(.23)	16.95(.25)
1955	21.72(.39)	18.50(.52)	21.01(.85)	19.01(.37)	17.89(.85)	16.67(.30)
1956	19.90(.44)	17.64(.82)	21.66(.46)	20.71(.29)	19.90(.41)	19.22(.29)
1957	19.47(.47)	24.83(.48)	25.26(.21)	24.53(.37)	24.76(.48)	23.15(.27)
1958	23.15(.11)	25.00(.19)	24.52(.25)	22.83(.30)	21.63(.35)	20.42(.18)
1959	20.45(.21)	23.08(.18)	24.49(.15)	21.54(.25)	20.90(.18)	19.26(.25)
1960	21.97(.18)	22.74(.18)	22.70(.19)	20.58(.18)	19.09(.14)	18.22(.18)
1961	22.30(.15)	23.24(.20)	21.61(.21)	19.94(.15)	20.24(.21)	18.67(.15)
1962	21.29(.14)	22.12(.18)	20.37(.18)	19.41(.18)	18.68(.18)	18.92(.12)
1963	20.72(.24)	22.67(.17)	22.15(.16)	20.21(.17)	21.01(.13)	18.98(.10)
1964	21.44(.12)	22.41(.14)	20.91(.22)	20.66(.37)	18.38(.26)	17.35(.24)
1965	21.75(.26)	23.09(.27)	23.96(.15)	24.54(.21)	24.08(.20)	22.11(.14)
1966	22.09(.20)	23.62(.20)	21.96(.25)	20.85(.24)	19.88(.24)	18.67(.16)
1967	20.01(.22)	22.12(.22)	21.86(.23)	20.61(.19)	19.11(.24)	18.13(.30)
1968	19.67(.21)	22.21(.21)	21.78(.22)	18.60(.20)	18.49(.30)	17.31(.20)
1969	22.28(.23)	22.36(.23)	24.25(.18)	23.51(.23)	22.94(.25)	20.92(.22)
1970	21.71(.26)	21.94(.43)	22.51(.26)	20.40(.33)	18.73(.21)	16.85(.14)
1971	19.70(.19)	20.34(.29)	19.70(.25)	21.63(.36)	19.80(.32)	18.46(.46)
1972	20.94(.25)	24.38(.41)	25.17(.37)	22.97(.24)	23.05(.22)	21.68(.24)
1973	24.22(.25)	24.40(.39)	22.52(.20)	19.54(.31)	19.16(.37)	17.36(.35)
1974	20.72(.30)	22.00(.36)	22.10(.31)	21.35(.36)	21.36(.24)	19.51(.19)
1975	21.25(.28)	22.41(.24)	23.41(.19)	22.21(.27)	20.81(.21)	18.67(.18)
1976	21.16(.30)	23.38(.64)	22.96(.33)	22.45(.35)	21.64(.28)	21.23(.30)
1977	23.69(.22)	23.46(.19)	22.44(.32)	20.44(.28)	19.77(.24)	19.66(.27)
1978	21.06(.24)	23.46(.25)	22.57(.25)	22.69(.32)	20.07(.34)	19.95(.49)
1979	22.42(.19)	23.11(.28)	23.62(.22)	22.71(.26)	20.37(.31)	20.61(.45)
1980	21.69(.25)	23.22(.21)	24.21(.21)	22.48(.29)	21.81(.17)	20.84(.13)
1981	20.90(.26)	22.80(.22)	22.10(.24)	20.99(.28)	20.73(.20)	19.44(.16)
1982	21.33(.22)	22.62(.30)	21.65(.23)	21.20(.24)	21.01(.22)	21.15(.41)
1983	26.42(.19)	27.38(.19)	27.99(.14)	27.93(.20)	27.72(.15)	25.93(.30)
1984	22.13(.22)	22.78(.29)	21.92(.26)	20.95(.33)	19.17(.31)	19.49(.28)

	Jul	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*
1953	19.78(.27)	19.06(.21)	18.20(.34)	18.24(.35)	18.72(.40)	18.81(.41)
1954	14.60(.35)	15.57(.41)	14.91(.31)	14.22(.29)	17.11(.26)	19.24(.54)
1955	17.68(.53)	15.54(.45)	15.71(.28)	14.69(.37)	17.09(.24)	18.12(.37)
1956	18.94(.24)	17.65(.37)	17.48(.29)	16.75(.19)	18.38(.29)	19.23(.40)
1957	22.43(.34)	19.28(.34)	18.94(.19)	19.23(.17)	19.07(.16)	20.75(.16)
1958	19.63(.26)	17.37(.10)	17.80(.15)	17.90(.13)	18.98(.18)	20.25(.31)
1959	17.55(.15)	16.80(.12)	16.64(.18)	17.77(.20)	19.04(.20)	19.35(.15)
1960	17.65(.10)	17.42(.12)	17.17(.11)	17.53(.18)	18.78(.24)	20.59(.17)
1961	18.04(.22)	17.62(.11)	16.87(.11)	17.36(.16)	18.54(.14)	19.39(.17)
1962	17.30(.09)	17.27(.10)	16.77(.10)	16.89(.10)	18.08(.12)	19.49(.21)
1963	18.70(.13)	18.24(.17)	18.00(.11)	17.55(.16)	18.54(.28)	19.72(.17)
1964	17.10(.18)	16.11(.20)	16.11(.14)	16.40(.15)	18.31(.32)	19.76(.19)
1965	20.59(.20)	20.00(.20)	17.79(.16)	18.26(.23)	18.76(.13)	21.49(.15)
1966	18.00(.12)	16.75(.13)	16.81(.10)	17.37(.12)	18.13(.17)	19.77(.20)
1967	17.40(.16)	16.46(.17)	15.76(.13)	16.09(.21)	16.90(.18)	18.22(.21)
1968	17.64(.23)	17.05(.17)	18.26(.38)	17.65(.17)	17.67(.16)	20.82(.24)
1969	18.44(.20)	18.01(.17)	17.36(.19)	18.24(.16)	18.39(.13)	19.49(.15)
1970	15.72(.12)	16.19(.13)	16.33(.28)	16.36(.25)	17.94(.16)	18.29(.21)
1971	18.00(.28)	17.27(.23)	16.32(.26)	17.05(.27)	18.34(.15)	19.81(.35)
1972	21.18(.36)	21.77(.23)	19.29(.36)	19.17(.35)	20.61(.32)	21.73(.31)
1973	16.88(.32)	16.04(.16)	15.80(.22)	16.11(.31)	17.27(.24)	19.01(.30)
1974	18.12(.15)	17.48(.15)	16.70(.31)	16.91(.32)	18.96(.23)	19.83(.35)
1975	18.46(.25)	17.68(.36)	15.71(.24)	15.59(.20)	16.24(.15)	18.74(.24)
1976	21.18(.20)	19.51(.55)	19.00(.23)	19.19(.25)	20.04(.23)	21.46(.15)
1977	18.54(.25)	17.23(.22)	17.21(.28)	18.49(.28)	18.95(.16)	19.45(.24)
1978	18.49(.35)	16.91(.33)	17.27(.25)	18.11(.25)	19.40(.30)	20.49(.24)
1979	18.73(.25)	18.30(.26)	19.01(.28)	18.53(.23)	19.25(.27)	21.04(.38)
1980	20.04(.11)	18.35(.13)	17.77(.15)	18.39(.23)	18.95(.27)	20.21(.21)
1981	18.08(.17)	18.24(.11)	17.67(.24)	17.86(.23)	18.98(.15)	20.29(.15)
1982	19.65(.18)	18.34(.23)	19.00(.36)	20.61(.22)	23.03(.17)	25.19(.21)
1983	23.24(.23)	21.26(.21)	19.57(.25)	19.89(.14)	20.25(.22)	21.54(.27)
1984	19.52(.23)	18.37(.13)	18.44(.18)	18.27(.28)	19.70(.31)	20.20(.31)

Table 3. Total cloud amount. Values indicate mean fraction of sky obscured. The standard error of the mean appears in parentheses to the right of each mean value.

	Jan	Feb	Mar	Apr	May	Jun
1953	.66(.06)	.58(.06)	.43(.06)	.43(.08)	.54(.06)	.76(.10)
1954	.59(.05)	.75(.05)	.69(.07)	.35(.04)	.85(.05)	.74(.07)
1955	.55(.07)	.61(.06)	.60(.09)	.06(.04)	.69(.08)	.90(.04)
1956	.66(.05)	.46(.10)	.40(.06)	.53(.06)	.65(.08)	.89(.06)
1957	.48(.07)	.80(.05)	.56(.03)	.57(.05)	.55(.06)	.76(.04)
1958	.60(.03)	.68(.03)	.63(.03)	.32(.04)	.54(.04)	.83(.03)
1959	.40(.03)	.58(.02)	.66(.02)	.60(.03)	.83(.03)	.78(.04)
1960	.50(.03)	.50(.03)	.38(.02)	.44(.03)	.51(.03)	.63(.05)
1961	.65(.03)	.44(.03)	.65(.03)	.50(.03)	.49(.04)	.79(.03)
1962	.55(.02)	.54(.03)	.48(.03)	.56(.03)	.53(.04)	.79(.03)
1963	.50(.04)	.52(.03)	.61(.02)	.52(.03)	.66(.03)	.81(.02)
1964	.64(.03)	.66(.03)	.57(.04)	.51(.04)	.72(.06)	.63(.06)
1965	.54(.04)	.49(.04)	.61(.02)	.60(.03)	.63(.03)	.64(.03)
1966	.56(.03)	.44(.03)	.57(.03)	.45(.03)	.62(.03)	.76(.03)
1967	.72(.03)	.51(.05)	.56(.03)	.51(.03)	.46(.04)	.82(.04)
1968	.52(.04)	.52(.03)	.45(.03)	.38(.03)	.65(.04)	.75(.03)
1969	.57(.04)	.55(.04)	.58(.03)	.57(.04)	.70(.05)	.81(.03)
1970	.59(.04)	.43(.04)	.37(.03)	.43(.05)	.62(.04)	.81(.02)
1971	.51(.03)	.58(.04)	.48(.03)	.52(.05)	.68(.06)	.85(.06)
1972	.53(.04)	.49(.04)	.64(.03)	.53(.04)	.69(.04)	.78(.04)
1973	.67(.03)	.61(.05)	.60(.04)	.49(.04)	.40(.05)	.70(.05)
1974	.59(.03)	.52(.04)	.53(.03)	.53(.05)	.77(.03)	.84(.02)
1975	.69(.04)	.50(.04)	.60(.02)	.54(.03)	.72(.03)	.86(.03)
1976	.61(.04)	.59(.08)	.63(.03)	.55(.05)	.62(.04)	.87(.04)
1977	.54(.05)	.68(.03)	.55(.04)	.34(.03)	.53(.04)	.71(.04)
1978	.53(.04)	.65(.04)	.45(.04)	.57(.04)	.54(.05)	.68(.07)
1979	.50(.03)	.53(.04)	.56(.03)	.44(.03)	.67(.04)	.79(.05)
1980	.57(.03)	.53(.03)	.58(.03)	.48(.04)	.57(.03)	.80(.02)
1981	.66(.03)	.63(.03)	.51(.03)	.57(.03)	.66(.03)	.80(.03)
1982	.60(.03)	.58(.03)	.55(.03)	.52(.03)	.58(.04)	.84(.04)
1983	.52(.04)	.47(.02)	.63(.03)	.70(.03)	.75(.03)	.74(.04)
1984	.42(.04)	.43(.03)	.45(.03)	.40(.04)	.34(.05)	.74(.04)
	Jul	Aug	Sep	Oct	Nov	Dec
1953	.65(.14)	.91(.04)	.74(.07)	.74(.07)	.81(.06)	.67(.07)
1954	.79(.05)	.86(.07)	.92(.05)	.89(.04)	.72(.05)	.75(.08)
1955	.97(.02)	.90(.04)	.90(.04)	.80(.05)	.61(.08)	.44(.10)
1956	.85(.05)	.82(.08)	.84(.05)	.62(.05)	.73(.05)	.49(.08)
1957	.79(.06)	.72(.08)	.85(.04)	.72(.03)	.72(.03)	.64(.03)
1958	.79(.05)	.80(.03)	.90(.02)	.81(.03)	.52(.04)	.45(.06)
1959	.78(.03)	.78(.03)	.79(.04)	.79(.03)	.63(.04)	.51(.03)
1960	.72(.03)	.81(.03)	.90(.02)	.89(.03)	.63(.05)	.67(.04)
1961	.94(.01)	.83(.02)	.90(.02)	.78(.03)	.61(.02)	.60(.03)
1962	.90(.02)	.93(.02)	.86(.03)	.88(.02)	.77(.02)	.46(.04)
1963	.80(.03)	.80(.04)	.88(.02)	.82(.04)	.77(.04)	.68(.05)
1964	.87(.03)	.87(.03)	.86(.03)	.88(.02)	.77(.04)	.51(.03)
1965	.88(.03)	.90(.02)	.92(.02)	.86(.03)	.75(.02)	.61(.03)
1966	.77(.03)	.83(.03)	.85(.02)	.89(.02)	.83(.03)	.61(.03)
1967	.88(.03)	.91(.03)	.84(.03)	.85(.04)	.86(.03)	.47(.04)
1968	.80(.05)	.93(.02)	.88(.03)	.83(.03)	.76(.03)	.50(.04)
1969	.86(.04)	.83(.03)	.91(.02)	.82(.03)	.68(.03)	.56(.04)
1970	.87(.04)	.91(.03)	.85(.03)	.95(.02)	.59(.03)	.64(.04)
1971	.94(.02)	.88(.03)	.91(.03)	.85(.05)	.65(.04)	.65(.06)
1972	.83(.05)	.80(.04)	.87(.04)	.78(.04)	.86(.05)	.67(.05)
1973	.82(.03)	.91(.02)	.87(.03)	.80(.04)	.81(.03)	.72(.04)
1974	.91(.02)	.89(.03)	.88(.03)	.75(.05)	.72(.04)	.57(.05)
1975	.86(.03)	.89(.03)	.89(.03)	.77(.04)	.78(.04)	.64(.04)
1976	.80(.04)	.93(.03)	.77(.03)	.81(.03)	.78(.04)	.53(.04)
1977	.89(.03)	.86(.04)	.83(.04)	.81(.03)	.72(.02)	.41(.05)
1978	.95(.01)	.84(.04)	.80(.04)	.81(.04)	.68(.04)	.50(.03)
1979	.85(.03)	.81(.03)	.83(.03)	.81(.03)	.80(.03)	.49(.06)
1980	.90(.01)	.90(.02)	.81(.02)	.82(.02)	.69(.04)	.48(.04)
1981	.87(.02)	.83(.02)	.92(.02)	.67(.03)	.63(.03)	.51(.03)
1982	.80(.04)	.88(.03)	.82(.03)	.76(.03)	.75(.03)	.58(.03)
1983	.72(.03)	.68(.03)	.66(.06)	.80(.02)	.58(.04)	.49(.04)
1984	.81(.03)	.75(.03)	.86(.03)	.91(.03)	.70(.05)	.52(.04)

Table 4. Atmospheric pressure at sea level. Add 1000.0 to the mean values in the table to yield pressure in millibars. The standard error of the mean appears in parentheses to the right of each mean value; the standard errors are given (directly) in millibars.

	Jan	*Feb*	*Mar*	*Apr*	*May*	*Jun*
1953	11.2(.3)	10.4(.1)	11.1(.3)	13.2(.5)	12.5(.2)	14.5(.5)
1954	12.3(.2)	12.2(.4)	10.2(.4)	11.3(.3)	13.5(.3)	14.7(.3)
1955	12.5(.3)	10.9(.2)	10.4(.4)	11.9(.5)	13.6(.2)	15.2(.2)
1956	11.5(.2)	10.7(.4)	11.1(.3)	10.9(.3)	12.0(.2)	10.0(.6)
1957	12.8(.2)	8.6(.3)	10.9(.3)	9.9(.3)	12.3(.2)	12.3(.2)
1958	11.9(.2)	11.5(.2)	7.2(.4)	9.8(.3)	11.5(.2)	13.2(.1)
1959	12.0(.2)	10.9(.1)	11.5(.2)	11.2(.1)	13.3(.2)	14.2(.2)
1960	11.6(.2)	11.5(.2)	11.3(.2)	11.5(.1)	12.7(.1)	13.7(.2)
1961	10.6(.4)	10.6(.2)	10.6(.2)	11.2(.4)	12.9(.1)	13.6(.2)
1962	13.0(.1)	11.8(.2)	12.0(.1)	12.8(.2)	14.0(.2)	15.3(.1)
1963	12.9(.2)	13.6(.2)	11.2(.1)	13.5(.4)	13.2(.1)	14.2(.1)
1964	12.3(.1)	10.5(.1)	11.2(.2)	12.2(.2)	12.7(.4)	14.2(.2)
1965	11.7(.1)	10.2(.2)	11.0(.2)	11.5(.1)	11.3(.2)	12.9(.2)
1966	10.6(.2)	10.2(.2)	10.2(.1)	11.8(.2)	13.2(.1)	14.6(.1)
1967	11.5(.2)	12.3(.2)	12.0(.2)	11.3(.2)	13.1(.2)	14.3(.2)
1968	11.3(.2)	11.7(.1)	12.6(.2)	12.9(.1)	14.3(.2)	15.6(.1)
1969	11.2(.3)	9.6(.1)	11.4(.2)	11.3(.1)	11.5(.2)	13.5(.2)
1970	12.8(.2)	11.0(.2)	11.8(.1)	11.7(.2)	14.5(.2)	14.4(.1)
1971	11.9(.2)	10.8(.2)	10.8(.2)	12.3(.2)	13.8(.3)	15.3(.4)
1972	10.9(.2)	11.0(.3)	10.3(.2)	11.5(.2)	11.8(.2)	12.1(.2)
1973	10.5(.4)	11.8(.2)	10.7(.2)	11.5(.3)	13.0(.3)	14.5(.2)
1974	11.9(.5)	11.8(.2)	12.5(.2)	12.6(.3)	13.7(.3)	14.2(.2)
1975	11.5(.3)	11.9(.2)	11.4(.1)	11.9(.2)	13.5(.1)	14.0(.1)
1976	12.1(.3)	11.6(.7)	10.6(.1)	11.9(.2)	12.5(.2)	12.0(.2)
1977	10.4(.3)	11.2(.1)	10.0(.2)	12.0(.4)	12.6(.2)	13.7(.2)
1978	13.9(.3)	10.1(.7)	12.0(.2)	12.3(.2)	12.8(.2)	15.0(.3)
1979	12.2(.1)	11.9(.3)	11.4(.2)	11.0(.3)	13.3(.3)	15.5(.5)
1980	11.9(.2)	12.3(.2)	9.3(.2)	10.5(.2)	12.9(.2)	14.5(.3)
1981	13.9(.3)	10.8(.2)	11.4(.2)	12.1(.2)	14.3(.2)	13.8(.4)
1982	12.6(.5)	11.4(.2)	10.4(.2)	12.1(.2)	12.6(.2)	12.9(.3)
1983	9.1(.3)	9.7(.2)	9.1(.2)	9.5(.2)	9.6(.3)	11.6(.2)
1984	12.5(.2)	10.7(.3)	10.7(.5)	13.1(.3)	13.7(.7)	13.9(.2)

	Jul	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*
1953	13.7(.5)	13.4(.2)	13.0(.2)	15.0(.5)	14.0(.3)	13.2(.4)
1954	13.8(.3)	14.3(.4)	13.8(.3)	14.8(.2)	14.5(.2)	13.0(.3)
1955	15.7(.3)	15.1(.3)	15.4(.3)	16.1(.3)	14.0(.2)	13.1(.5)
1956	14.9(.3)	13.7(.4)	14.4(.3)	14.1(.2)	14.2(.5)	9.4(.6)
1957	13.0(.3)	14.0(.3)	12.5(.3)	13.4(.2)	12.8(.2)	12.2(.2)
1958	14.1(.3)	13.8(.2)	14.0(.3)	12.7(.2)	12.8(.2)	10.6(1.7)
1959	13.6(.1)	14.1(.2)	13.1(.2)	13.7(.2)	13.3(.2)	12.2(.3)
1960	14.5(.1)	14.5(.2)	14.1(.1)	14.0(.2)	13.1(.2)	13.5(.3)
1961	14.4(.2)	14.4(.1)	14.7(.1)	13.5(.1)	14.7(.2)	13.2(.1)
1962	14.4(.1)	15.2(.2)	13.9(.3)	15.3(.2)	10.6(1.4)	13.8(.2)
1963	14.3(.2)	13.6(.3)	13.8(.4)	14.4(.1)	15.4(.4)	12.4(.2)
1964	14.8(.1)	14.8(.2)	14.2(.2)	14.3(.2)	13.1(.2)	13.2(.1)
1965	12.6(.2)	14.0(.2)	14.1(.2)	13.9(.2)	12.1(.2)	11.6(.1)
1966	14.0(.1)	14.9(.1)	14.8(.1)	14.1(.2)	13.6(.2)	12.3(.1)
1967	14.2(.2)	14.5(.2)	15.2(.2)	14.0(.2)	13.4(.2)	13.0(.2)
1968	14.8(.2)	15.2(.1)	14.0(.3)	13.5(.2)	14.1(.1)	12.6(.2)
1969	14.3(.2)	14.9(.2)	13.0(.1)	13.8(.1)	13.2(.2)	12.2(.1)
1970	15.5(.1)	14.4(.2)	13.8(.2)	13.9(.3)	13.9(.1)	11.0(.2)
1971	13.7(.3)	14.3(.7)	14.5(.4)	15.3(.2)	14.0(.1)	12.3(.3)
1972	12.5(.6)	12.8(.3)	12.9(.3)	13.1(.2)	12.2(.3)	11.8(.6)
1973	14.7(.4)	14.8(.2)	15.2(.3)	15.1(.2)	14.3(.2)	14.8(.2)
1974	13.8(.4)	14.7(.2)	14.9(.2)	14.0(.2)	13.7(.1)	12.6(.2)
1975	15.2(.2)	15.1(.3)	15.5(.2)	15.3(.2)	15.1(.2)	13.5(.2)
1976	13.3(.2)	14.6(.6)	13.3(.4)	13.7(.3)	13.9(.2)	10.4(.2)
1977	13.5(.3)	14.3(.2)	14.7(.2)	14.2(.2)	13.7(.2)	12.4(.2)
1978	13.9(.4)	14.1(.2)	14.5(.2)	13.8(.2)	12.3(.2)	12.3(.2)
1979	14.9(.2)	14.2(.3)	14.7(.3)	14.8(.2)	14.1(.3)	12.5(.9)
1980	15.1(.2)	15.2(.2)	14.1(.4)	13.8(.3)	13.8(.2)	13.7(.5)
1981	15.0(.3)	16.0(.2)	14.8(.2)	13.9(.2)	13.4(.2)	11.9(.1)
1982	12.0(.2)	12.9(.2)	14.1(.3)	12.9(.2)	10.6(.2)	10.0(.2)
1983	11.8(.2)	14.2(.4)	15.0(.5)	13.6(.2)	13.3(.7)	14.2(.4)
1984	12.6(.4)	15.3(.3)	14.8(.5)	14.5(.3)	14.2(.1)	11.8(.3)

Table 5. Alongshore component (positive equatorward) of wind stress on the sea surface. Units are dynes per square centimeter. The standard error of the mean appears in parentheses to the right of the mean alongshore stress value. Values in this table multiplied by the factor 3.95 (see text) yield offshore Ekman transport in cubic meters per second across each meter width.

	Jan	*Feb*	*Mar*	*Apr*	*May*	*Jun*
1953	.36(.06)	.32(.05)	.44(.07)	.99(.20)	.83(.09)	.37(.10)
1954	.24(.03)	.41(.14)	.10(.02)	.46(.05)	.56(.08)	.46(.08)
1955	.40(.09)	.16(.03)	.53(.18)	.18(.08)	.63(.11)	.45(.09)
1956	.16(.02)	.25(.07)	.67(.10)	.83(.09)	.85(.13)	.50(.05)
1957	.31(.06)	.53(.11)	.76(.05)	.86(.10)	.57(.06)	.76(.07)
1958	.40(.05)	.42(.05)	.45(.05)	.61(.06)	.57(.07)	.46(.04)
1959	.34(.03)	.28(.02)	.40(.03)	.42(.04)	.30(.03)	.59(.07)
1960	.23(.03)	.27(.02)	.41(.03)	.49(.04)	.53(.09)	.45(.04)
1961	.20(.02)	.27(.03)	.39(.04)	.48(.03)	.70(.06)	.48(.05)
1962	.42(.02)	.34(.03)	.47(.03)	.52(.04)	.51(.04)	.60(.04)
1963	.32(.04)	.39(.03)	.61(.03)	.47(.03)	.59(.04)	.33(.03)
1964	.49(.04)	.44(.03)	.51(.05)	.71(.07)	.63(.07)	.58(.12)
1965	.29(.04)	.40(.05)	.40(.03)	.53(.06)	.97(.07)	.58(.04)
1966	.60(.04)	.61(.06)	.46(.04)	.75(.06)	.59(.05)	.62(.04)
1967	.40(.04)	.36(.04)	.29(.03)	.30(.03)	.37(.04)	.71(.10)
1968	.15(.02)	.40(.05)	.36(.03)	.36(.03)	.34(.05)	.65(.05)
1969	.29(.04)	.26(.04)	.47(.04)	.56(.04)	.45(.07)	.89(.08)
1970	.33(.04)	.16(.05)	.40(.05)	.56(.06)	.55(.05)	.52(.04)
1971	.17(.04)	.36(.04)	.34(.03)	.59(.08)	.43(.07)	.73(.23)
1972	.29(.03)	.34(.04)	.56(.11)	.55(.04)	.42(.04)	.67(.08)
1973	.57(.06)	.38(.05)	.73(.05)	.68(.08)	.67(.11)	.51(.07)
1974	.32(.04)	.42(.05)	.48(.04)	.68(.07)	.71(.05)	.66(.07)
1975	.40(.04)	.35(.04)	.72(.05)	.63(.05)	.74(.04)	.63(.06)
1976	.21(.04)	.17(.04)	.51(.05)	.77(.07)	.72(.07)	.56(.08)
1977	.32(.06)	.56(.06)	.38(.04)	.57(.05)	.47(.05)	.67(.05)
1978	.37(.05)	.47(.06)	.62(.07)	.71(.08)	.59(.07)	.72(.12)
1979	.49(.05)	.54(.09)	.54(.04)	.68(.05)	.69(.07)	.92(.14)
1980	.44(.04)	.47(.05)	.49(.04)	.49(.05)	.89(.07)	.58(.03)
1981	.52(.04)	.30(.03)	.46(.04)	.54(.04)	.53(.05)	.84(.08)
1982	.35(.04)	.47(.04)	.63(.04)	.55(.04)	.65(.06)	.91(.12)
1983	.69(.06)	.66(.04)	.46(.05)	.74(.08)	.75(.06)	1.07(.09)
1984	.26(.04)	.53(.11)	.80(.13)	.31(.11)	.83(.18)	.87(.13)

	Jul	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*
1953	.70(.22)	.36(.05)	.46(.06)	.53(.08)	.62(.08)	.27(.05)
1954	.52(.07)	.89(.21)	.83(.09)	.24(.02)	.30(.04)	.20(.04)
1955	.46(.09)	.88(.14)	.66(.10)	.65(.12)	.60(.08)	.11(.04)
1956	.69(.09)	.52(.13)	.64(.05)	.50(.08)	.45(.04)	.45(.08)
1957	1.01(.11)	.54(.08)	.75(.07)	.56(.06)	.44(.04)	.56(.04)
1958	.51(.05)	.71(.06)	.49(.04)	.43(.04)	.26(.03)	.39(.05)
1959	.38(.04)	.53(.04)	.48(.07)	.44(.05)	.31(.03)	.23(.03)
1960	.59(.05)	.55(.04)	.51(.04)	.48(.06)	.34(.03)	.36(.04)
1961	.67(.06)	.50(.04)	.50(.04)	.40(.03)	.38(.02)	.31(.03)
1962	.60(.04)	.49(.04)	.60(.06)	.49(.04)	.51(.04)	.23(.02)
1963	.54(.05)	.48(.06)	.72(.05)	.72(.11)	.53(.06)	.36(.04)
1964	.62(.05)	.71(.09)	.73(.08)	.57(.04)	.36(.05)	.42(.04)
1965	.63(.05)	.84(.07)	.87(.07)	.60(.07)	.49(.03)	.49(.04)
1966	.76(.04)	.74(.06)	.59(.03)	.52(.04)	.26(.03)	.26(.02)
1967	.54(.05)	.72(.07)	.74(.09)	.73(.09)	.46(.05)	.55(.06)
1968	.90(.10)	.72(.08)	.64(.08)	.59(.03)	.51(.03)	.63(.08)
1969	.58(.06)	.71(.08)	.59(.05)	.42(.04)	.28(.03)	.37(.04)
1970	.57(.06)	.52(.05)	.45(.04)	.50(.07)	.41(.03)	.27(.05)
1971	.46(.08)	.77(.11)	.64(.12)	.71(.08)	.43(.05)	.49(.09)
1972	.90(.11)	.81(.10)	1.32(.19)	.49(.05)	.35(.04)	.72(.15)
1973	.70(.11)	1.16(.12)	1.01(.11)	.71(.09)	.58(.05)	.37(.06)
1974	.73(.05)	.64(.08)	.72(.07)	.67(.07)	.68(.05)	.45(.06)
1975	.64(.07)	.91(.10)	.73(.05)	.51(.05)	.36(.04)	.35(.05)
1976	.59(.05)	.69(.16)	.80(.06)	.67(.06)	.64(.06)	.52(.06)
1977	.94(.11)	.83(.10)	.47(.06)	.46(.04)	.57(.04)	.55(.06)
1978	.87(.14)	.69(.08)	.73(.09)	.54(.06)	.51(.06)	.47(.05)
1979	.65(.07)	.66(.09)	.71(.07)	.65(.05)	.54(.05)	.46(.07)
1980	1.01(.04)	.74(.04)	.75(.06)	.65(.05)	.47(.04)	.49(.06)
1981	.77(.07)	.64(.04)	.85(.09)	.41(.04)	.57(.04)	.42(.03)
1982	.89(.08)	.63(.06)	.96(.12)	.84(.06)	.73(.04)	.66(.05)
1983	.86(.06)	.69(.06)	.77(.07)	.60(.05)	.38(.10)	.23(.05)
1984	.61(.06)	.76(.06)	.64(.07)	.60(.04)	.86(.06)	.58(.05)

Table 6. Onshore component of wind stress on the sea surface. Units are dynes per square centimeter. The standard error of the mean appears in parentheses to the right of each mean onshore stress value.

	Jan	*Feb*	*Mar*	*Apr*	*May*	*Jun*
1953	.10(.03)	.02(.03)	.00(.05)	-.12(.04)	.02(.04)	-.06(.05)
1954	.04(.01)	.07(.05)	.00(.01)	.10(.02)	-.04(.03)	.04(.02)
1955	-.04(.03)	.02(.01)	.19(.07)	.09(.08)	-.01(.03)	-.01(.03)
1956	.06(.03)	.08(.03)	.08(.08)	.01(.04)	.01(.05)	.10(.04)
1957	.05(.02)	-.06(.05)	-.06(.02)	-.04(.03)	.00(.04)	.06(.03)
1958	.07(.01)	.08(.02)	.09(.02)	.01(.02)	.02(.02)	.08(.02)
1959	.05(.01)	.07(.01)	.01(.02)	.06(.01)	.04(.02)	.17(.03)
1960	.07(.01)	.04(.01)	.05(.01)	.04(.02)	.03(.01)	.02(.02)
1961	.03(.01)	.01(.01)	.06(.02)	.05(.01)	.03(.02)	.04(.02)
1962	.08(.01)	.01(.02)	.04(.01)	.02(.02)	.02(.02)	-.03(.01)
1963	.06(.01)	.02(.02)	.08(.01)	.01(.01)	.01(.02)	.01(.01)
1964	.05(.02)	.03(.01)	.04(.02)	-.07(.03)	.00(.04)	.06(.03)
1965	.06(.02)	.05(.02)	.01(.01)	.06(.02)	-.08(.03)	.03(.02)
1966	.05(.02)	.06(.02)	.09(.03)	-.06(.02)	.03(.02)	.06(.02)
1967	.02(.02)	.08(.02)	.02(.02)	.03(.01)	.09(.02)	.08(.05)
1968	.03(.01)	.02(.02)	.04(.01)	.02(.01)	.01(.03)	.01(.02)
1969	.04(.01)	.04(.02)	.00(.01)	.03(.02)	.05(.03)	-.03(.03)
1970	.04(.02)	-.08(.05)	.05(.02)	.10(.03)	.08(.02)	.03(.01)
1971	.05(.02)	.04(.02)	.00(.02)	.03(.04)	-.03(.02)	-.08(.07)
1972	.04(.01)	-.06(.05)	-.06(.07)	.03(.02)	.00(.02)	.06(.04)
1973	.13(.03)	.07(.02)	-.02(.02)	.13(.04)	-.02(.04)	.15(.05)
1974	.04(.02)	.02(.02)	-.04(.02)	.02(.04)	-.01(.02)	.03(.03)
1975	.02(.02)	.07(.02)	-.05(.02)	-.04(.02)	.00(.02)	-.01(.02)
1976	.03(.01)	.03(.04)	.01(.02)	-.06(.04)	.01(.02)	.03(.04)
1977	.07(.02)	-.03(.03)	.06(.02)	.07(.03)	.02(.02)	-.01(.03)
1978	.04(.03)	.09(.03)	.05(.03)	-.03(.02)	.03(.02)	-.07(.05)
1979	.03(.02)	-.08(.04)	.08(.03)	.03(.02)	-.03(.03)	-.04(.04)
1980	.08(.02)	.06(.02)	.02(.02)	.03(.03)	-.05(.03)	-.08(.02)
1981	.02(.02)	.00(.02)	.05(.02)	-.01(.02)	.01(.02)	.01(.03)
1982	.06(.02)	.10(.03)	.00(.02)	-.01(.02)	.06(.03)	-.09(.06)
1983	.15(.03)	.00(.02)	-.03(.03)	-.01(.07)	.07(.03)	.05(.04)
1984	.06(.02)	-.04(.02)	-.08(.06)	-.10(.06)	.08(.07)	.14(.05)

	Jul	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*
1953	.15(.04)	.06(.02)	.12(.03)	.07(.07)	.08(.03)	.04(.02)
1954	.06(.03)	-.02(.11)	.19(.08)	.04(.01)	.21(.05)	.08(.02)
1955	.08(.04)	.04(.06)	.09(.04)	.09(.02)	.12(.05)	.05(.01)
1956	.02(.06)	.31(.08)	.13(.04)	.14(.03)	.06(.03)	.06(.02)
1957	-.05(.09)	.18(.05)	.05(.03)	.07(.02)	.10(.02)	.11(.02)
1958	.12(.03)	.23(.05)	.12(.02)	.20(.03)	.05(.01)	.06(.02)
1959	.04(.02)	.12(.02)	.17(.06)	.05(.01)	.05(.01)	.04(.01)
1960	.06(.02)	.07(.02)	.06(.02)	.07(.02)	.02(.01)	.06(.02)
1961	.04(.02)	.03(.01)	.08(.02)	.15(.03)	.03(.01)	.04(.01)
1962	.05(.01)	.12(.02)	.10(.02)	.08(.02)	.08(.01)	.09(.02)
1963	.03(.02)	.01(.02)	.09(.02)	.05(.03)	.03(.04)	.07(.02)
1964	.04(.02)	.05(.05)	.10(.03)	.11(.02)	.05(.02)	.04(.02)
1965	.01(.03)	-.02(.02)	.10(.03)	.17(.04)	.13(.03)	.08(.02)
1966	.05(.02)	.15(.03)	.08(.02)	.15(.02)	.06(.01)	.02(.01)
1967	.08(.02)	.06(.04)	-.01(.03)	.09(.03)	.03(.02)	.12(.03)
1968	.03(.04)	.09(.03)	.12(.05)	.11(.02)	.08(.01)	-.06(.04)
1969	.02(.02)	-.02(.02)	.08(.02)	.04(.01)	.07(.01)	.09(.02)
1970	.07(.02)	.08(.02)	.10(.02)	.18(.04)	.12(.03)	.09(.03)
1971	.01(.03)	.14(.04)	-.01(.03)	.00(.03)	.06(.02)	-.02(.04)
1972	.04(.04)	.07(.03)	.12(.08)	.10(.03)	.19(.04)	.14(.03)
1973	-.03(.04)	.01(.05)	.01(.06)	.01(.05)	.01(.02)	.06(.03)
1974	.02(.02)	.04(.03)	.13(.03)	.12(.03)	.03(.03)	.13(.03)
1975	.06(.03)	.03(.05)	.06(.03)	.11(.03)	.08(.03)	.04(.02)
1976	.03(.04)	-.01(.06)	.09(.03)	.15(.03)	.02(.04)	.13(.04)
1977	.05(.07)	-.10(.04)	.10(.03)	.08(.02)	.07(.01)	.02(.03)
1978	-.11(.05)	.04(.04)	.07(.03)	.08(.03)	.07(.02)	.05(.02)
1979	-.01(.03)	.10(.03)	-.02(.04)	.07(.02)	.08(.03)	.06(.06)
1980	-.12(.02)	-.02(.03)	.04(.03)	.05(.02)	.06(.02)	-.01(.02)
1981	-.04(.03)	-.05(.01)	.01(.03)	.07(.02)	.05(.02)	-.04(.01)
1982	.05(.04)	.04(.02)	.01(.06)	.15(.04)	.09(.02)	.08(.02)
1983	-.03(.02)	-.01(.03)	-.10(.03)	.02(.03)	.04(.03)	.04(.03)
1984	.07(.05)	-.12(.05)	.03(.04)	.02(.04)	-.09(.03)	-.01(.03)

Table 7. "Wind cubed" index of rate of addition to the water column, by the wind, of turbulent mixing energy. The standard errors of the mean appear in parentheses to the right of each mean index value. Nominal units are m³sec⁻³.

	Jan	Feb	Mar	Apr	May	Jun
1953	130(34)	107(19)	162(35)	473(140)	354(44)	130(47)
1954	75(16)	205(85)	19(4)	186(32)	210(46)	174(41)
1955	132(40)	37(9)	316(101)	93(22)	238(67)	177(50)
1956	58(15)	91(30)	287(46)	355(51)	377(68)	182(25)
1957	101(22)	220(44)	310(23)	375(64)	201(27)	337(42)
1958	184(48)	171(32)	181(25)	260(37)	244(46)	192(21)
1959	116(13)	94(8)	143(14)	154(18)	104(16)	300(47)
1960	84(11)	86(10)	151(15)	207(18)	307(95)	161(19)
1961	71(9)	83(11)	173(24)	178(13)	301(37)	204(26)
1962	156(12)	127(16)	171(14)	220(24)	197(20)	226(19)
1963	113(19)	141(19)	252(17)	176(14)	230(20)	113(13)
1964	188(20)	156(14)	198(27)	295(36)	248(41)	315(117)
1965	100(17)	155(33)	144(16)	238(51)	467(45)	232(20)
1966	247(26)	263(30)	213(25)	312(35)	252(34)	263(24)
1967	147(16)	143(25)	94(13)	102(11)	140(20)	387(80)
1968	47(10)	172(30)	126(15)	120(11)	142(25)	272(25)
1969	97(16)	113(19)	174(18)	206(23)	193(34)	432(68)
1970	121(17)	148(36)	166(38)	232(35)	227(25)	218(20)
1971	92(16)	128(25)	120(15)	266(42)	155(30)	404(162)
1972	102(14)	146(33)	346(70)	214(25)	146(18)	315(51)
1973	247(29)	136(21)	292(26)	333(49)	314(75)	279(52)
1974	121(17)	155(24)	181(20)	308(62)	300(29)	295(39)
1975	135(18)	140(22)	308(24)	251(21)	304(24)	272(33)
1976	76(22)	68(19)	196(27)	326(39)	308(36)	248(53)
1977	134(44)	251(40)	158(21)	265(27)	191(27)	263(30)
1978	150(22)	214(33)	280(44)	316(54)	246(35)	327(91)
1979	202(33)	250(54)	241(23)	282(29)	331(38)	459(122)
1980	179(19)	212(32)	203(21)	194(23)	441(47)	241(18)
1981	205(22)	104(13)	195(19)	212(21)	226(27)	431(73)
1982	134(21)	199(20)	259(19)	201(20)	300(29)	491(97)
1983	319(31)	262(18)	203(21)	420(117)	373(35)	539(61)
1984	118(21)	307(120)	534(117)	288(110)	636(159)	522(116)

	Jul	Aug	Sep	Oct	Nov	Dec
1953	332(129)	125(26)	179(34)	217(43)	243(50)	74(16)
1954	207(37)	445(135)	439(73)	64(8)	161(33)	59(13)
1955	179(41)	460(100)	308(76)	322(79)	266(42)	30(13)
1956	324(56)	346(65)	261(29)	237(56)	184(23)	158(35)
1957	484(66)	253(52)	331(45)	261(38)	189(24)	238(22)
1958	214(25)	474(56)	214(26)	228(30)	92(16)	152(26)
1959	138(16)	233(23)	303(76)	164(23)	108(15)	82(13)
1960	260(32)	222(25)	201(19)	198(35)	99(12)	144(24)
1961	290(39)	191(17)	211(20)	199(24)	136(12)	100(12)
1962	265(22)	236(23)	267(32)	199(20)	212(19)	96(15)
1963	220(26)	176(25)	320(31)	376(72)	222(33)	131(19)
1964	250(25)	385(89)	372(58)	242(22)	132(20)	164(21)
1965	263(29)	392(45)	442(52)	319(44)	240(21)	193(20)
1966	317(29)	388(39)	245(18)	243(28)	95(12)	83(10)
1967	222(28)	336(41)	357(59)	369(57)	180(30)	280(45)
1968	442(61)	352(56)	326(62)	243(19)	192(16)	283(42)
1969	237(33)	312(52)	272(29)	154(26)	104(13)	151(23)
1970	248(34)	212(28)	186(22)	251(50)	194(24)	139(22)
1971	190(49)	425(71)	258(66)	302(49)	169(23)	199(57)
1972	423(63)	400(67)	805(139)	220(27)	156(25)	407(157)
1973	369(81)	784(81)	675(74)	348(66)	237(28)	179(37)
1974	299(28)	317(57)	352(45)	295(42)	274(28)	195(31)
1975	284(35)	461(58)	316(31)	235(35)	143(24)	147(23)
1976	264(36)	377(87)	370(33)	328(37)	270(49)	235(43)
1977	529(95)	392(59)	229(37)	189(21)	241(17)	220(34)
1978	434(85)	310(54)	350(82)	226(29)	237(49)	203(28)
1979	290(51)	433(73)	350(51)	274(33)	233(28)	226(50)
1980	458(27)	354(31)	382(35)	271(28)	181(22)	188(30)
1981	420(49)	244(21)	457(60)	166(18)	249(22)	146(13)
1982	438(52)	270(40)	549(82)	454(57)	316(22)	275(30)
1983	379(34)	330(39)	318(43)	277(33)	227(111)	122(32)
1984	334(58)	415(88)	328(46)	242(30)	350(27)	229(22)

Table 8. Daily total (both direct and diffuse) solar radiation absorbed by the ocean, Q_S. The standard error of the mean appears in parentheses to the right of each mean value. Units are watts/m^2. (Values may be converted to units of cal cm^{-2} day^{-1} by multiplying by the factor 2.064.)

	Jan	*Feb*	*Mar*	*Apr*	*May*	*Jun*
1953	239(12)	253(9)	262(11)	258(15)	193(9)	182(22)
1954	240(9)	214(10)	227(12)	241(6)	141(7)	158(11)
1955	250(12)	254(12)	236(17)	282(8)	182(17)	125(5)
1956	255(16)	269(16)	257(31)	230(12)	181(14)	121(3)
1957	264(12)	203(11)	243(7)	221(8)	190(10)	153(7)
1958	244(5)	236(8)	243(9)	248(9)	202(8)	148(6)
1959	287(7)	247(8)	241(9)	208(10)	169(12)	144(6)
1960	268(9)	269(4)	283(3)	236(4)	204(4)	167(7)
1961	242(5)	276(5)	228(5)	221(4)	205(6)	140(4)
1962	258(5)	257(4)	260(4)	214(4)	192(6)	143(3)
1963	263(6)	265(5)	240(4)	217(0)	176(4)	139(3)
1964	243(6)	236(4)	242(6)	223(6)	162(8)	161(7)
1965	257(8)	268(7)	236(4)	218(4)	183(4)	165(4)
1966	252(5)	279(5)	246(5)	236(4)	182(5)	148(4)
1967	218(5)	264(8)	244(5)	230(4)	207(6)	138(5)
1968	250(7)	263(5)	265(5)	244(4)	174(6)	149(4)
1969	248(7)	257(6)	238(4)	216(5)	168(7)	140(4)
1970	245(7)	274(7)	280(4)	236(7)	178(5)	140(2)
1971	264(6)	255(6)	261(5)	230(7)	169(8)	130(6)
1972	256(6)	271(7)	237(6)	221(5)	170(6)	145(6)
1973	236(7)	247(9)	237(5)	229(7)	216(7)	151(7)
1974	250(6)	268(7)	257(5)	219(8)	156(4)	131(3)
1975	234(7)	268(6)	240(4)	224(5)	163(4)	131(3)
1976	245(7)	248(13)	234(5)	218(8)	178(6)	130(5)
1977	259(8)	235(4)	244(6)	253(4)	187(5)	154(5)
1978	258(8)	240(7)	265(6)	217(6)	190(6)	153(9)
1979	270(5)	264(7)	246(5)	238(5)	171(5)	142(7)
1980	248(6)	261(5)	244(5)	231(7)	187(4)	156(5)
1981	233(5)	241(5)	249(5)	218(5)	183(6)	142(3)
1982	246(6)	257(5)	246(4)	230(5)	187(5)	139(6)
1983	260(8)	273(4)	236(5)	201(5)	163(4)	149(5)
1984	263(9)	268(7)	260(10)	223(10)	204(29)	142(6)

	Jul	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*
1953	170(20)	142(3)	204(12)	227(16)	211(13)	266(15)
1954	149(8)	144(5)	158(5)	192(7)	225(19)	184(11)
1955	123(2)	154(7)	159(2)	217(10)	241(15)	263(26)
1956	134(7)	157(11)	184(9)	198(10)	195(9)	261(31)
1957	143(11)	170(12)	186(8)	211(6)	216(8)	235(6)
1958	154(11)	165(5)	173(7)	218(9)	254(8)	278(13)
1959	154(6)	169(8)	190(8)	218(13)	226(7)	256(6)
1960	163(4)	171(6)	171(4)	185(5)	219(11)	235(7)
1961	126(2)	159(3)	170(2)	210(6)	243(4)	240(5)
1962	133(2)	148(2)	173(5)	193(4)	211(4)	258(6)
1963	145(4)	167(6)	177(4)	204(6)	212(6)	229(9)
1964	138(4)	154(5)	183(5)	191(3)	210(7)	257(6)
1965	135(4)	148(3)	169(3)	197(5)	219(4)	241(5)
1966	151(4)	162(4)	181(3)	191(3)	202(4)	241(5)
1967	137(4)	148(3)	184(5)	195(5)	196(5)	258(6)
1968	145(5)	145(3)	180(5)	201(4)	218(5)	256(7)
1969	137(5)	158(4)	165(3)	205(5)	226(5)	246(6)
1970	134(4)	152(4)	181(4)	180(3)	244(5)	235(7)
1971	127(2)	151(4)	171(7)	193(7)	236(6)	233(10)
1972	138(7)	161(6)	183(8)	209(6)	195(7)	229(9)
1973	142(4)	149(3)	174(5)	205(7)	208(5)	221(6)
1974	127(2)	154(4)	175(4)	218(8)	222(6)	250(8)
1975	134(4)	156(5)	173(4)	212(7)	211(7)	234(6)
1976	147(5)	143(6)	194(6)	206(6)	212(8)	257(8)
1977	134(4)	155(5)	187(6)	204(5)	223(4)	270(8)
1978	126(2)	160(5)	187(6)	205(7)	231(7)	264(6)
1979	138(4)	167(5)	179(5)	217(8)	210(6)	252(12)
1980	139(5)	158(4)	196(5)	208(5)	231(8)	266(9)
1981	139(4)	168(6)	169(2)	205(6)	241(4)	255(4)
1982	150(6)	151(4)	186(6)	215(5)	218(5)	253(6)
1983	156(5)	161(7)	184(12)	198(4)	258(12)	246(10)
1984	157(7)	165(6)	175(16)	185(6)	246(16)	242(9)

Table 9. Radiative heat loss, Q_s. The standard error of the mean appears in parentheses to the right of each mean value. Units are watts/m^2. (Values may be converted to units of cal cm^{-2} day^{-1} by multiplying by the factor 2.064.)

	Jan	*Feb*	*Mar*	*Apr*	*May*	*Jun*
1953	23(2)	28(2)	32(3)	41(5)	33(3)	33(10)
1954	26(2)	16(2)	22(3)	43(2)	16(3)	30(5)
1955	30(3)	27(3)	29(5)	60(5)	29(7)	10(2)
1956	33(5)	34(5)	38(13)	41(5)	28(5)	7(1)
1957	33(3)	13(2)	26(2)	29(2)	28(3)	21(2)
1958	24(1)	22(2)	27(2)	39(3)	36(2)	20(2)
1959	43(2)	24(2)	28(2)	29(3)	22(4)	18(2)
1960	32(2)	33(1)	44(1)	37(1)	38(1)	31(3)
1961	26(1)	34(1)	25(1)	34(1)	39(2)	19(1)
1962	31(1)	31(1)	36(1)	30(1)	35(2)	21(1)
1963	33(1)	31(1)	27(1)	34(0)	27(1)	18(1)
1964	27(1)	23(1)	30(1)	34(2)	23(3)	30(3)
1965	33(2)	34(2)	27(1)	27(1)	27(1)	28(1)
1966	30(1)	37(1)	29(1)	38(1)	29(1)	21(1)
1967	20(1)	33(2)	30(1)	34(1)	38(2)	19(2)
1968	33(2)	33(1)	36(1)	44(1)	28(2)	23(2)
1969	29(2)	30(1)	28(1)	29(1)	23(2)	18(1)
1970	29(2)	35(2)	42(1)	37(2)	29(2)	19(1)
1971	34(1)	30(1)	35(1)	34(2)	26(3)	15(2)
1972	32(1)	32(2)	24(1)	31(2)	24(2)	18(2)
1973	22(1)	24(2)	27(1)	36(2)	43(2)	25(3)
1974	30(1)	33(2)	33(1)	34(2)	20(1)	14(1)
1975	23(1)	32(1)	27(1)	32(1)	23(1)	15(1)
1976	27(1)	30(5)	25(1)	31(2)	29(2)	14(2)
1977	30(2)	22(1)	29(1)	43(1)	33(2)	25(2)
1978	31(2)	24(2)	34(1)	31(2)	33(2)	25(4)
1979	33(1)	30(1)	27(1)	36(1)	25(2)	20(3)
1980	30(1)	29(1)	28(1)	34(2)	31(1)	25(2)
1981	24(1)	24(1)	31(1)	31(1)	28(2)	18(1)
1982	29(1)	28(1)	0(1)	35(1)	32(2)	16(2)
1983	28(2)	31(1)	22(1)	20(1)	18(1)	19(2)
1984	29(2)	31(2)	32(3)	29(3)	37(10)	17(2)

	Jul	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*
1953	30(9)	9(1)	22(4)	26(5)	20(4)	34(3)
1954	20(3)	11(3)	10(2)	14(2)	23(5)	12(3)
1955	8(0)	14(3)	8(1)	22(3)	31(5)	39(10)
1956	16(3)	18(5)	15(3)	19(4)	15(3)	35(9)
1957	17(5)	19(4)	18(2)	21(2)	22(2)	25(1)
1958	22(4)	20(2)	14(2)	25(3)	35(2)	43(4)
1959	22(2)	19(3)	21(3)	24(5)	25(2)	34(1)
1960	27(1)	23(2)	15(1)	11(1)	23(3)	27(2)
1961	10(0)	17(1)	13(0)	20(2)	31(1)	29(1)
1962	14(0)	11(0)	15(1)	15(1)	20(1)	37(2)
1963	19(1)	19(2)	14(1)	18(2)	21(2)	26(2)
1964	15(1)	15(2)	16(1)	15(1)	20(2)	35(1)
1965	14(1)	13(1)	12(0)	15(1)	22(1)	29(1)
1966	22(1)	18(1)	16(1)	14(1)	17(1)	29(1)
1967	15(1)	13(1)	17(2)	16(2)	15(1)	39(2)
1968	20(3)	11(1)	14(1)	17(1)	22(1)	34(2)
1969	15(2)	17(1)	12(1)	18(1)	26(1)	31(1)
1970	15(2)	13(1)	16(1)	10(1)	32(1)	29(2)
1971	11(1)	13(1)	12(2)	17(3)	28(2)	26(3)
1972	15(2)	19(2)	15(2)	20(2)	15(2)	25(2)
1973	17(1)	12(1)	15(1)	20(2)	18(1)	23(1)
1974	13(1)	14(1)	15(1)	23(2)	23(2)	32(2)
1975	15(1)	14(2)	14(1)	23(2)	30(2)	28(2)
1976	19(2)	11(1)	20(1)	18(1)	19(2)	33(2)
1977	14(1)	16(2)	17(2)	19(1)	23(1)	41(2)
1978	9(0)	17(2)	19(2)	19(2)	25(2)	34(1)
1979	16(2)	19(2)	15(1)	22(2)	19(2)	32(4)
1980	13(1)	15(1)	20(1)	19(1)	27(2)	38(2)
1981	15(1)	19(2)	11(0)	29(2)	30(1)	35(1)
1982	19(2)	13(1)	17(2)	21(1)	20(1)	30(1)
1983	24(2)	17(2)	15(3)	15(1)	33(3)	28(3)
1984	21(2)	22(2)	18(8)	11(1)	29(5)	29(3)

Table 10. Evaporative heat loss, Q_c. The standard error of the mean appears in parentheses to the right of each mean value. Units are watts/m^2. (Values may be converted to units of cal cm^{-2}day^{-1} by multiplying by the factor 2.064.)

	Jan	Feb	Mar	Apr	May	Jun
1953	3(6)	34(10)	39(8)	62(16)	97(11)	8(9)
1954	-23(5)	15(4)	8(3)	-24(4)	27(5)	33(4)
1955	22(7)	-26(5)	39(16)	14(10)	-14(12)	6(5)
1956	17(6)	-27(13)	-1(25)	39(11)	23(9)	33(6)
1957	-11(3)	43(9)	46(10)	68(13)	59(8)	64(11)
1958	22(4)	65(7)	31(8)	37(6)	49(11)	40(5)
1959	15(3)	15(4)	59(9)	42(7)	21(10)	35(6)
1960	11(2)	18(2)	32(4)	22(3)	15(1)	24(4)
1961	9(2)	22(2)	15(4)	18(2)	34(4)	36(4)
1962	22(2)	33(3)	16(3)	16(4)	26(3)	50(3)
1963	16(3)	24(2)	35(3)	31(0)	46(3)	31(2)
1964	25(3)	25(2)	19(3)	34(7)	28(5)	30(6)
1965	34(6)	46(5)	45(3)	57(5)	109(7)	62(3)
1966	36(4)	63(6)	30(4)	51(6)	44(4)	40(3)
1967	17(2)	33(4)	22(3)	14(2)	15(3)	52(8)
1968	6(1)	36(4)	24(3)	12(2)	26(4)	38(4)
1969	28(4)	19(3)	44(3)	51(5)	57(6)	69(5)
1970	29(4)	31(11)	34(4)	22(6)	22(4)	24(2)
1971	14(2)	11(4)	6(4)	40(6)	39(6)	46(10)
1972	20(3)	48(8)	62(9)	48(4)	62(6)	31(6)
1973	47(12)	28(7)	39(4)	30(6)	28(8)	32(9)
1974	26(3)	26(5)	40(4)	58(9)	70(5)	42(4)
1975	26(5)	21(3)	55(4)	54(6)	70(4)	44(4)
1976	10(2)	48(22)	32(6)	62(9)	64(6)	57(6)
1977	25(4)	43(5)	15(4)	13(5)	21(4)	39(6)
1978	21(3)	38(4)	34(6)	54(6)	23(3)	62(11)
1979	27(4)	35(6)	30(4)	38(6)	45(5)	40(6)
1980	28(6)	24(5)	37(4)	15(3)	57(5)	31(4)
1981	12(5)	19(3)	14(3)	29(5)	42(5)	51(4)
1982	18(2)	21(5)	39(5)	28(3)	46(5)	87(23)
1983	71(5)	97(5)	87(4)	110(10)	124(5)	125(14)
1984	4(10)	31(7)	49(15)	41(15)	-11(15)	32(8)

	Jul	Aug	Sep	Oct	Nov	Dec
1953	41(13)	53(4)	29(6)	33(8)	32(7)	8(8)
1954	6(6)	38(10)	17(6)	-8(4)	15(8)	25(12)
1955	46(10)	2(11)	8(5)	-9(8)	9(4)	2(5)
1956	69(11)	35(10)	49(7)	21(4)	69(8)	-9(3)
1957	111(19)	39(11)	54(7)	42(3)	35(4)	18(6)
1958	56(6)	35(3)	31(4)	40(5)	21(4)	27(5)
1959	26(2)	12(3)	30(7)	24(11)	13(1)	2(1)
1960	38(3)	28(3)	28(2)	23(4)	27(5)	20(5)
1961	34(5)	37(2)	28(2)	18(2)	27(2)	14(2)
1962	33(2)	27(2)	26(3)	24(2)	28(2)	15(2)
1963	40(3)	38(4)	43(3)	37(4)	36(4)	24(3)
1964	40(4)	37(4)	31(3)	30(3)	17(3)	27(3)
1965	60(4)	64(5)	36(3)	29(4)	36(2)	33(3)
1966	53(3)	29(2)	32(2)	26(2)	19(2)	13(1)
1967	36(2)	34(4)	22(2)	19(4)	24(3)	26(3)
1968	63(6)	29(3)	34(3)	29(2)	22(2)	33(6)
1969	41(4)	43(4)	31(4)	16(3)	10(1)	15(3)
1970	19(3)	23(3)	21(3)	15(3)	19(2)	15(3)
1971	39(4)	44(6)	31(7)	34(5)	19(3)	31(5)
1972	66(10)	105(10)	70(12)	40(4)	37(5)	42(8)
1973	42(7)	27(6)	29(4)	31(5)	15(5)	15(4)
1974	61(3)	32(3)	25(5)	28(5)	37(4)	33(7)
1975	54(6)	54(6)	23(5)	18(3)	4(2)	16(3)
1976	74(5)	30(17)	50(4)	45(7)	38(6)	34(3)
1977	48(6)	32(4)	19(3)	48(7)	23(2)	18(2)
1978	36(12)	30(9)	32(3)	31(5)	25(6)	24(4)
1979	39(4)	26(3)	37(3)	27(4)	37(7)	20(5)
1980	28(4)	29(4)	28(3)	34(6)	20(4)	15(4)
1981	41(6)	29(3)	27(4)	21(3)	21(3)	19(2)
1982	71(9)	30(6)	34(10)	59(4)	66(5)	68(10)
1983	91(8)	18(15)	46(17)	40(4)	42(7)	15(10)
1984	54(8)	37(5)	54(20)	19(8)	13(17)	26(8)

Table 11. Net atmosphere - ocean heat exchange, Q_N. The standard error of the mean appears in parentheses to the right of each mean value. Units are watts/m^2. (Values may be converted to units of cal cm^{-2} day^{-1} by multiplying by the factor 2.064.)

	Jan	*Feb*	*Mar*	*Apr*	*May*	*Jun*
1953	220(13)	193(13)	196(13)	152(24)	51(16)	142(10)
1954	261(11)	187(10)	200(9)	247(9)	101(8)	89(10)
1955	194(13)	273(11)	164(22)	211(16)	192(20)	115(8)
1956	208(12)	286(25)	232(22)	150(15)	137(18)	79(9)
1957	258(11)	143(16)	176(16)	125(17)	103(11)	63(16)
1958	203(7)	146(9)	189(15)	171(10)	110(16)	81(8)
1959	236(7)	215(9)	155(13)	139(13)	125(18)	92(9)
1960	228(8)	220(4)	209(6)	182(5)	153(4)	113(7)
1961	211(5)	221(4)	193(7)	175(4)	133(7)	83(6)
1962	210(5)	195(5)	216(6)	177(6)	135(6)	69(4)
1963	219(7)	213(5)	185(5)	156(0)	100(6)	88(3)
1964	196(6)	192(4)	199(6)	156(10)	111(11)	104(10)
1965	190(8)	187(8)	164(4)	135(7)	35(9)	69(6)
1966	188(7)	179(7)	187(6)	145(9)	108(6)	86(5)
1967	183(5)	202(6)	196(4)	187(4)	157(5)	62(9)
1968	214(5)	196(5)	207(4)	196(4)	118(6)	86(5)
1969	195(6)	209(6)	164(5)	134(7)	82(10)	41(8)
1970	185(8)	212(13)	203(7)	184(10)	130(7)	101(3)
1971	220(5)	219(8)	230(7)	155(9)	99(9)	67(13)
1972	205(5)	188(12)	150(11)	142(7)	77(10)	99(10)
1973	173(16)	203(11)	172(7)	171(11)	153(11)	95(13)
1974	197(6)	211(8)	187(6)	128(13)	63(7)	75(5)
1975	187(8)	217(6)	157(7)	138(9)	62(7)	66(6)
1976	215(6)	166(22)	179(9)	124(14)	78(9)	58(8)
1977	209(9)	174(6)	210(9)	218(9)	142(7)	92(9)
1978	209(8)	185(7)	200(9)	130(10)	139(7)	64(15)
1979	213(8)	204(9)	192(7)	166(10)	101(8)	82(9)
1980	198(9)	217(8)	184(6)	190(8)	99(8)	103(6)
1981	211(8)	202(6)	214(5)	166(9)	114(7)	75(5)
1982	207(5)	220(9)	182(6)	172(5)	111(7)	26(31)
1983	161(8)	139(7)	121(7)	66(14)	8(6)	-8(17)
1984	240(14)	213(11)	180(17)	158(19)	197(24)	101(14)

	Jul	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*
1953	91(26)	74(6)	151(11)	171(16)	157(14)	227(19)
1954	135(14)	93(15)	138(9)	201(8)	183(19)	143(16)
1955	58(14)	152(18)	140(9)	222(15)	215(13)	226(17)
1956	34(15)	97(15)	109(8)	166(9)	98(13)	245(22)
1957	12(23)	110(18)	108(12)	144(6)	158(7)	200(9)
1958	69(12)	112(6)	127(8)	149(9)	198(8)	204(11)
1959	104(5)	139(6)	140(11)	174(18)	189(5)	224(5)
1960	95(5)	120(6)	129(4)	152(7)	172(12)	193(7)
1961	80(7)	103(4)	130(3)	173(5)	189(4)	203(5)
1962	89(3)	111(3)	140(6)	157(4)	167(4)	211(5)
1963	83(5)	106(7)	120(6)	155(7)	155(7)	183(8)
1964	78(6)	102(7)	138(5)	145(4)	173(6)	198(5)
1965	58(7)	66(7)	121(5)	154(6)	161(4)	180(5)
1966	70(5)	114(4)	131(3)	151(3)	166(4)	200(4)
1967	85(4)	97(5)	144(5)	169(7)	156(5)	196(6)
1968	55(9)	108(4)	135(5)	157(5)	174(4)	192(7)
1969	75(6)	93(6)	121(6)	170(5)	192(4)	203(5)
1970	102(4)	117(5)	146(5)	165(5)	195(5)	198(7)
1971	71(6)	92(10)	128(11)	142(8)	194(6)	176(9)
1972	51(15)	23(13)	98(17)	145(7)	147(8)	171(10)
1973	77(11)	120(10)	144(7)	157(9)	187(9)	191(7)
1974	46(5)	106(6)	141(7)	175(9)	166(8)	183(12)
1975	63(8)	79(10)	144(8)	178(5)	197(5)	195(6)
1976	52(8)	116(25)	122(8)	148(9)	162(9)	195(7)
1977	72(9)	111(6)	156(7)	131(10)	181(4)	222(7)
1978	89(16)	118(14)	138(6)	158(8)	191(10)	208(7)
1979	86(7)	133(6)	131(6)	171(7)	158(10)	207(10)
1980	105(8)	117(7)	154(6)	156(10)	192(9)	220(9)
1981	83(8)	119(6)	139(5)	191(6)	196(5)	207(4)
1982	59(12)	114(8)	144(14)	132(6)	129(7)	155(13)
1983	34(10)	139(19)	136(25)	145(7)	184(15)	216(15)
1984	78(12)	108(10)	121(36)	166(14)	228(25)	190(11)

uncommon in the figure with the notable exception of the early 1970s and again in the early 1980s. The main point is that features in Fig. 4L seem unrelated to any major features apparent in the other series plotted in Fig. 4. Thus, the major effect of uneven distribution of reports appears to be in increasing sampling variance rather than in introducing long-term nonhomogeneity in the various time series.

Discussion

Since the 12-month running mean filter used to highlight the long-term variations in Fig. 4 incorporates no data more than 6 months previous or following, the indicated multiyear features are certainly real, and in no way represent artifacts of filtering and smoothing procedures. Moreover, the interyear variations of annual mean values tend to be of similar magnitude to the cyclic seasonal components (Figs. 2 and 3), making the separation of these scales in analysis of effects (e.g., on the biota) a difficult problem. For example, the impact of long-term variability will generally depend on phase relationships with the seasonal variation. Additional complications involve the adaptations of the biota, not only the long-term evolutionary adaptations of life cycle processes to regular cyclic effects, but also lagged responses of community composition, etc., to events of the recent past (see Mendelsohn and Mendo, this vol.).

This area of the world's ocean may be uniquely troublesome in these respects. Because the Pacific Ocean is so large, it is much less subject to continental effects which amplify seasonalities due to the low heat storage capacities of continents relative to oceans. The apparent consequence is much less forcing of Pacific Ocean processes to follow a regular seasonal cycle than may be the case, for example, in the Atlantic; the result is the dominance of interyear variation in the Pacific (Picaut 1985). The location so near to the eastern terminus of the equatorial wave guide results in a focusing of variability initiated in various portions of the great Pacific ocean-atmosphere coupled system to particularly impact the ocean habitat off Peru. Indeed, this may constitute part of the explanation for the enormous biomasses of pelagic fishes that have inhabited the region; i.e., because of the intense irregular environmental variability, a single, rather unspecialized fish species with very rapid population responses may be able to dominate the system relatively free from predation and competition from more specialized, less responsive species that would be more subject to the inefficiencies of multiple food-chain steps.

We have noted that the interyear variations tend to involve groups of years. In fact single features, e.g., the 1982-1983 El Niño, the 1954-1955 cold period, etc., so dominate the series that the entire series length becomes a dominant scale of variability. The result is that any sort of assumption of stationarity must be somewhat unrealistic; the real degrees of freedom useful for empirical analysis nearly vanish with respect to such features. It is also apparent from even casual inspection of Fig. 4 that the index series presented in this paper are all highly interrelated in terms of major interyear features, further exacerbating the problems of empirically sorting the various effects. Any available mechanistic constraints, provided by established physical or biological principles, that can be imposed on empirical analysis, would of course be very helpful in this situation.

Variable vs. Constant Transfer Coefficient Formulations

Some differences in the results of variable and constant transfer coefficient formulations in the wind stress estimates (Equation 1) and in the estimates of certain of the heat exchange components (Equations 4, 5 and 6) have been noted in the discussions of both seasonal and interyear variability. The differences have mainly been in magnitude of the particular index, with temporal aspects of the variability appearing to be relatively unaffected. An exception was the conductive component of heat exchange, Q_C, where the effect of stability in the atmospheric boundary layer introduced major discrepancies between the alternate formulations (Fig. 3E). Fortunately, Q_C is by far the smallest heat exchange component. Some summary information concerning gross effects of the differences in the various series with respect to time series properties is indicated in Fig. 5.

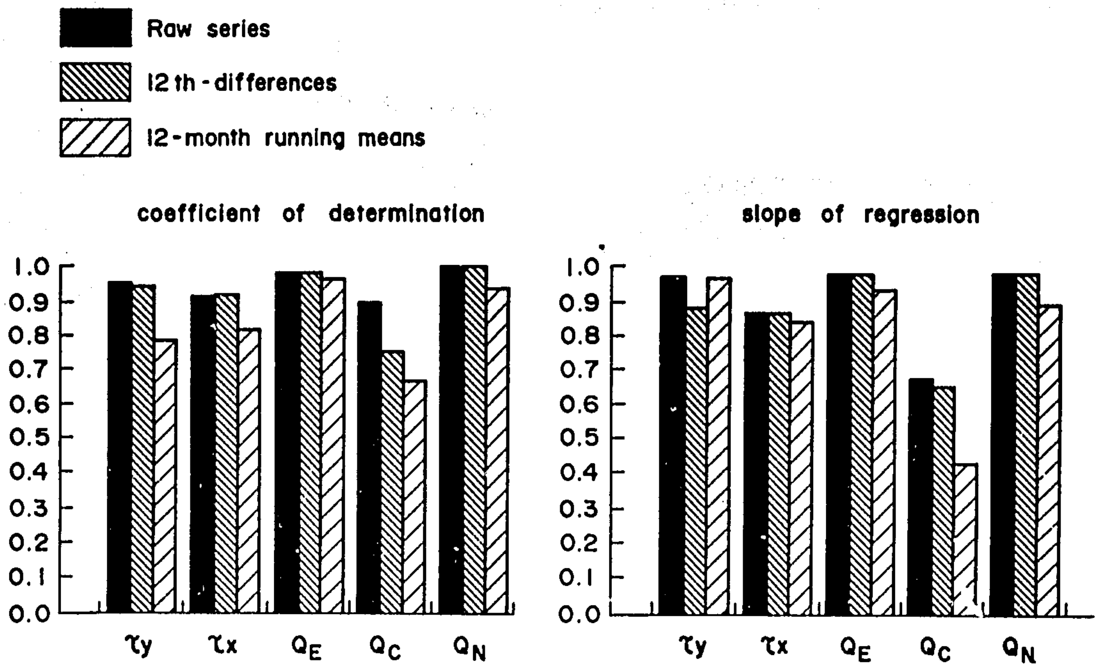

Fig. 5. Graphs of r^2 (= coefficient of determination, i.e., proportion of variation in one series 'explained' by other series) and slope of the regression of the variable transfer coefficient formulation versus the constant transfer coefficient formulation of alongshore stress (τ_x), onshore stress (τ_y), evaporative heat loss (Q_E), conductive heat loss (Q_C) and net atmosphere-ocean heat exchange (Q_N).

In the case of alongshore component of wind stress, the raw monthly series computed according to the two types of drag coefficient formulation are well correlated, each accounting for more than 95% of the variance in the other. When 12th-differencing was employed to remove the cyclic seasonal variations, the correlation dropped only slightly; this lower than expected drop in r^2 must be due to a strong seasonality in the differences resulting from the two formulations. Note that both the raw and 12th-differenced series pairs were much more highly correlated than the pair of 12-month running mean filtered series (which can be viewed in terms of directly proportional offshore Ekman transport in Fig. 4G). The slope of the regression of the variable coefficient alongshore stress series on the constant coefficient series is nearly one to one in the raw series; it drops to below 0.9 in the 12-differenced series, but is above 0.95 in the filtered series.

Slightly lower degrees of relationship are seen for the onshore component which tends to be much the smaller of the two stress components. The respective formulations of evaporative heat loss (Q_E) were very highly correlated in raw and 12th-differenced series. The degree of relationship fell only slightly after the 12-month running mean was applied. In the case of the conductive heat loss term (Q_C), the two formulations gave substantially greater differences, particularly after 12th-differencing or filtering. In the case of net heat exchange (Q_N) the differences between the results of the two formulations appear not to be appreciable. Note that in all cases the raw and 12-differenced series were more highly correlated between the constant and variable coefficient formulations than were the corresponding 12-month running mean filtered versions of the respective series; thus the degree of relationship is even higher in the case of the unsmoothed series, even after the seasonality is removed, than can be seen in the comparative examples of filtered series in Fig. 4.

In view of the time series similarities, the constant transfer coefficient versions of the respective index series are the only ones presented herein in tabular form (Tables 5, 6, 10 and 11). In view of the larger relative effect of the uncertainties as to proper formulation of the transfer coefficient for conductive heat loss, and because its very small magnitude makes it relatively unimportant in any case, no tabular series of Q_C is included. Of course, it would be possible to assemble the constant coefficient version of the Q_C series from the values in Tables 8 to 11.

Offshore Ekman Velocity of the Mixed Layer

In discussing the inference of Parrish et al. (1983) that the offshore Ekman transport should ideally be divided by the effective mixed layer depth, to yield the net rate of offshore transport of drifting larvae which are passively mixed through the layer, Bakun (1985) stressed the importance of the qualification "ideally". Ekman transport is estimated from relatively abundant surface wind reports, which reflect the fairly large spatial scales of atmospheric variation. Mixed layer depth may vary on much shorter oceanic length scales and must be determined from generally much less abundant subsurface observations. In cases where the estimate of effective mixed layer depth may be very imprecise, the derived estimate of offshore Ekman velocity of the mixed layer could constitute a less reliable indicator of variability in this process than the Ekman transport alone.

On long time scales, mixed layer depth and wind stress observations are likely to be substantially correlated. However, within any given month it is probably not too bad an assumption to regard observations used to estimate these quantities (surface wind and subsurface temperature structure) as largely independent samples of the respective monthly distributions, particularly since there will normally be many more surface than subsurface reports. In this case, combining the standard errors according to the rules for a quotient of independently observed quantities (e.g., Beers 1953) should provide a reasonable gauge of precision. Thus the ratio of the standard error to the monthly mean derived net offshore Ekman velocity of the mixed layer might be reasonably estimated as being equivalent to the square root of the sum of the squares of the respective ratios of the standard errors to the monthly mean values of the Ekman transport and mixed layer depth components of the calculation.

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Monthly Turbulence and Ekman Transport Indexes, 1953 to 1985, Based on Local Wind Records from Trujillo and Callao, Peru

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Abstract

Mean monthly turbulence and Ekman transport (upwelling) indexes have been computed based on subdaily wind records from Trujillo and Callao airports, Peru, for the period 1953 to 1985.

The seasonal and interannual variability of these indexes are discussed, with special references to differences between inshore and offshore winds, the differences between Trujillo and Callao and their relevance to the spawning of pelagic fishes off Peru.

Introduction

An important feature of the upwelling region off the Peruvian coast is the variability of both its physical characteristics and its living resources. This region supports large fish populations, such as the anchoveta *(Engraulis ringens)*, upon which one of the largest fishery resources in the world was based (Zuta and Guillen 1970; Guillen and Calienes 1981; Cushing 1982).

The causes of coastal upwelling can be several, some of which are: transport caused by wind, currents, internal waves, mixing, etc. Of these, wind-caused transport is, off Peru, the most important factor, due to its persistence and direction both of which are favorable for upwelling (Smith 1968; Schaffer 1982).

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*PROCOPA Contribution No. 47.

The physical processes that regulate coastal circulation, important for the upwelling, vary both in time and space (Calienes et al. 1985) and can greatly affect the fishery resources. This applies especially to reproductive processes, transport and survivorship of larvae and, thus, to recruitment of such resources (Bakun 1973, 1975, 1985; Lasker 1978, 1981; Bakun et al. 1982).

Currently, recruitment is that aspect of fish population dynamics that is most difficult to model and predict. Nevertheless, powerful hypotheses exist that try to explain the mechanisms that regulate recruitment. One of them, proposed by Hjort (1914), suggests that the strength of a cohort of fish is established by mortality during the larval phase, as regulated by the food available when the larvae begin feeding. Another hypothesis, proposed by Hunter (1976), suggests that predation of larvae by vertebrates and invertebrates regulates recruitment. Lasker and Smith (1977), however, concluded that larvae survivorship is related more to the coincidence than to the abundance of food and predators. Lasker (1978, 1981), finally, suggested that larval mortality is caused mainly by wind-generated turbulence, which leads to dispersion of particles necessary for first feeding of the larvae.

Several contributions have been published pinpointing some biological-environmental relationships in anchovies, such as the ones presented by Parrish and MacCall (1978), Bakun and Parrish (1980), Csirke (1980), Bailey (1981), Collins and MacCall (1977) and others, most of them referring to the current systems off California. However, the possibility exists that the environmental processes which regulate recruitment and population fluctuations of a group of species, are similar in all four Eastern Boundary Currents regions, i.e., California, Peru, Canaries and Benguela (Bakun and Parrish 1980; Parrish et al. 1981; Bakun 1985).

The present study presents the monthly averages of the upwelling and turbulence indices calculated on the basis of wind data recorded at the Trujillo (08°06'S) and Callao (12°00'S) airports (Fig.1), as a contribution to the identification of possible relationships between the environment and recruitment of fish stock in the Peruvian Current.

Material and Methods

Calculation of Upwelling and Turbulence Indexes

An upwelling index is essentially a quantitative expression of water mass transport with reference to the coastline. The transport generated by superficial wind is based on Ekman's theory (Ekman 1905). Under the assumption of a stable uniform movement and an infinite homogeneous ocean, the transport of masses by area unit of ocean surface is directed 90° to the left (in the southern hemisphere) of the direction towards which the wind is blowing. Hence, wind blowing parallel to the coastline will generate a net water transport perpendicular to it and, thus, the upwelling index will be greater than that of a wind blowing with equal intensity but not parallel to the coastline.

Ekman's transport is calculated according to Bakun (1973) using the wind-created stress (τ) on the surface and the Coriolis parameter (f) of the area:

$$E = \tau / f \qquad \ldots 1)$$

The wind stress is given by:

$$\tau = \rho_a C_D (V)^2 \qquad \ldots 2)$$

where "ρ_a" is the air density (= 1.2 kg m^{-3})
C_D is the empirical drag coefficient (= 0.0013) and
V is the wind velocity.

The direction of the stress is the direction from which the wind is blowing. The Coriolis parameter is dependent of the latitude of the area and is calculated by:

$$f = 2\, \Omega \sin \phi \qquad \ldots 3)$$

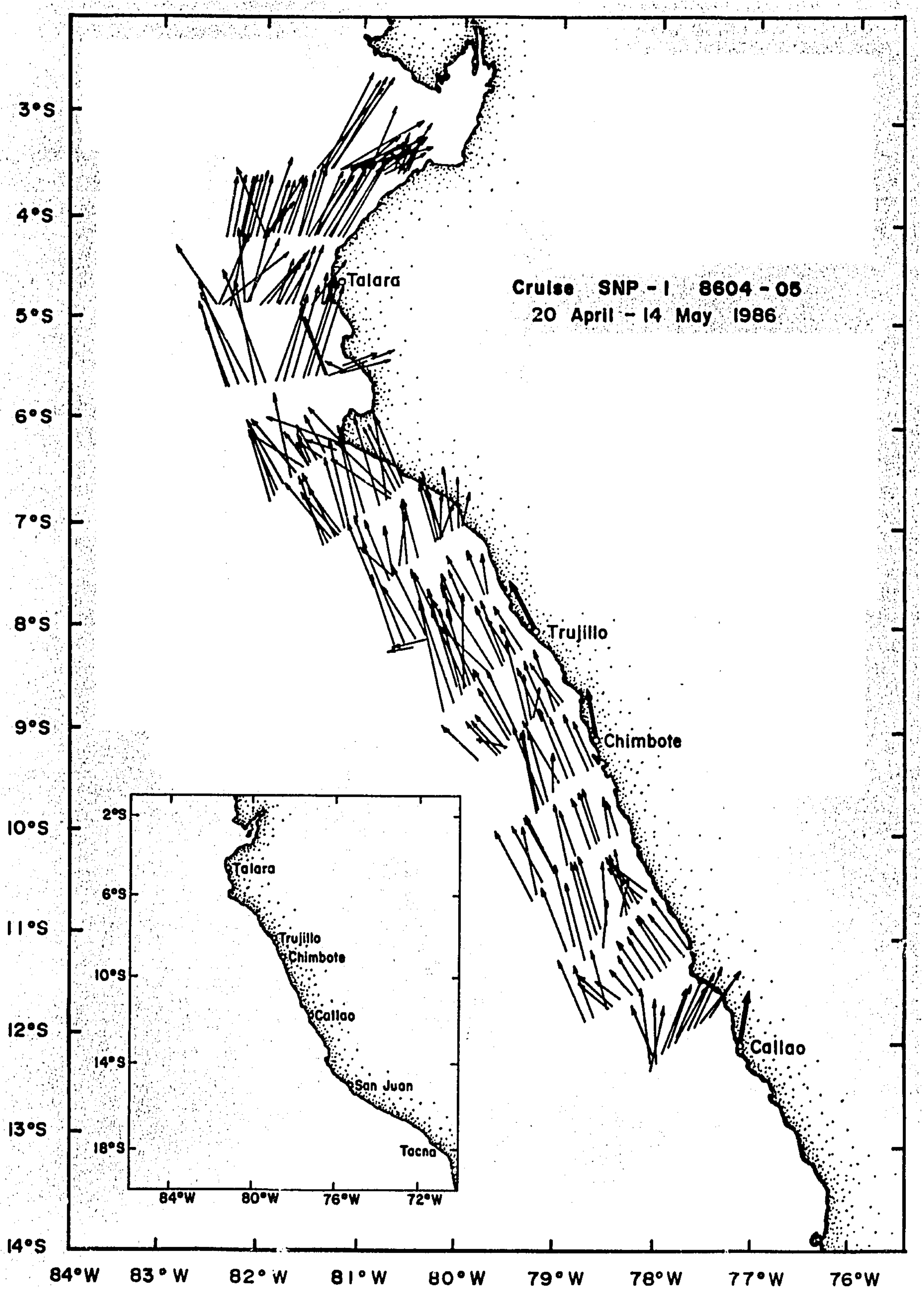

Fig. 1. Insert: Locations of Peruvian towns mentioned in this contribution. Larger Map: Wind strength and direction during a cruise on 20 April-14 May 1966 showing correspondence between wind records at Trujillo, Chimbote and Callao airports (thick arrows) and nearshore wind records (thin arrows).

where Ω is the earth's rotation angular velocity ($=7.2921 \times 10^{-5}$ rad sec^{-1}) and ϕ is the latitude in degrees (see Bakun, this vol.)

The upwelling index is calculated by:

$$IA = E \cos \alpha \qquad \ldots 4)$$

where α is the angle representing the difference between the coastline angle and the direction of the wind. The coastline angles used were 150° for Trujillo and 145° for Callao station.

The turbulence index in the upper water column, following Elsberry and Garwood (1978), is here defined as equal to the third power of the wind velocity ("wind cubed").

Source and Analysis of Data

A statistical analysis of the monthly average upwelling indices calculated on the basis of 24, 12, 8, 6, 3 and 1 (prevailing average) observations per day, taken during one year (1970) at Trujillo and Callao stations was performed and the results are shown on Table 1.

All but one of the chi-squared values were lower than the critical value, the only exception being 1 observation per day (i.e., "daily prevailing wind") at Trujillo. Moreover, as we can see in Fig. 2, the trends of the daily means based on different numbers of observations per day are similar to those obtained using 24 observations per day. We performed the analysis of our data by computing the indices with 6 to 8 observations per day as suggested by A. Bakun (pers. comm.). The data were entered into an HP-100 computer and processed using a routine based on the program of Navaluna et al. (1984).

Table 1. Chi-square test for the monthly upwelling indices (IA) computed using 24, 12, 8, 6, 3 and 1 (prevailing wind, PV) observations per day as recorded by CORPAC at Trujillo and Callao during 1970. The chi-squared values for 12, 8, 6, 3 observations and for PV were computed with reference to the IA values for 24 observations per day. The critical value of the chi-squared statistics for P = 0.05 and 0.01 and 11 d.f. are 19.68 and 24.7, respectively.

	Trujillo											Callao										
	Number of observations											Number of observations										
	24	12		8		6		3		1		24	12		8		6		3		1	
	IA	IA	CHI-2	IA	CHI-2	IA	CHI-2	IA	CHI-2	IA	CHI-2	IA	IA	CHI-2	IA	CHI-2	IA	CHI-2	IA	CHI-2	IA	CHI-2
Jan	241	242	0.00	234	0.20	240	0.00	246	0.10	230	0.50	75	72	0.12	71	0.21	71	0.21	72	0.12	62	2.25
Feb	248	252	0.06	246	0.02	254	0.15	268	1.60	227	1.78	76	78	0.05	75	0.01	76	0.00	78	0.05	69	0.64
Mar	290	294	0.06	295	0.09	290	0.00	305	0.78	263	2.51	73	74	0.01	69	0.22	75	0.06	85	1.97	65	0.87
Apr	331	334	0.03	330	0.00	333	0.01	341	0.30	266	12.76	58	53	0.43	54	0.28	51	0.85	51	0.85	45	2.91
May	294	296	0.01	290	0.01	296	0.01	298	0.05	258	4.41	32	33	0.03	32	0.00	32	0.00	30	0.13	27	0.78
Jun	275	271	0.06	274	0.00	267	0.23	260	0.82	251	2.09	21	21	0.00	23	0.19	16	1.19	12	3.86	20	0.05
Jul	264	265	0.00	261	0.03	261	0.03	252	0.55	254	0.38	34	36	0.12	35	0.03	35	0.03	30	0.47	22	4.24
Aug	251	248	0.04	248	0.04	258	0.20	246	0.10	259	0.26	39	38	0.03	40	0.03	38	0.03	37	0.10	33	0.92
Sep	285	289	0.06	279	0.13	296	0.42	293	0.22	266	1.27	59	61	0.07	57	0.07	58	0.02	59	0.00	52	0.83
Oct	286	285	0.00	283	0.03	278	0.22	283	0.03	260	0.90	70	72	0.06	68	0.06	72	0.06	74	0.23	59	1.73
Nov	228	234	0.16	231	0.04	227	0.00	241	0.74	212	1.12	47	48	0.02	48	0.02	47	0.00	52	0.53	43	0.34
Dec	271	271	0.00	261	0.37	270	0.00	256	0.83	230	6.20	55	58	0.16	55	0.00	56	0.02	60	0.46	51	0.30
Chi-square (Σ)			0.49		0.99		1.28		6.13		34.18			1.1		1.112		2.45		8.76		15.86

The calculation of the daily upwelling and turbulence indices was obtained by computing these indices for each observation (i.e., for each period of 3-4 hours) with subsequent averaging. The monthly averages were obtained by taking the mean of the daily indices. This same procedure was used by Bakun (1973, 1975) to calculate daily, weekly, and monthly upwelling indices for the North American western coast.

Positive values indicate upwelling and negative values indicate downwelling. A data volume was prepared (Mendo et al. 1987) which presents, on a daily basis, the data used here.

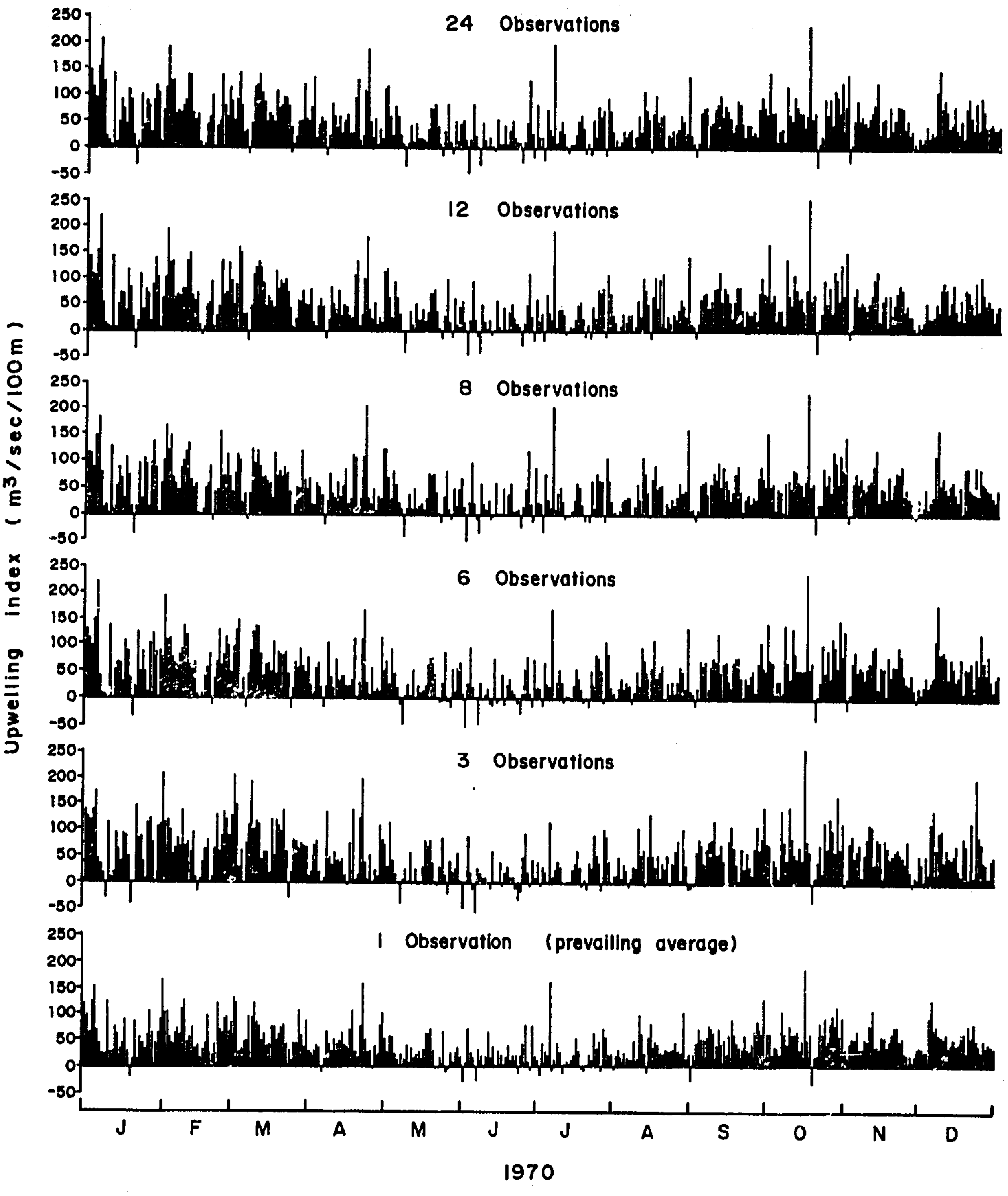

Fig. 2. Effect of using less and less subdaily observations when computing daily mean upwelling indices. Note that basic features of time series are maintained when 6-8 observations per day are used. (Data refer to Callao, 1970; see also Table 1 and text).

Results and Discussion

Inshore-Offshore Differences

The difference between the winds recorded at the airports and those from off the coast is one of the key points in this study. Enfield (1981a, 1981b) suggests that the differences between the seasonality of the easterlies, with a maximum in winter-spring and a minimum in summer (see Wyrtki and Meyers 1976; Barnett 1977), and the wind record at the Chimbote, Callao and Tacna airports (see Fig. 1) are due to land-sea thermal variations. Nevertheless, the Talara and San Juan winds, he points out, do have seasonal trends similar to those of the easterlies.

Brink et al. (1980) also found a reasonable match between winds measured at the airports and those measured over the shelf near 15oS. Based on these results, Schaffer (1982) used wind data recorded at the Trujillo, Chimbote and Callao airports to calculate mean stress vectors and to correlate these with the currents 50 km off Chimbote.

During a cruise to the north and central part of the Peruvian coast in April and May 1986, wind data (direction and velocity) were recorded every half hour until approximately 113 km off the coast. Fig. 1 shows the vectors of the wind records. As may be seen, there is a considerable uniformity in the winds off Trujillo, Chimbote and Callao, at least up to 48 km off the coast. Likewise, the airport records for the abovementioned localities resemble this neighboring sea-based wind vectors. This suggests that the winds recorded at the airports, up to a not yet determined distance from the coast (possibly 32 to 48 km), tend to be similar.

Considering that the coastal strip within 50 km is the area where upwelling occurs (Zuta and Guillen 1970; Guillen and Calienes 1981) and where the most important activities (e.g., spawning) of the different resources species take place, it appears that wind records from the two selected airports can be used for the calculation of upwelling and coastal turbulence indexes.

Monthly Variation of the Upwelling and Turbulence Indexes

Tables 2, 3, 4 and 5 and Fig. 3 and 4 show that the monthly variations of the upwelling and turbulence indexes have similar tendencies at each of the two stations considered here . In Trujillo, minimum values occur more frequently in winter (July-August) and summer (January-February-March) months. Maximum values tend to occur, on the other hand, at the end of winter (September) and in spring (October-November-December). In Trujillo, minimum and maximum monthly values tend to vary from one year to the other.

In Callao, the minimum and maximum values of upwelling and turbulence indices have a more regular seasonality than in Trujillo. The minimum values occur with a 70% incidence in

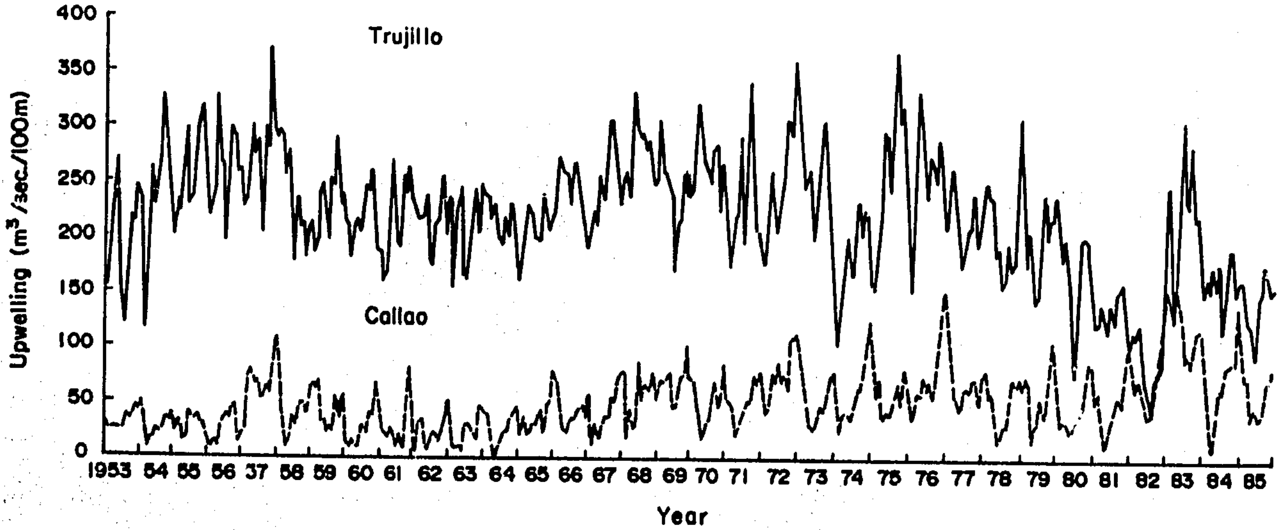

Fig. 3. Monthly variation of the upwelling index, Trujillo and Callao, 1953 to 1985.

the fall (May-June) months, and the maximum values in the spring (November-December) and summer (January-February) months.

The monthly patterns obtained by averaging the monthly values of every year analyzed differ between both stations (Fig. 5). In Trujillo low values occur in summer and winter while in Callao, low values are observed in fall. A greater seasonality in the indices can be observed for Callao than for Trujillo.

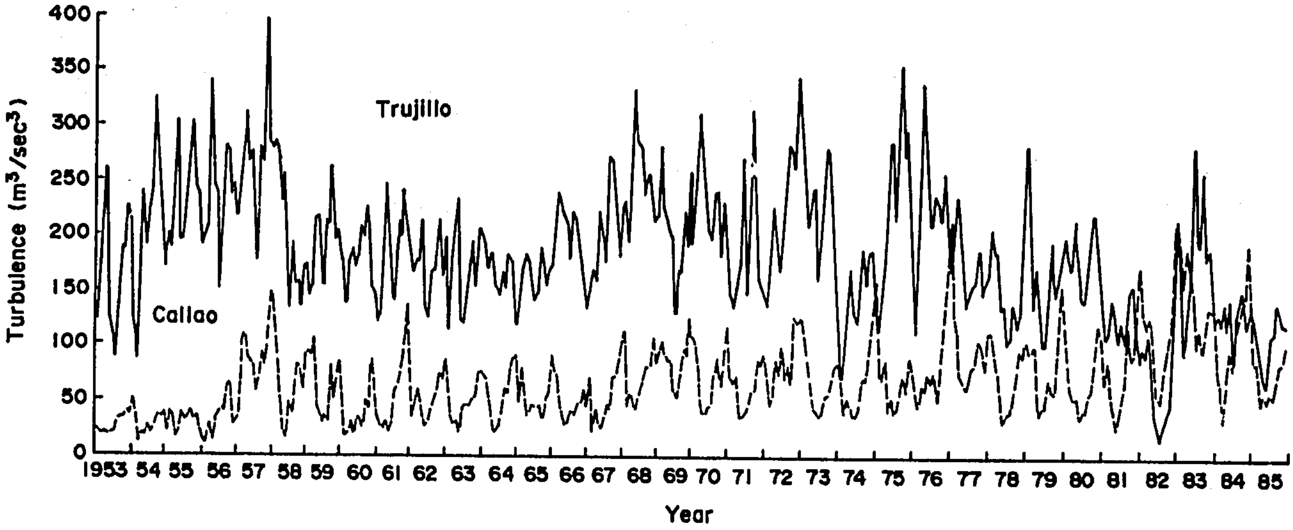

Fig. 4. Monthly variation of the turbulence index, Trujillo and Callao, 1953 to 1985.

Table 2. Monthly upwelling indices for Trujillo (m^3/sec/100 m coastline).

Trujillo (08°06'S 79°03'W)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
1953	164	155	208	243	270	163	138	122	166	221	213	241	192
1954	237	152	117	197	265	229	250	266	330	293	267	229	236
1955	204	235	223	246	301	229	237	260	300	310	265	256	256
1956	219	225	241	332	269	268	197	270	302	295	[illegible]	257	261
1957	228	240	271	304	274	291	267	207	301	280	373	291	277
1958	290	299	292	257	280	215	180	238	212	215	184	202	239
1959	216	189	203	244	251	231	200	255	248	292	231	237	233
1960	219	214	184	212	217	207	222	249	242	264	231	183	220
1961	190	162	171	213	275	236	196	192	257	241	265	232	219
1962	227	219	221	220	238	184	177	212	217	241	256	195	217
1963	236	159	226	232	247	167	164	196	217	245	207	244	212
1964	242	240	218	231	222	202	197	219	202	232	220	179	217
1965	164	181	287	229	224	202	203	200	241	225	207	209	214
1966	225	259	273	263	263	257	231	270	264	253	231	213	250
1967	192	208	226	214	258	246	236	307	309	291	269	224	248
1968	256	263	237	267	333	301	294	295	280	291	274	239	278
1969	255	309	262	261	250	244	173	212	216	258	237	267	245
1970	237	244	284	324	287	271	264	250	282	285	227	261	268
1971	236	193	176	213	226	294	196	260	345	251	208	196	233
1972	186	177	215	263	243	207	235	256	310	308	296	348	254
1973	319	276	247	267	264	201	215	272	306	298	256	175	258
1974	124	106	117	162	203	177	167	185	235	203	227	220	177
1975	167	155	184	210	300	298	145	317	371	307	323	234	251
1976	204	156	220	336	290	252	240	275	270	254	207	220	250
1977	213	244	265	242	199	176	191	209	215	240	195	199	216
1978	218	252	240	239	186	[illegible]	159	165	200	174	179	220	202
1979	314	247	177	209	180	144	149	188	244	202	220	215	207
1980	241	211	182	201	172	152	90	161	200	202	199	164	181
1981	137	123	125	141	129	118	142	125	153	156	161	117	136
1982	105	118	113	124	102	68	57	42	62	81	91	197	97
1983	251	231	129	157	200	318	239	232	291	222	224	174	222
1984	154	168	159	178	158	182	121	154	178	195	153	160	163
1985	167	155	130	124	110	98	150	157	178	167	156	154	146
Mean	213	205	207	229	233	213	192	219	247	242	230	217	220

Table 3. Monthly upwelling indices for Callao (m^3/sec/100 m coastline).

Callao (12°00'S 77°07'W)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
1953	35	27	24	27	25	25	25	27	39	34	39	45	31
1954	41	52	37	8	17	16	25	22	24	29	36	33	28
1955	41	23	34	32	16	18	41	34	37	38	28	33	31
1956	22	9	12	17	11	33	37	42	35	49	49	14	28
1957	22	26	76	81	73	67	71	52	60	69	60	81	62
1958	112	92	47	38	9	16	42	31	43	52	51	41	48
1959	58	70	63	71	34	35	24	30	25	58	38	56	47
1960	60	15	11	17	12	11	30	32	24	43	40	68	30
1961	53	28	24	19	29	24	11	24	12	12	49	82	31
1962	34	8	34	37	17	9	17	26	25	16	28	34	24
1963	56	38	12	11	14	7	32	34	31	25	20	48	27
1964	48	44	42	17	7	1	17	25	28	29	40	42	28
1965	50	21	44	24	26	35	33	42	45	24	50	54	37
1966	81	75	66	36	28	27	35	39	37	46	48	49	47
1967	38	61	15	35	21	20	35	42	38	59	53	71	41
1968	83	81	23	47	30	33	38	56	70	68	64	78	56
1969	56	70	75	72	77	80	49	49	63	78	79	105	71
1970	76	77	74	54	32	21	35	39	60	71	48	55	54
1971	87	54	54	49	22	35	43	50	54	54	79	71	54
1972	82	64	44	49	82	71	91	70	79	63	111	109	76
1973	118	103	79	60	34	30	28	37	51	43	65	75	60
1974	82	61	26	43	45	41	39	47	66	64	77	87	57
1975	130	76	58	76	40	46	41	45	58	72	49	80	64
1976	75	51	38	63	61	76	65	74	56	72	105	123	72
1977	154	102	92	59	53	47	66	67	65	76	76	50	76
1978	77	84	58	63	45	19	28	34	34	57	77	69	54
1979	77	67	79	72	19	35	37	58	44	41	74	110	59
1980	96	68	35	39	36	27	33	36	46	47	73	91	52
1981	88	56	64	31	20	17	35	44	62	56	54	87	51
1982	103	86	65	76	71	56	41	44	76	79	104	142	79
1983	157	149	134	160	145	133	90	100	88	102	120	119	125
1984	114	72	59	11	49	68	65	84	90	91	91	141	78
1985	103	77	78	41	51	46	52	46	61	74	77	90	66
Mean	76	60	51	47	38	37	41	45	49	54	62	74	53

Table 4. Monthly turbulence indices for Trujillo (m^3/sec^3).

Trujillo (08°06'S 79°03')

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
1953	145	133	204	244	284	136	114	96	139	208	204	240	179
1954	231	128	95	178	261	206	238	264	357	299	267	221	229
1955	186	220	204	236	334	215	[illegible]	254	308	328	264	253	251
1956	209	214	231	371	267	258	167	264	306	302	257	261	259
1957	236	257	281	342	290	302	[illegible]	193	305	288	433	301	291
1958	303	309	293	251	282	186	[illegible]	211	171	173	149	177	221
1959	190	157	169	237	237	204	167	235	228	283	212	220	212
1960	209	189	150	193	205	187	196	228	216	245	214	159	199
1961	162	133	139	186	271	205	164	155	232	219	263	211	195
1962	202	184	195	192	234	148	137	181	184	205	233	167	188
1963	218	124	194	210	255	134	131	158	189	213	166	223	185
1964	212	210	185	203	193	167	160	185	164	201	192	149	185
1965	128	144	274	200	194	167	154	162	209	185	168	179	180
1966	189	229	261	245	238	230	195	243	236	221	192	177	221
1967	147	167	187	174	243	210	192	296	294	270	250	191	218
1968	246	254	213	270	365	313	306	289	260	281	259	224	273
1969	238	309	247	239	225	219	140	185	183	245	209	262	225
1970	211	220	283	341	283	252	225	216	261	263	198	244	250
1971	209	161	146	174	192	294	161	229	344	219	178	163	206
1972	158	146	194	247	[illegible]	184	213	244	308	305	284	361	239
1973	315	267	226	244	263	174	193	255	300	290	233	151	243
1974	94	75	86	135	186	144	132	148	207	170	200	203	148
1975	139	125	162	197	311	311	235	312	382	300	325	226	252
1976	182	125	198	370	290	236	228	259	252	232	285	197	238
1977	184	228	259	231	181	151	162	170	175	205	161	169	190
1978	180	226	203	203	146	150	113	118	152	129	141	200	163
1979	307	229	147	189	144	110	113	152	214	158	186	191	178
1980	218	200	185	236	207	158	155	180	214	241	228	192	201
1981	150	118	125	158	136	115	136	114	150	165	172	113	138
1982	96	109	100	124	90	42	33	19	32	45	52	172	76
1983	237	210	103	134	173	311	217	210	284	196	208	153	203
1984	134	143	136	153	130	158	94	140	151	168	129	137	139
1985	147	139	115	92	77	72	122	124	154	145	134	128	121
Mean	[illegible]	184	188	210	224	192	170	197	229	224	214	200	203

Table 5. Monthly turbulence indices for Callao (m^3/sec^3).

Callao (12°00'S 77°07'W)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
1953	33	25	24	23	23	21	22	23	35	38	37	43	29
1954	41	56	40	13	22	19	29	21	26	34	40	37	31
1955	42	24	45	41	18	24	44	36	37	45	34	38	36
1956	26	13	13	32	14	37	41	48	44	68	72	30	36
1957	36	42	111	122	98	93	92	62	77	101	89	118	87
1958	167	143	69	55	25	19	54	42	65	90	88	65	73
1959	102	104	100	117	51	42	32	40	34	89	53	82	70
1960	93	28	20	23	34	19	38	36	29	54	46	93	43
1961	65	38	30	28	35	25	30	64	69	85	94	147	59
1962	68	37	59	67	42	30	32	42	53	60	83	73	54
1963	96	71	39	33	35	23	47	50	50	56	59	79	53
1964	83	80	78	45	31	25	29	42	67	62	88	92	60
1965	99	52	88	51	40	50	49	48	50	37	56	61	57
1966	101	87	81	52	37	29	35	45	41	53	53	62	56
1967	48	78	24	47	31	29	39	52	47	78	79	96	54
1968	113	124	48	65	54	46	55	66	82	90	89	113	79
1969	93	100	113	99	95	95	64	59	80	105	100	144	96
1970	119	118	111	77	44	42	48	50	81	99	67	84	78
1971	138	79	73	80	38	40	43	53	65	66	97	91	71
1972	101	80	51	56	95	79	110	75	92	71	139	129	90
1973	138	128	96	77	52	43	40	46	62	62	78	89	76
1974	93	79	40	58	52	40	40	45	78	76	100	119	68
1975	177	97	74	98	41	59	43	48	66	81	62	95	78
1976	90	64	47	72	66	85	74	86	53	83	131	163	84
1977	235	141	128	82	73	68	76	89	91	115	110	81	107
1978	124	124	99	88	64	36	44	44	57	75	108	96	80
1979	116	103	107	110	43	50	50	79	66	63	112	164	89
1980	130	96	69	59	60	41	47	46	63	70	104	129	76
1981	119	72	98	61	49	29	52	66	131	98	102	145	85
1982	189	141	128	140	131	87	60	55	89	104	119	181	119
1983	202	200	171	208	183	164	103	129	104	126	149	143	157
1984	146	86	72	36	80	106	90	126	135	150	158	205	116
1985	132	96	97	54	65	57	66	60	77	94	96	115	84
Mean	107	85	74	69	55	50	52	57	67	78	88	103	74

The marked irregularity of seasonal patterns, for the period covered by this study, suggests that the average monthly values and seasonal cycles presented here for both Trujillo and Callao should be viewed with caution. Likewise, the large differences found between both stations make it difficult to define a monthly pattern, say, for all of the northern zone of Peru.

On the other hand, a preliminary calculation of the upwelling indices for Chimbote (9°S) based on daily mean prevailing winds gave a monthly pattern similar to that of Trujillo, with the exception of a slightly more pronounced seasonality (Fig. 6). This allows us to assume that the wind-generated transport and turbulence could remain similar over coastal stretches of 2° and more. The extent of such coherence would depend, obviously, on interferences caused by coastal topography.

Annual Variations of the Upwelling and Turbulence Indexes

Tables 2, 3, 4 and 5 and Fig. 7 present the interannual transport and turbulence variations for the 1953-1985 period. Trujillo has higher values for both indices than does Callao, due mainly to a greater intensity of the winds. The interannual trends of both stations are almost opposite: while Trujillo experiences a rather regular decrease, Callao shows an increase in the values of both indices through the 33 years analyzed. Trujillo has its higher values during 1957, 1968 and 1983, and the lowest in 1953, 1974, 1981 and 1982. On the other hand, in Callao, an increase can be observed for the years 1957, 1966, 1969, 1972, 1976-1977 and 1983, all characterized by El Niño events.

This increase, in El Niño years in Callao, is a product of the wind intensification recorded by several authors such as Wyrtki (1975), Enfield (1981a and 1981b), Brink et al. (1983) and Smith (1983), among others. In Trujillo, this anomaly is not clearly observed (Fig. 5). However, the relaxation observed in 1982 matches the description of Wooster (1960) who noted a weakening of the easterlies during El Niño years.

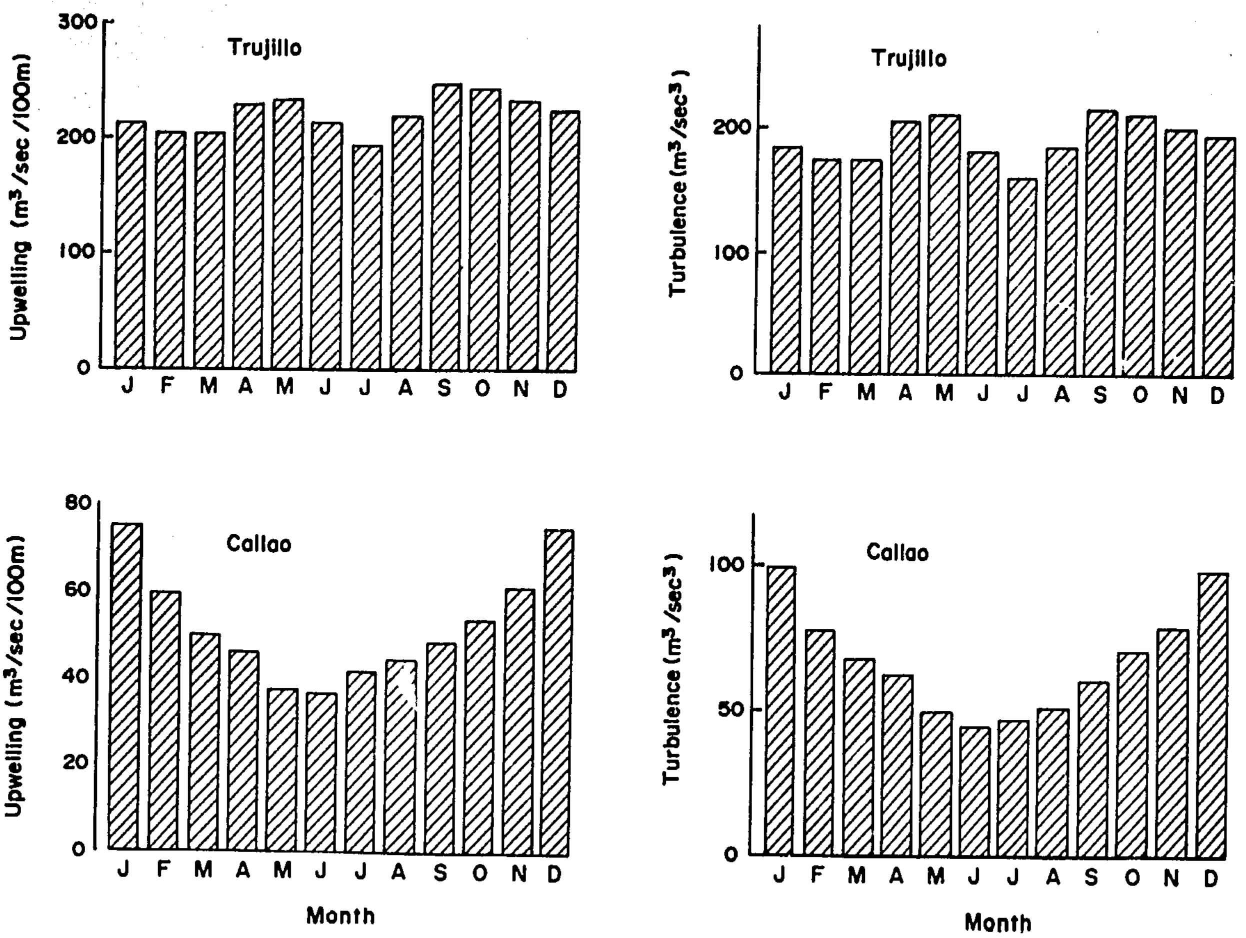

Fig. 5. Monthly cycles of turbulence and upwelling at Trujillo and Callao, based on 33-year means of monthly values (1953 to 1985).

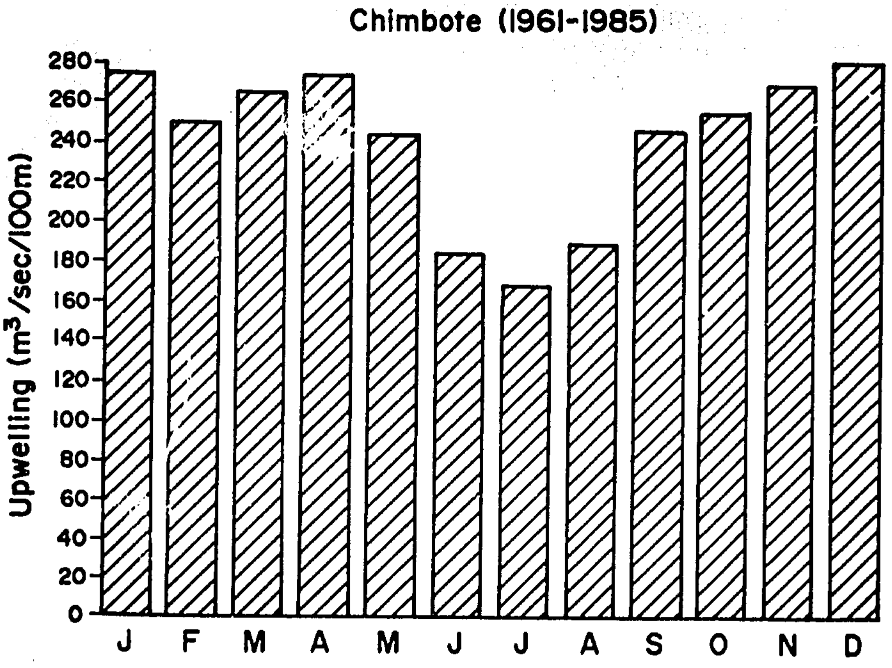

Fig. 6. Monthly cycle of upwelling for Chimbote. Based on 25-year means of monthly values.

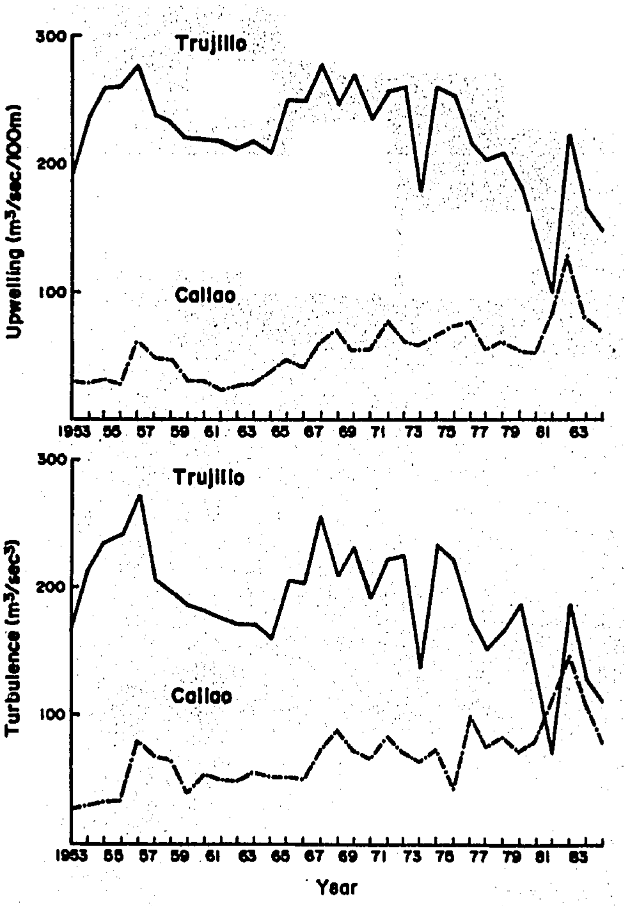

Fig. 7. Interyear variations of upwelling and turbulence indices for Trujillo and Callao, 1953 to 1984.

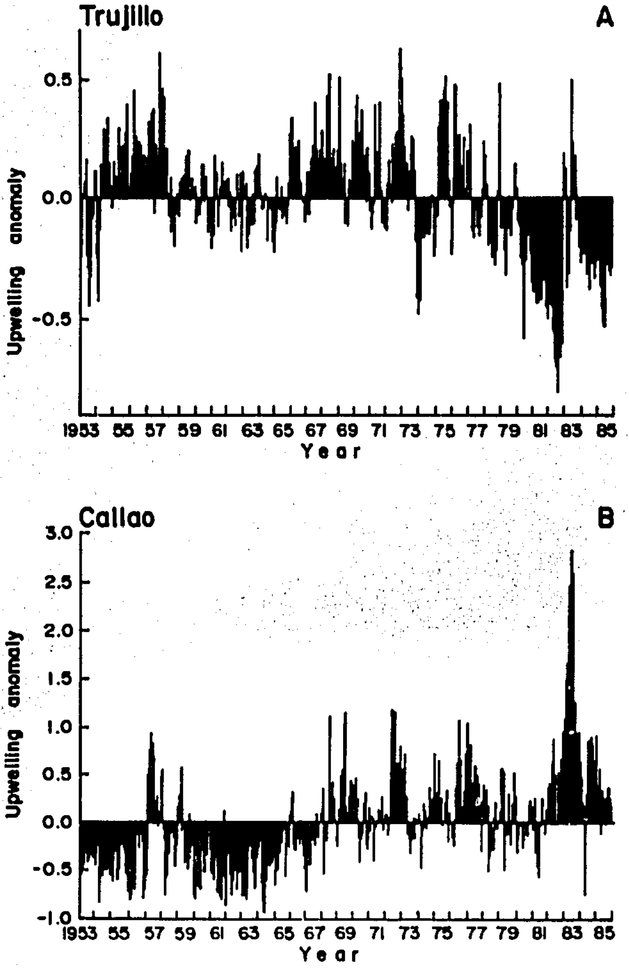

Fig. 8. Monthly upwelling anomalies, at Trujillo and Callao stations, Peru, 1953 to 1985.

Upwelling Index and the El Niño Phenomenon

The years characterized by the occurrence of El Niño events show positive and negative anomalies in Trujillo (Fig. 8) i.e., positive anomalies in 1955-1977, 1967, 1969 and 1976, and negative anomalies in 1981-1985.

On the other hand, in Callao only the years with positive anomalies correspond to El Niño events (e.g., 1957, 1969, 1972-1973, 1976-1977 and 1982-1983). In addition, a positive anomaly occurred during 1984-1985.

Ekman Transport and Turbulence Indexes Related to Spawning Seasons in Eastern Boundary Current Systems

Parrish et al. (1983), after comparing the four eastern boundary systems, concluded that spawning rarely occurs in areas of strong turbulent mixing of the upper water column. Indeed, spawning grounds are characterized by weak to moderate values of the turbulent index.

Fig. 9 (adapted from Parrish et al. 1983) shows the upwelling and turbulence indices for spawning areas in the Peru Current System, with our new values for including the values for Trujillo and Callao (33 years monthly means) added for comparison. The graph shows that Trujillo as well as Callao are characterized by relative low turbulence and strong transport. The

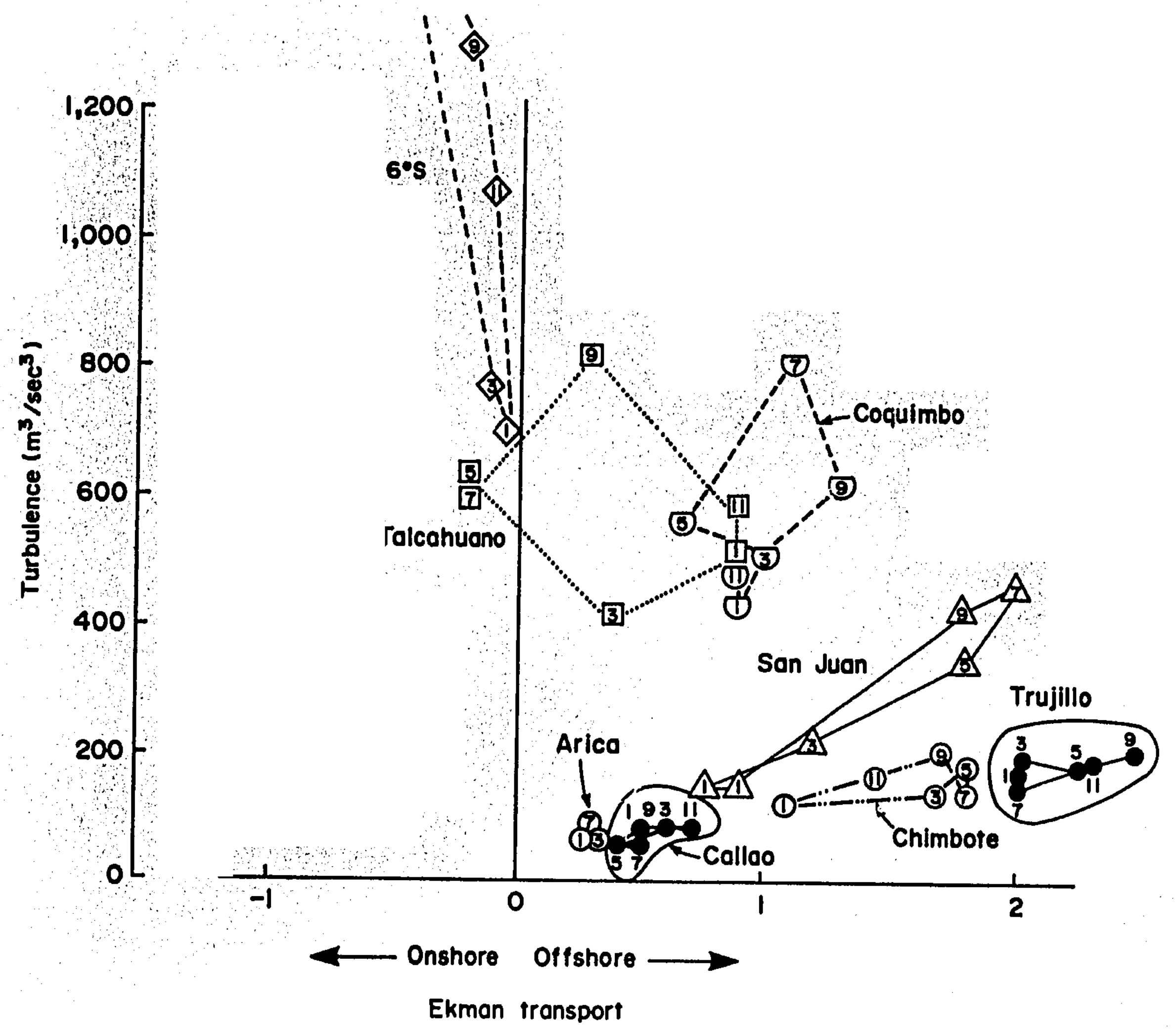

Fig. 9. Seasonal cycles of turbulence and upwelling at various locations in the Peru Current. Each numbered symbol represents a 2-month climatological sample, with the number corresponding to the first of the pair of months. Seasons and/or area with low turbulence and offshore transport may be assumed to be appropriate for survival of fry (redrawn from Parrish et al. 1983, with data for Callao and Trujillo added).

spawning peak of the Peruvian anchovy occurs during the austral winter when offshore Ekman transport is strong. Likewise, we know that the offshore transport off Chimbote is stronger than in the California Current System (Bakun 1985).

This fact suggests that spawning success of the Peruvian anchoveta off Chimbote and Trujillo should be influenced more by transport than turbulence.

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Monthly Catch and Catch Composition of Peruvian Anchoveta *(Engraulis ringens)* (Northern-Central Stock, 4-14°S), 1953 to 1982*

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TSUKAYAMA, I. and M.L.D. PALOMARES. 1987. Monthly catch and catch composition of Peruvian anchoveta *(Engraulis ringens)* (northern-central stock, 4-14°S), 1953 to 1982, p. 89-108. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

This paper presents an uninterrupted time series of monthly catch data on Peruvian anchoveta *(Engraulis ringens)* covering the northern/central stock (4-14°S) and the period from January 1953 to December 1982. Also presented is a monthly, largely uninterrupted time series, also covering 1953 to 1982, of % length-frequency data representing the catch composition by 1 cm class of the fishery and the anchoveta consumed by major predators such as the guano birds. This paper presents, finally, a time series of monthly "condition factors", i.e., of the multiplicative factor (c.f.) in length-weight relationships of the form $W = (cf/100) \cdot L^3$. These c.f. values can be used to turn the data presented here into monthly catch-at-length data, i.e., absolute numbers of fish caught by length and month, from 1953 to 1982. The methods used to obtain and standardize these data are briefly presented, along with potential source of errors.

Introduction

The anchoveta (*Engraulis ringens*) which, from the mid-1960s to the early 1970s formed the basis of the largest single-species fishery in the world, has been the focus of numerous studies both on its biology and population dynamics and on the environmental factors that affect these (Clark 1954; Jordan 1959; Boerema et al. 1965; Schaefer 1967; see also contributions in UNESCO 1980; Glantz and Thompson 1981 and references in Pauly and Tsukayama, this vol.). The fishery has a well documented history dating back to the start of the fish meal and oil industries,which use anchoveta as raw material,in the 1950s (Freyre 1967),resulting in increased demand for anchoveta and a corresponding increase in the number of commercial vessels (Doucet and Einarsson 1967 and Aguero, this vol.). The rapid growth of the fishery led to various government interventions, notably the creation of fishery research institutions, i.e., the Consejo de Investigaciones Hidrobiologicas in 1954, the Instituto de Investigacion de los Recursos Marinos in 1960 and the Instituto del Mar del Peru (IMARPE) in 1964, whose aim was to study the fishery and to propose development and management schemes for the fishery (Schaefer 1967 and see Castillo and Mendo, this vol.).

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* ICLARM Contribution No. 380.

In the early 1970s, IMARPE, based on a large volume of catch, length-frequency, environmental, economic and ancillary data, organized a series of meetings that were aimed at assessing the status of the anchoveta stock (IMARPE 1970, 1973, 1974a, 1974b). In 1974, following the 1972 collapse of the fishery, a research scheme was proposed at an international workshop for the study of the effects of fishing on the anchoveta stock and the contributing effects of environmental factors, such as the "El Niño" phenomenon and predation pressure (see Anon.1975 and contributions in UNESCO 1980).

Pauly and Tsukayama (1983) presented a preliminary analysis of a time series of catch-at-length data covering, on a monthly basis, the years 1961 to 1982 for the northern anchoveta stock. Their analysis brought to the fore the importance of a long time series to identify and quantify the factors which affect growth, mortality, recruitment, and thus, biomass and catches. Continuous and consistent series of catch and catch composition data are also needed to demonstrate monthly variability of stock sizes indicative of seasonal fluctuations in the physical environment and changes in biological processess.

This paper presents a number of time series needed for these purposes. These have been derived in a two-phase process also used in some other contributions included in this volume:

a) collection and initial data standardization at IMARPE, and

b) final data standardization and filling of gaps at ICLARM.

Material and Methods

The Catch Data

Three data sources were used to construct the time series of monthly catch covering the years 1953 to 1982:

i) for the years 1953 to 1958, we used annual catches in Table 2 of Murphy (1972), put on a monthly basis using monthly weighting factors based on the monthly catch data in Fig. 1 of Doucet and Einarsson (1967), which cover the years 1959 to 1964 (1963 and 1984 were not used

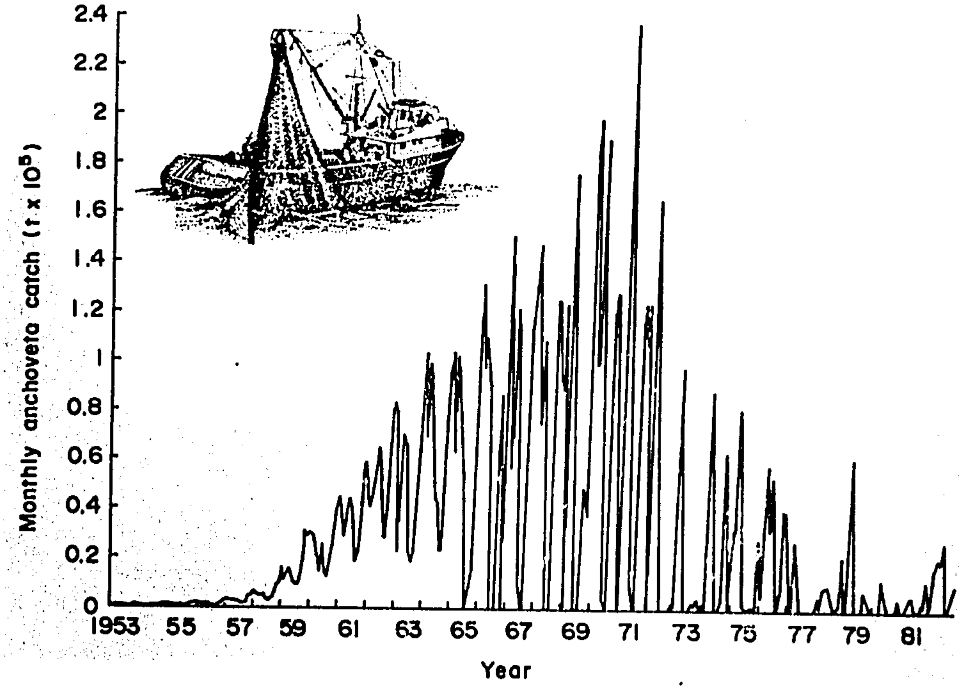

Fig. 1. Monthly nominal catch of Peruvian anchoveta *(Engraulis ringens)* (northern/central stock, 4-14°S) from January 1953 to December 1982.

due to the occurrence of a strike in January 1963 and to noncoverage of later months in 1964, respectively).

ii) for the period from January 1959 to February 1961 we used the catch data in Fig. 1 of Doucet and Einarsson (1967), which pertains to the whole of the Peruvian coast. These data were therefore adjusted to the narrower stretch from 4 to 14^{o}S using a factor of 96%, computed from the data in Fig. 2 in Doucet and Einarsson (1967); this factor was also applied to the data in (i).

iii) the catch data covering the period from March 1961 to December 1982 were collected by staff of the Instituto del Mar del Peru and its predecessor, the Instituto del Investigaciones de Recursos Marinos.

The time series of catch presented here is uninterrupted in the sense that a catch figure is given for every month during which fishing activities occurred. Months with zero, or near zero catches refer either to a strike *(huelga)* or a closure of the fishery *(veda),* a measure which became increasingly necessary during the 1970s (the very low catch values during *veda* periods refer mainly to the small catches made by the survey ships themselves).

It must be realized that the catch figures presented here (see Tables 1 to 30) represent *nominal* catches, i.e., figures which may considerably underestimate the actual catches (see Castillo and Mendo, this vol.).

The Length-Frequency Data

The length-frequency data presented in 1 cm classes in Tables 1 to 30 stem from four different sources:

i) from the archives of the Instituto del Investigaciones de Recursos Marinos, and referring to standard length (SL) samples collected at Callao, Casma, Chimbote, Don Martin, Huacho and Samanco. These samples, representing individual fish measured to the nearest mm, were converted to total length (TL) using a regression established by Clark (1954), i.e.,

$$TL = 2.5 + 1.154\ SL \qquad \ldots 1)$$

where L is expressed in mm. These data refer to the period ranging from October 1953 to February 1961 (see Tables 1-9).

ii) Jordan (1959, Figs. 5a-5d) presented detailed size-frequency data representing fishery catches from the Huacho area and anchoveta consumed by cormorants (the most important guano bird of Peru, see Tovar et al., this vol.), as reconstructed from regurgitated otoliths collected on Don Martin Island (see Tovar et al., this vol. for location). Jordan (1959) also showed that the size distribution of these two groups of samples largely overlap (see also Muck and Pauly, this vol.). These samples, originally presented as standard length in graphic forms, were read off, coverted to total length and regrouped in 1 cm classes as was done in (i). They cover the period from June 1954 to June 1958; whenever they were taken in the same month as a sample from (i), an average sample was constructed for the month in question (see Tables 2 to 6).

iii) the bulk of the length-frequency data presented here for the period from March 1961 to December 1982 have been collected by IMARPE staff generally following the sampling procedure described in Saetersdal and Valdivia (1964). These authors also presented data suggesting that for the stretch of coastline covering the northern and central part of Peru, within port variability of length-frequency samples was less than variability due to different sampling periods. Monthly samples representative of the stock as a whole were thus obtained by pooling, within each month, daily samples representing about 30% of the landing and most of the fishing areas covered by the fleet.

Generally, one single sample was taken from each vessel sampled. The sample consisted of the content of a two-liter container, of which all anchoveta were measured and weighted. The data were originally in 0.5 cm classes, defined such that, upon regrouping into 1 cm classes, class medians (or "midlengths") of 4.25, 5.25,...20.25 cm emerged. This is the reason why the data in (i) and (ii) were also regrouped within the somehow unconventional class limits that the above midlengths imply.

iv) to complement the data in (iii) obtained from fishery catches, length-frequency data were obtained, from 1972 onward during scientific surveys such as the EUREKA surveys, conducted during closures of the fishery (Villanueva 1975 and Tables 20-27).

The length-frequency data obtained from (i) to (iv) were then expressed as percentages of the total monthly frequencies. These percent frequencies as presented in Tables 1-30 may, in some case, not add up exactly to 100% because of rounding off errors and cases where the original sample included fish smaller than 4.25 cm, excluded from the tables presented here. It should also be noted that on all these tables, dashes represent zero frequencies and "0.000" represents frequencies less than 0.0005%.

Overall, the length-frequency data presented here cover 270 of 360 possible months, i.e., the time series is 75% complete. Standardization to 1 cm length classes and a single definition of length (here total length (TL), led to certain features such as the consistency of the time of recruitment of young fish, the shift of modes reflective of growth phenomena and a trend toward larger sizes, from 1953 to 1982 to become immediately visible (see Tables 1 to 30). These themes are investigated in greater detail in Palomares et al. (this vol.).

The Condition Factors

"Condition factors" (c.f.) are here defined as the multiplicative term in a length-weight relationship of the form

$$W = (c.f./100) \cdot L^3 \qquad ...2)$$

where weight (W) is expressed in g live weight and length (L) as total length in cm. The exponent of 3 implies isometry which is assumed here for the sake of having all temporal changes in the length-weight relationship of anchoveta "concentrated", as it were, in their monthly c.f. values (see Pauly 1984).

In earlier analyses of the length-frequency data from March 1961 to December 1982 presented in Tables 9-30, the weights of samples of fish that had been measured by IMARPE field staff had also been used to raise these samples to the total catch. Because these sample weights were not available to directly estimate c.f. values at the time this contribution was written, we have proceeded "backward", i.e., used the catch-at-length estimates to obtain approximations of the underlying condition factors. This was done on the basis of a length-weight relationship of the form

$$W = aL^3 \qquad ...3)$$

with (a · 100) arbitrarily set equal to 1 (one). The "pseudo-weight" of the fish of a given class (j) was then estimated as

$$PW_j = (L_{j1}^3 + L_{j2}^3)/2 \qquad ...4)$$

where L_{j2} is the upper limit of length class (j) and L_{j1} its lower limit (e.g., for say a midlength of 10.25, $L_{j1} = 9.75$ and $L_{j2} = 10.75$ cm). The values of PW_j were then multiplied, for each month separately, by the available catch-at-length data. This resulted in pseudo total weight of the monthly catch. Finally, the ratio of the real catch to the pseudo monthly catch was computed, corresponding to the ratio between real c.f. values and the values of a · 100.

The c.f. values so estimated are given in Tables 9-30. They were also plotted by Palomares et al. (this vol.) against the mean sea surface temperature (T_i, see Table 2 in Pauly and Tsukayama, this vol.) of the corresponding month (i) This resulted in

$$c.f._i = 0.851 - 0.000974T_i \qquad ...5)$$

which was used for all years (i.e., 1953 to 1960, see Tables 1-8) and months for which "real" c.f. could not be estimated from catch-at-length data using the method described above.

Results and Discussion

Tables 1-30 present the monthly catch of Peruvian anchoveta *(Engraulis ringens)*, northern/central stock (4-14°S), from January 1953 to December 1982.

As might be seen from Fig. 1, this catch fluctuated enormously from month to month, this phenomenon being strengthened since 1972 by seasonal closures of the fishery.

Palomares et al. (this vol.) present an analysis of the time series of catch composition data and condition factors compiled in Tables 1-30, while Castillo and Mendo (this vol.) discuss possible sources of bias in the nominal catch presented here. We leave it thus to the reader to consult these authors for a detailed discussion of the data in Tables 1-30.

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Table 1. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S), 1953.

Midlength (TL, cm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct[a]	Nov[a]	Dec[a]
4.25												
5.25												
6.25												
7.25												
8.25										0.614	0.255	0.845
9.25										5.522	0.610	15.080
10.25										8.589	5.688	25.320
11.25										14.720	26.520	16.140
12.25										41.720	36.800	20.580
13.25										26.380	19.380	16.790
14.25										1.840	9.321	4.680
15.25										0.614	1.276	0.194
16.25											0.255	0.194
17.25												
18.25												
19.25												
20.25												
Catch[b]	6.330	5.270	4.990	4.940	4.740	4.800	3.270	2.780	3.370	5.470	8.900	9.140
c.f.[c]	(0.662)	(0.645)	(0.630)	(0.641)	(0.660)	(0.676)	(0.678)	(0.686)	(0.684)	(0.688)	(0.686)	(0.680)

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[a] % frequencies based on data collected at Callao, Casma, Chimbote, Don Martin, Huacho, Pisco and Samanco by staff of the Instituto de Investigacion de Recursos Marinos.

[b] Monthly catch in 1,000 t adapted from annual catch data in Murphy (1972) and mean seasonality of catch adapted from Figs. 1 and 2 in Doucet and Einarsson (1967).

[c] Condition factors in brackets estimated from the linear relationship between temperature and condition factors in Palomares et al. (this vol.).

Table 2. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S), 1954.

Midlength (TL, cm)	Jan	Feb	Mar	Apr[a]	May[a]	Jun	Jul	Aug[b]	Sep[b]	Oct[a]	Nov[a]	Dec[a]
4.25												
5.25												
6.25												
7.25												
8.25				0.532	0.506					3.000		
9.25				2.660	5.823	1.954				2.000	1.581	
10.25				4.787	13.860	8.388		0.333	0.333	-	0.500	0.195
11.25				25.000	43.880	31.050		3.872	1.943	5.380	0.250	1.253
12.25				32.980	23.740	28.680		11.410	12.800	29.070	3.866	5.764
13.25				22.870	11.430	22.750		21.560	33.790	24.740	24.660	1.460
14.25				10.640	0.506	5.665		40.130	39.150	15.860	33.550	49.520
15.25				0.532	0.253	0.505		19.800	11.450	19.630	25.140	9.288
16.25						0.505		2.660	0.536	4.753	6.820	0.942
17.25						0.505		0.236		0.571	0.216	
18.25												
19.25												
20.25												
Catch[c]	8.60	7.17	6.79	6.72	6.44	6.52	4.44	3.78	4.58	7.43	12.10	12.40
c.f.[d]	(0.671)	(0.666)	(0.672)	(0.685)	(0.693)	(0.702)	(0.697)	(0.710)	(0.706)	(0.705)	(0.698)	(0.674)

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[a] % frequencies per length class based on data collected at Callao, Casma, Chimbote, Don Martin, Huacho, Pisco and Samanco by staff of the Instituto de Investigacion de Recursos Marinos.

[b] Mean of % frequencies from (a) and from Jordan (1959).

[c] Monthly catch in 1,000 t adapted from annual catch data in Murphy (1972) and mean seasonality of catch adapted from Figs. 1 and 2 in Doucet and Einarsson (1967).

[d] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 3. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S), 1955.

Midlength (TL, cm)	Jan[b]	Feb[b]	Mar[b]	Apr[b]	May[b]	Jun[b]	Jul[b]	Aug[b]	Sep[a]	Oct[a]	Nov[b]	Dec[b]
4.25												
5.25												
6.25		0.447			0.617						2.510	
7.25		10.220	1.457	2.576	9.259						5.688	
8.25	0.084	13.040	4.399	6.040	12.120	2.664					3.072	
9.25	0.689	5.168	1.321	3.642	7.411	6.782	33.010				0.938	
10.25	1.983	5.689	6.717	2.433	5.704	6.687	22.440				0.502	0.844
11.25	13.090	11.630	17.580	9.830	19.640	20.410	11.730	0.543	10.000	20.710	5.165	14.910
12.25	21.230	11.600	21.330	27.710	21.600	35.290	18.400	4.417	29.000	31.820	12.600	30.200
13.25	20.610	14.440	22.090	20.200	13.780	22.850	9.395	20.450	40.340	30.300	24.810	28.000
14.25	31.660	20.420	21.830	22.230	8.454	4.982	4.000	66.800	19.330	16.160	32.430	19.310
15.25	10.460	6.999	3.194	5.168	1.247	0.333	1.023	7.792	1.333	1.010	11.100	6.317
16.25	0.175	0.345	0.082	0.167	0.166						1.186	0.422
17.25												
18.25												
19.25												
20.25												
Catch[c]	10.50	8.73	8.27	8.18	7.84	7.95	5.42	4.60	5.59	9.05	14.70	15.20
c.f.[d]	(0.648)	(0.660)	(0.678)	(0.672)	(0.686)	(0.688)	(0.690)	(0.697)	(0.693)	(0.700)	(0.695)	(0.688)

[a] % frequencies based on data collected at Callao, Casma, Chimbote, Don Martin, Huacho, Pisco and Samanco by staff of the Instituto de Investigacion de Recursos Marinos.

[b] Mean of % frequencies from (a) and from Jordan (1959).

[c] Monthly catch in 1,000 t adapted from annual catch data in Murphy (1972) and mean seasonality of catch adapted from Figs. 1 and 2 in Doucet and Einarsson (1967).

[d] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 4. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S), 1956.

Midlength (TL, cm)	Jan[b]	Feb[c]	Mar[b]	Apr[a]	May[a]	Jun[b]	Jul[b]	Aug[b]	Sep[a]	Oct[a]	Nov[c]	Dec[b]
4.25												
5.25												
6.25							1.334					
7.25				1.000		0.453	8.107					
8.25				40.000		2.493	18.880	0.333				
9.25		0.507	0.751	8.500	0.250	1.662	14.030	1.667	3.000	2.000		0.487
10.25	1.907	1.015	2.336	1.754	5.000	6.568	8.007	5.471	8.500	9.667	4.362	1.468
11.25	11.630	17.290	4.703	2.881	9.250	16.250	6.450	10.710	5.500	10.000	12.820	19.800
12.25	17.080	25.220	13.970	5.515	23.750	36.480	16.730	23.830	21.000	20.000	12.420	39.790
13.25	25.740	23.120	34.640	20.420	39.000	29.560	17.360	20.020	34.000	28.000	26.920	26.960
14.25	30.300	22.200	34.410	17.420	20.260	6.280	7.508	12.300	25.000	19.000	31.260	9.500
15.25	11.030	9.131	8.582	2.506	2.500	0.251	0.817	16.670	2.500	2.000	10.480	1.750
16.25	2.244	1.522	0.607				0.334	4.000	0.000	3.000	1.742	0.250
17.25	0.067						0.445	5.000	0.500	6.333		
18.25												
19.25												
20.25												
Catch[d]	16.10	13.40	12.70	12.60	12.10	12.20	8.33	7.07	8.59	13.90	22.60	23.30
c.f.[e]	(0.672)	(0.658)	(0.654)	(0.668)	(0.674)	(0.678)	(0.680)	(0.686)	(0.690)	(0.694)	(0.692)	(0.694)

[a] % frequencies based on data collected at Callao, Casma, Chimbote, Don Martin, Huacho, Pisco and Samanco by staff of the Instituto de Investigacion de Recursos Marinos.

[b] Frequencies per length class adapted from Jordan (1959), referring either to fish eaten by birds or fishery catch.

[c] Means of (a) and (b).

[d] Monthly catch in 1,000 t adapted from annual catch data in Murphy (1972) and mean seasonality of catch adapted from Figs. 1 and 2 in Doucet and Einarsson (1967).

[e] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 5. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S), 1957.

Midlength (TL, cm)	Jan[b]	Feb[b]	Mar[b]	Apr[b]	May[b]	Jun[b]	Jul[b]	Aug[a]	Sep[b]	Oct[b]	Nov[b]	Dec[b]
4.25										15.580		
5.25	0.244				0.996					1.154		
6.25	0.244				2.986	1.377	2.515	0.483		0.000		
7.25	0.244				9.790	7.606	9.356	14.980	4.488	0.939		
8.25	0.489		0.236		3.982	6.372	9.054	14.980	16.150	5.886		
9.25	1.244		0.486	1.202	0.000	1.995	6.036	7.740	13.190	7.050	3.146	3.146
10.25	5.718	3.246	1.800	9.240	3.570	0.776	6.640	16.040	12.020	19.520	9.585	6.085
11.25	11.860	11.600	20.380	27.300	15.780	5.293	11.070	13.870	20.240	19.180	24.315	18.815
12.25	28.400	36.240	44.380	36.870	31.200	21.230	19.620	15.890	27.360	15.600	31.650	37.400
13.25	25.320	32.440	24.610	18.635	22.960	37.650	26.150	10.540	6.167	10.380	23.670	23.670
14.25	21.010	12.980	6.635	4.500	8.232	16.590	9.557	0.365	0.386	2.466	7.389	10.889
15.25	4.228	3.495	0.972	0.750	0.500	1.115		–		0.947	0.250	
16.25	–			0.250				0.365		–		
17.25	1.000		0.500	1.250				4.745		1.300		
18.25												
19.25												
20.25												
Catch[c]	33.70	28.10	26.60	26.30	25.20	25.60	17.40	14.80	18.00	29.10	47.40	48.80
c.f.[d]	(0.678)	(0.633)	(0.635)	(0.638)	(0.634)	(0.644)	(0.653)	(0.669)	(0.679)	(0.677)	(0.677)	(0.650)

[a] % frequencies from Jordan (1959), referring either to fish eaten by birds or fishery catch.

[b] Means of (a) and of data collected by staff of the Instituto de Investigacion de los Recursos Marinos.

[c] Monthly catch in 1,000 t adapted from annual catch data in Murphy (1972) and mean seasonality of catch adapted from Figs. 1 and 2 in Doucet and Einarsson (1967).

[d] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 6. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S), 1958.

Midlength (TL, cm)	Jan[b]	Feb[b]	Mar[b]	Apr[a]	May[b]	Jun[b]	Jul[a]	Aug[a]	Sep[a]	Oct	Nov[a]	Dec[a]
4.25												
5.25											1.974	
6.25											24.010	
7.25	8.330		0.973								6.908	
8.25	7.520		9.730		3.732	3.333			8.889		0.329	
9.25	10.330		6.130		11.230	8.717		7.000	23.330		–	3.646
10.25	18.800	4.347	18.240	18.000	12.260	15.250		33.000	25.550		2.960	7.085
11.25	23.310	24.560	38.660	56.000	24.060	23.020	4.000	42.000	16.670		38.490	10.820
12.25	17.800	48.280	16.600	26.000	17.510	36.540	50.000	14.000	16.670		22.700	24.900
13.25	6.690	17.890	5.148		25.190	9.883	38.000	4.000	8.889		2.303	40.660
14.25	2.220	4.591	2.772		6.022	3.254	8.000				–	12.890
15.25	–	0.334	–								–	
16.25	–		–								–	
17.25	5.000		1.750								0.329	
18.25												
19.25												
20.25												
Catch[c]	66.3	55.2	52.3	51.7	49.6	50.2	34.2	29.1	35.3	57.2	93.1	95.8
c.f.[d]	(0.638)	(0.634)	(0.636)	(0.655)	(0.668)	(0.674)	(0.676)	(0.686)	(0.686)	(0.685)	(0.681)	(0.686)

[a] % frequencies based on data collected at Callao, Casma, Chimbote, Don Martin, Huacho, Pisco and Samanco by staff of the Instituto de Investigacion de los Recursos Marinos.

[b] Mean of % frequencies from (a) and from Jordan (1959).

[c] Monthly catch in 1,000 t adapted from annual catch data in Murphy (1972) and mean seasonality of catch adapted from Figs. 1 and 2 in Doucet and Einarsson (1967).

[d] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 7. Monthly catch[a] and percent catch composition[b] of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S), 1959.

Midlength (TL, cm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25			1.282									
5.25			5.128		5.769							
6.25			0.641	1.923	42.300	0.784			0.485			
7.25	13.460	1.639	20.510	10.000	35.580	9.412		1.429	0.971			
8.25	34.620	15.410	30.760	21.920	11.540	29.800	11.540	2.857	–	0.560	0.279	1.923
9.25	27.400	32.460	16.030	16.540	1.923	30.200	26.920	3.571	–	0.840	12.810	0.962
10.25	12.020	25.570	16.030	24.620	1.923	20.339	34.620	5.714	–	17.070	48.470	25.960
11.25	8.654	11.480	7.051	10.770	–	5.098	15.380	2.143	5.825	41.470	28.970	32.690
12.25	3.365	9.180	1.923	8.846	–	3.922	7.692	28.570	39.320	30.540	8.078	19.230
13.25	0.481	4.262	0.641	4.231	0.962	0.392	3.846	42.860	44.180	9.244	1.393	17.310
14.25				1.154				11.430	9.223	0.280		1.923
15.25								1.429				
16.25												
17.25												
18.25												
19.25												
20.25												
Catch	164	108	132	157	137	104	96	88	102	171	304	286
c.f.[c]	(0.666)	(0.644)	(0.650)	(0.660)	(0.669)	(0.678)	(0.687)	(0.690)	(0.688)	(0.684)	(0.680)	(0.670)

[a] Monthly catch in 1,000 t adapted from annual catch data in Murphy (1972) and mean seasonality of catch adapted from Figs. 1 and 2 in Doucet and Einarsson (1967).

[b] % frequencies based on data collected at Callao, Casma, Chimbote, Don Martin, Huacho, Pisco and Samanco by staff of the Instituto de los Recursos Marinos.

[c] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 8. Monthly catch[a] and percent catch composition[b] of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S), 1960.

Midlength (TL, cm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25												
5.25											0.481	
6.25										0.481	–	
7.25	1.282	0.769				0.386				–	0.481	
8.25	0.641	1.923	6.667	1.905	12.500	13.900				1.923	0.962	
9.25	3.846	6.154	25.560	–	20.190	23.940				0.489	0.154	
10.25	51.280	53.070	21.110	6.667	42.310	17.760				7.283	3.904	0.222
11.25	35.900	27.300	23.330	27.620	20.190	14.290				12.790	15.440	1.222
12.25	5.969	6.923	20.000	36.190	3.846	18.150				8.940	28.360	16.330
13.25	1.282	3.846	3.333	23.810	0.962	10.420				24.290	35.950	40.010
14.25				3.810		1.158				25.470	13.350	37.440
15.25										15.550	0.769	3.880
16.25										2.740	0.154	0.889
17.25										0.048		
18.25												
19.25												
20.25												
Catch	303	292	279	182	137	258	138	117	158	223	348	397
c.f.[c]	(0.666)	(0.661)	(0.664)	(0.676)	(0.684)	(0.685)	(0.690)	(0.688)	(0.689)	(0.690)	(0.690)	(0.680)

[a] Monthly catch in 1,000 t adapted from annual catch data in Murphy (1972) and mean seasonality of catch adapted from Figs. 1 and 2 in Doucet and Einarsson (1967).

[b] % frequencies based on data collected at Callao, Casma, Chimbote, Don Martin, Huacho, Pisco and Samanco by staff of the Instituto de los Recursos Marinos.

[c] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 9. Monthly catch[a] and percent catch composition[b] of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S), 1961.

Midlength (TL, cm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25												
5.25												
6.25			0.017	0.009	0.007							
7.25			0.124	1.342	0.230	0.0902						0.036
8.25		0.125	0.402	2.910	2.341	0.945	0.084	0.227				0.049
9.25	0.091	0.375	2.161	2.670	5.374	3.670	2.650	1.437	0.010	0.017		0.227
10.25	0.911	1.000	7.954	3.243	7.695	7.262	8.936	4.074	0.455	0.142	0.022	0.542
11.25	0.820	2.000	14.570	12.770	13.470	14.480	12.050	9.046	1.851	2.510	0.486	1.296
12.25	10.660	10.750	14.350	18.140	20.290	20.260	13.090	13.810	6.682	9.227	4.634	6.282
13.25	40.530	38.380	17.880	17.700	21.330	21.100	22.200	17.860	22.610	17.810	17.980	21.120
14.25	43.260	34.120	26.990	25.420	20.280	20.690	27.270	31.020	41.340	34.580	42.380	46.330
15.25	3.734	2.875	13.890	13.940	7.948	10.140	12.290	19.840	24.190	30.140	30.320	22.000
16.25		4.500	1.652	1.839	1.005	1.332	1.426	2.666	2.801	5.479	4.082	2.095
17.25		5.125	0.011	0.018	0.036	0.034	0.006	0.019	0.059	0.096	0.096	0.026
18.25		0.750										
19.25												
20.25												
Catch	447	379	283	364	439	343	233	183	208	375	571	591
c.f.[c]	(0.666)	(0.650)	0.682	0.696	0.688	0.667	0.644	0.672	0.718	0.724	0.700	0.672

[a] Monthly catch in 1,000 t for January and February adapted from annual catch data in Murphy (1972) and mean seasonality of catch adapted from Figs. 1 and 2 in Doucet and Einarsson (1967); catch for March-December are based on samples collected by IMARPE staff.

[b] % frequencies for January and February are based on data collected at Callao, Casma, Chimbote, Don Martin, Huacho, Pisco and Samanco by staff of the Instituto de Investigacion de los Recursos Marinos while that for March-December are based on samples collected by IMARPE staff.

[c] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 10. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1962.

Midlength (TL, cm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25												
5.25	0.042											
6.25	0.324	0.190	0.008									
7.25	0.587	1.178	0.192	0.002	0.021							0.065
8.25	0.874	2.840	2.232	0.367	0.811	0.882	0.256				0.028	0.898
9.25	0.957	3.829	4.744	3.791	5.307	10.670	5.586	0.032	0.012		0.047	1.108
10.25	1.280	3.964	6.139	7.543	10.580	17.250	12.020	1.726	1.292	0.004	0.028	0.301
11.25	1.900	4.444	6.708	8.173	15.140	17.010	15.700	8.202	8.087	1.420	0.304	0.103
12.25	4.821	5.702	6.944	6.579	12.860	12.220	13.530	15.880	15.430	15.490	5.639	1.884
13.25	14.910	19.180	12.100	11.030	14.380	11.520	13.920	20.600	17.060	20.720	21.570	15.280
14.25	42.110	39.010	34.080	34.850	24.120	18.050	23.520	29.150	24.780	20.960	36.900	34.600
15.25	28.540	18.070	23.940	24.410	14.680	11.030	13.640	21.300	27.720	30.070	27.580	35.600
16.25	3.526	1.557	2.841	3.234	2.058	1.330	1.802	2.946	5.563	10.940	7.652	9.750
17.25	0.134	0.034	0.068	0.016	0.039	0.041	0.028	0.117	0.060	0.395	0.249	0.406
18.25												0.005
19.25												
20.25												
Catch	432	404	450	549	647	432	351	275	324	498	800	832
c.f.	0.690	0.664	0.696	0.684	0.663	0.636	0.642	0.673	0.709	0.722	0.736	0.720

Table 11. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1963.

Midlength (TL, cm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25												
5.25											0.006	0.015
6.25	0.009										0.230	0.320
7.25	0.431		0.596	0.043	0.255	0.056				0.298	0.909	2.292
8.25	1.964		6.143	0.861	1.136	1.154	0.366	0.036	0.067	0.448	2.500	7.561
9.25	3.086	0.009	8.364	7.331	3.336	5.569	1.643	1.036	0.614	0.163	3.672	13.120
10.25	5.010	0.773	6.970	15.440	6.388	13.030	6.699	5.325	2.184	0.601	3.257	10.980
11.25	2.569	2.114	6.498	11.800	12.220	19.470	12.230	11.020	6.018	3.878	1.371	5.712
12.25	6.867	2.365	8.277	5.990	8.780	15.520	18.680	16.490	15.740	18.990	7.039	2.491
13.25	22.460	16.360	22.540	15.700	12.000	12.290	18.360	20.110	22.720	36.500	27.540	13.410
14.25	30.930	34.800	25.730	28.450	35.180	19.680	23.660	27.300	33.460	30.030	38.190	29.980
15.25	21.630	32.160	12.480	12.120	18.580	11.080	16.040	15.540	16.540	8.158	13.650	12.630
16.25	4.924	10.900	2.322	2.185	2.065	2.050	2.298	3.008	2.591	0.844	1.621	1.446
17.25	0.116	0.522	0.077	0.087	0.060	0.099	0.026	0.136	0.067	0.093	0.012	0.054
18.25												
19.25												
20.25												
Catch	780	229	629	701	652	346	191	178	232	388	624	733
c.f.	0.681	0.660	0.657	0.704	0.708	0.481	0.680	0.653	0.656	0.730	0.732	0.731

Table 12. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1964.

Midlength (TL, cm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25												
5.25	0.038											0.001
6.25	0.881	0.297	0.007	0.004	0.013	0.010					0.100	0.257
7.25	3.342	3.017	0.348	0.030	0.270	0.659	0.175	0.009		0.089	1.110	1.795
8.25	6.573	11.670	3.149	0.487	0.250	3.483	1.377	0.303		0.158	1.206	3.790
9.25	10.310	20.800	14.180	4.108	0.654	3.589	5.254	1.645		0.030	0.801	5.381
10.25	9.197	18.580	24.800	16.290	6.831	5.099	7.478	3.230	0.116	0.000	0.337	6.993
11.25	10.710	13.200	20.890	25.960	22.680	15.540	11.490	6.745	0.293	0.098	0.061	6.879
12.25	15.140	9.954	15.190	23.620	30.220	24.770	21.220	8.780	2.203	2.058	0.999	3.337
13.25	22.640	11.750	10.650	17.590	22.870	26.660	25.850	18.420	20.110	16.300	11.770	9.555
14.25	16.410	8.518	8.098	8.852	12.190	15.880	21.370	37.910	48.240	43.760	44.530	32.110
15.25	4.400	2.094	2.520	2.916	3.735	4.026	5.171	20.190	26.050	32.940	34.440	26.160
16.25	0.266	0.120	0.159	0.226	0.288	0.281	0.506	2.719	2.949	4.438	4.575	3.677
17.25	0.003		0.003	0.004		0.003		0.0433	0.036	0.128	0.068	0.048
18.25												
19.25												
20.25												
Catch	1,026	691	996	865	657	437	417	226	237	662	895	968
c.f.	0.643	0.640	0.668	0.690	0.729	0.714	0.716	0.731	0.709	0.710	0.747	0.721

Table 13. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1965.

Midlength (TL, cm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug[a]	Sep	Oct	Nov	Dec
4.25												0.007
5.25											0.102	0.048
6.25	0.217	0.107	0.079	0.080	0.093	0.010			0.033		0.384	0.769
7.25	2.868	0.574	0.302	0.662	0.886	0.195	0.517		0.214		1.880	4.964
8.25	11.700	3.300	1.397	2.009	2.278	1.251	3.516		0.429		2.327	10.090
9.25	17.300	9.241	5.616	7.016	4.812	6.656	11.480		3,313	0.016	2.215	8.414
10.25	13.400	14.000	8.995	11.330	9.875	14.080	15.410		22.500	0.447	3.009	9.013
11.25	8.039	13.170	12.000	14.960	18.060	17.940	22.750		31.610	8.884	4.137	6.458
12.25	3.166	8.240	9.468	11.360	19.410	20.910	21.100		23.650	34.120	24.730	10.240
13.25	6.498	8.169	8.675	9.079	13.910	16.330	12.000		11.340	33.220	36.350	24.510
14.25	16.950	21.160	25.090	20.990	15.610	12.380	5.688		4.846	17.060	18.090	20.160
15.25	16.720	18.950	24.580	19.530	12.950	8.539	6.101		1.731	5.407	5.840	4.823
16.25	3.041	3.013	3.682	2.949	2.085	1.682	1.448		0.313	0.817	0.906	0.487
17.25	0.100	0.077	0.058	0.031	0.033	0.023			0.016	0.024	0.025	0.012
18.25											0.007	
19.25												
20.25												
Catch	1,037	634	1,019	760	650	486	11.4	0.00	65,1	199	629	1,146
c.f.[b]	0.690	0.618	0.642	0.643	0.635	0.632	0.683	(0.672)	0.652	0.704	0.710	0.712

[a] Month with closure of fishery *(veda)*.

[b] Condition factor in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 14. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1966.

Midlength (TL, cm)	Jan	Feb	Mar	Apr	May	Jun[a]	Jul[a]	Aug[a]	Sep	Oct	Nov[b]	Dec
4.25		0.004										
5.25	0.010	0.006										
6.25	0.566	0.250	0.017	0.013	0.015							0.040
7.25	7.840	4.840	1.128	0.920	0.220				0.008			0.466
8.25	22.780	19.670	5.912	5.232	2.209				0.027			1.421
9.25	26.400	30.880	15.440	10.470	7.939				0.053	0.051		1.386
10.25	14.680	20.210	21.360	16.080	13.720				0.099	0.076		1.116
11.25	5.958	8.057	24.140	24.780	16.540				0.209	0.244		0.159
12.25	3.418	2.445	17.650	24.120	23.760				0.396	2.412		0.048
13.25	9.855	6.017	6.844	14.520	21.720				9.468	13.780		0.936
14.25	7.047	6.093	5.747	3.484	12.160				48.800	41.400		14.950
15.25	1.290	1.306	1.576	0.339	1.644				36.630	36.140		55.610
16.25	0.144	0.214	0.184	0.035	0.035				4.264	5.777		22.980
17.25	0.005		0.006		0.005				0.038	0.125		0.884
18.25												
19.25												
20.25												
Catch	1,310	972	1,092	960	899	0.00	0.00	0.00	561	865	6.52	958
c.f.[c]	0.656	0.686	(0.664)	0.724	0.758	(0.688)	(0.692)	(0.694)	0.680	0.707	(0.691)	0.639

[a] Months with closure of fishery *(veda)*.

[b] Month with a strike *(huelga)*.

[c] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 15. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1967.

Midlength (TL, cm)	Jan	Feb	Mar	Apr	May	Jun	Jul[a]	Aug[a]	Sep	Oct	Nov	Dec
4.25												
5.25												
6.25	0.140	0.015	0.017	0.005								
7.25	1.418	3.475	2.081	1.352	0.617							
8.25	6.827	21.870	10.290	7.091	8.578	0.571						
9.25	15.190	25.780	19.360	12.000	17.700	9.706						
10.25	19.830	21.030	21.660	18.240	25.100	27.600				0.007		
11.25	10.060	10.810	14.060	22.890	20.280	23.290			0.163	0.044	0.020	0.021
12.25	1.437	2.536	7.919	17.600	14.520	17.260			17.360	5.762	2.190	0.792
13.25	1.340	0.905	3.114	7.434	7.781	13.390			35.810	38.320	29.990	9.377
14.25	8.971	3.040	2.142	2.332	2.428	6.223			29.100	31.970	38.380	34.360
15.25	24.020	6.515	12.010	5.450	0.986	1.123			15.260	19.430	24.900	45.230
16.25	10.440	3.889	7.004	5.290	1.734	0.657			1.789	3.688	4.115	9.661
17.25	0.329	0.130	0.334	0.315	0.275	0.171			0.506	0.753	0.384	0.552
18.25	0.003		0.006	0.001	0.007					0.024	0.010	0.009
19.25												
20.25												
Catch	1,506	570	876	1,210	1,082	126	0.00	0.00	232	1,109	1,238	1,365
c.f.	0.691	0.614	0.662	0.656	0.665	0.747	0.695	0.702	0.680	0.720	0.706	0.717

[a] Months with closure of fishery *(veda)*.

Table 16. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1968.

Midlength (TL, cm)	Jan	Feb	Mar	Apr	May	Jun[a]	Jul[a]	Aug[a]	Sep	Oct	Nov	Dec
4.25				0.017								0.009
5.25				0.024	0.003							0.037
6.25	0.015	0.389		0.098	0.075						0.164	0.536
7.25	1.918	2.976	0.010	0.436	0.888						0.442	3.178
8.25	17.970	6.052	3.596	1.252	3.894						0.281	7.762
9.25	22.770	24.110	17.900	4.016	7.384				0.172	0.003	0.023	10.060
10.25	10.020	26.200	24.180	7.635	17.430				1.045	0.12	–	4.961
11.25	2.809	8.030	24.580	20.740	15.900				1.249	0.513	0.094	0.878
12.25	0.658	2.259	9.528	27.800	14.800				3.582	1.901	2.595	0.174
13.25	2.376	1.146	1.722	14.700	18.690				15.320	10.480	11.010	2.370
14.25	18.880	11.860	5.681	5.473	8.894				36.770	34.820	23.800	20.420
15.25	18.920	14.280	10.020	10.810	6.330				28.620	36.760	35.660	37.550
16.25	3.481	2.565	2.655	6.554	5.171				11.100	12.840	20.800	10.690
17.25	0.176	0.120	0.127	0.423	0.538				2.084	2.506	4.956	1.366
18.25	0.001	0.002	0.006	0.006	0.006				0.049	0.056	0.177	0.011
19.25										0.005		
20.25												
Catch	1,469	900	744	1,079	952	0.00	0.00	0.00	1,246	1,242	939	880
c.f.[b]	0.681	0.665	0.674	0.728	0.692	(0.701)	(0.698)	(0.696)	0.652	0.654	0.712	0.709

[a] Months with closure of fishery *(veda)*.

[b] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 17. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1969.

Midlength (TL, cm)	Jan	Feb[a]	Mar	Apr	May	Jun[a]	Jul[a]	Aug[a]	Sep	Oct	Nov	Dec
4.25												
5.25	0.012											0.003
6.25	3.839		0.003	0.141	0.017						0.802	0.166
7.25	16.100		0.498	0.284	2.393						7.060	4.430
8.25	20.640		9.998	0.961	9.012				0.011		21.140	22.710
9.25	22.150		26.950	3.251	13.730				0.199	0.019	23.540	30.670
10.25	16.800		22.940	8.341	14.960				1.606	0.160	8.856	23.540
11.25	7.544		18.230	17.380	1.778				7.415	0.759	3.882	9.553
12.25	1.113		12.930	25.880	27.640				18.790	9.859	0.742	3.392
13.25	0.261		5.532	27.340	19.000				29.420	35.160	3.946	1.109
14.25	2.221		1.013	10.700	8.395				26.220	34.240	12.740	1.364
15.25	5.741		0.959	2.299	1.513				13.310	17.610	14.660	2.336
16.25	3.151		0.863	2.599	1.049				2.093	1.848	2.445	0.700
17.25	0.401		0.075	0.761	0.450				0.878	0.342	0.165	0.032
18.25	0.022		0.001	0.061	0.065				0.057	0.011	0.012	
19.25												
20.25												
Catch	1,226	0.00	1,762	1,232	790	0.00	0.00	0.00	482	470	373	1,802
c.f.[b]	0.659	(0.666)	0.633	0.686	0.797	(0.661)	(0.682)	(0.683)	0.677	0.639	0.675	0.652

[a] Months with closure of fishery *(veda)*.

[b] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 18. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1970.

Midlength (TL, cm)	Jan	Feb	Mar	Apr	May	Jun	Jul[a]	Aug[a]	Sep	Oct	Nov	Dec
4.25												
5.25												
6.25	0.003			0.006	0.013							0.394
7.25	0.157	0.050	0.126	0.820	0.121						0.044	2.130
8.25	4.637	1.372	0.773	6.756	0.223						0.067	11.600
9.25	24.270	10.530	1.653	13.340	2.936				0.013	[illegible]	0.067	15.830
10.25	36.790	25.190	17.360	16.030	12.780	0.047			0.177	0.010	0.047	9.244
11.25	20.640	30.520	23.510	18.000	20.580	3.198			0.765	0.122	0.023	2.182
12.25	7.415	15.720	25.270	19.100	19.790	17.830			2.580	0.401	0.584	0.517
13.25	2.857	7.362	19.490	15.230	23.480	38.900			7.557	4.483	8.390	6.420
14.25	1.224	3.167	7.809	7.344	15.620	28.930			20.140	23.400	27.510	19.760
15.25	1.469	3.827	2.929	2.542	3.747	9.784			37.830	43.140	35.910	17.990
16.25	0.510	2.169	0.975	0.780	0.580	1.223			26.930	25.140	23.050	11.460
17.25	0.020	0.098	0.105	0.046	0.080	0.094			4.280	3.220	4.116	2.360
18.25				0.003					0.168	0.074	0.189	0.108
19.25												
20.25												
Catch	1,998	986	995	1,900	830	40.8	9.81	0.00	1,178	1,267	995	731
c.f.[b]	0.627	0.671	0.717	0.675	0.693	(0.678)	(0.688)	(0.687)	0.708	0.732	0.738	0.755

[a] Months with closure of fishery *(veda)*; catch for July mainly from surveys.

[b] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 19. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1971.

Midlength (TL, cm)	Jan[a]	Feb[a]	Mar	Apr	May	Jun	Jul[a]	Aug[a]	Sep	Oct	Nov	Dec
4.25												
5.25												
6.25				0.009								
7.25			0.089	0.138								
8.25			1.954	1.024	0.008	0.015						
9.25			5.931	5.418	1.799	0.392			0.018			
10.25			13.150	14.630	8.110	2.249			1.094	0.018		
11.25			24.000	27.020	27.130	17.190			6.769	0.408		
12.25			24.100	28.250	33.770	37.590			21.050	4.800	0.108	0.046
13.25			18.780	16.460	16.760	22.240			32.410	16.360	2.586	5.133
14.25			5.609	4.916	6.593	11.760			26.780	38.710	27.360	23.070
15.25			1.711	0.852	2.444	4.831			9.543	31.070	49.200	47.320
16.25			2.902	0.538	1.599	2.437			1.543	6.582	18.880	21.750
17.25			1.683	0.662	1.661	1.219			0.696	1.787	1.644	2.440
18.25			0.078	0.087	0.128	0.073			0.097	0.263	0.228	0.247
19.25												
20.25												
Catch	0.00	0.00	2,366	1,453	636	92.0	0.00	0.00	1,118	1,229	1,066	1,224
c.f.[b]	(0.674)	(0.665)	0.646	0.609	0.626	0.615	(0.676)	(0.676)	0.669	0.713	0.761	0.726

[a] Months with closure of fishery *(veda)*.

[b] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 20. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1972.

Midlength (TL, cm)	Jan[a]	Feb[a]	Mar	Apr	May	Jun	Jul[b]	Aug[b, c]	Sep[b, c]	Oct[b, c]	Nov[b]	Dec
4.25												
5.25												
6.25			0.107							0.440		
7.25			0.100	0.136	0.017					0.396		0.168
8.25			0.175	0.888	0.729					0.106		1.344
9.25			0.119	1.632	5.316	0.368				–		4.370
10.25			2.936	1.289	12.610	7.042		0.468		–		7.395
11.25			6.444	2.030	12.850	27.690		4.062	0.010	0.387		6.723
12.25			2.276	2.427	16.280	30.080		41.880	4.156	1.945		3.193
13.25			1.337	2.704	17.370	17.430		42.220	19.330	3.547		5.714
14.25			7.869	6.497	9.736	7.115		6.417	19.390	2.200		13.280
15.25			35.520	36.140	14.520	4.899		2.131	17.720	15.390		42.020
16.25			35.710	39.480	9.084	4.440		1.645	5.824	16.790		14.620
17.25			7.023	6.576	1.429	0.837		0.940	25.580	43.400		1.176
18.25			0.381	0.193	0.069	0.101		0.232	7.988	15.400		
19.25				0.011								
20.25												
Catch	7.53	0.789	1,653	1,359	342	145	0.00	0.00	0.00	0.00	0.00	13.8
c.f.[d]	(0.670)	(0.650)	0.662	0.582	0.626	0.647	(0.645)	(0.656)	(0.667)	(0.666)	(0.663)	(0.777)

[a] Months without samples *(sin muestreo)*; catches refer to Callao only; the fishery was closed further north *(veda)*.

[b] Months with closure of fishery *(veda)*.

[c] % catch-composition data obtained from EUREKA surveys.

[d] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 21. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1973.

Midlength (TL, cm)	Jan^{a,b}	Feb^{b}	Mar	Apr	May^{b}	Jun^{a,b}	Jul	Aug^{a,b}	Sep^{a,b}	Oct^{b}	Nov^{a,b}	Dec^{b}
4.25						54.250					0.035	
5.25						43.780	0.467				1.133	
6.25			0.001			1.758	0.939				1.626	
7.25	2.652		0.017	0.028		0.011	0.962				3.301	
8.25	24.770		0.470	0.119		0.021	5.965	0.095			3.854	
9.25	36.280		3.515	0.154		0.012	70.860	0.318			2.138	
10.25	27.860		7.735	1.063		0.003	14.220	2.229	0.381		1.136	
11.25	7.956		14.760	3.197		–	3,022	20.240	2.796		0.424	
12.25	–		23.350	10.020		0.003	0,472	37.420	16.310		0.045	
13.25	–		29.890	27.100		0.009	1.150	34.570	36.280		0.136	
14.25	–		13.430	43.030		0.116	1.224	4.349	36.060		2.928	
15.25	–		4.902	12.540		0.065	0.502	0.532	7.254		36.560	
16.25	0.069		1.794	2.182			0.199	0.015	0.873		43.130	
17.25	0.138		0.134	0.546			0.017	0.232	0.038		3.503	
18.25	0.276		0.003	0.021							0.055	
19.25												
20.25												
Catch	0.00	0.00	1,193	357	0.00	0.00	0.00	3.33	20.2	12.6	36.2	0.00
c.f.^{c}	(0.624)	(0.626)	0.751	0.722^{d}	(0.682)	(0.690)	(0.696)	(0.701)	(0.699)	(0.694)	(0.685)	(0.692)

[a] Percent catch-composition data obtained from EUREKA surveys (January, September and November), "Prospeccíon Pesquera" (June and July) and "Exploracíon y Prospeccion Pesquera" (August).

[b] Months with closure of fishery *(veda);* catches mainly from surveys (August, September and October).

[c] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

[d] "Real" value was 0.927, which is far too high to be correct and was therefore replaced with an interpolated value representing the mean of itself, the preceeding and following values, and the values for April 1972 and April 1974.

Table 22. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1974.

Midlength (TL, cm)	Jan^{b}	Feb^{a,b}	Mar	Apr	May	Jun^{b}	Jul^{b}	Aug^{a,b}	Sep^{a,b}	Oct	Nov	Dec^{b}
4.25									26.810			
5.25								0.043	37.640			
6.25								0.823	19.620			
7.25			0.027	0.028				5.438	8.442			
8.25			0.304	0.421	0.154			4.029	3.092		0.066	
9.25			0.918	2.607	0.858			1.906	3.508		0.144	
10.25			3.177	8.929	2.696			0.433	0.892		0.126	
11.25		5.088	7.082	12.410	4.663			0.178		0.011	0.036	
12.25		27.680	14.910	9.663	5.156			0.022		0.006	0.006	
13.25		20.260	20.940	11.950	13.140			0.780		0.536	0.042	
14.25		9.053	12.040	14.750	19.450			0.802		9.811	3.225	
15.25		1.651	7.677	8.721	13.430			6.282		25.400	35.470	
16.25		12.520	12.390	8.071	10.480			8.860		23.930	37.350	
17.25		20.650	18.170	18.640	23.840			36.610		20.400	13.230	
18.25		3.092	2.341	3.792	6.091			32.320		18.750	9.123	
19.25			0.009	0.010	0.077			1.473		1.141	1.165	
20.25											0.012	
Catch	0.00	0.104	497	869	481	0.00	0.00	0.00	33.5	623	534	0.00
c.f.^{c}	(0.686)	(0.674)	0.718	(0.667)	(0.670)	(0.665)	(0.680)	(0.688)	(0.695)	0.740	0.748	(0.693)

[a] Percent catch-composition data obtained during EUREKA (August and September) and CATEO (February) surveys.

[b] Months with closure of fishery *(veda);* catches mainly from surveys (February and September).

[c] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 23. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1975.

Midlength (TL, cm)	Jan	Feb	Mar	Apr	May	Jun[a]	Jul[a]	Aug[a]	Sep[a]	Oct[b]	Nov[a]	Dec[c]
4.25												
5.25												
6.25		0.036										
7.25	0.026	0.127	0.022		0.005							5.556
8.25	0.642	0.555	0.069	0.036	0.024							5.556
9.25	3.604	1.074	0.259	0.209	0.267							
10.25	11.320	6.438	0.735	0.554	1.300							
11.25	19.360	27.110	7.358	2.300	1.820							
12.25	23.190	31.950	21.580	13.140	4.556							
13.25	8.976	19.820	28.930	30.470	20.640					0.483		
14.25	1.704	6.999	21.840	32.090	37.980					5.797		
15.25	9.081	2.214	7.539	11.200	20.890					28.980		5.556
16.25	13.020	2.232	7.008	5.912	6.599					46.380		50.000
17.25	6.827	1.170	3.715	3.236	4.348					15.460		33.332
18.25	2.202	0.272	0.922	0.824	1.499					2.415		
19.25	0.039		0.028	0.030	0.068					0.483		
20.25												
Catch	174	305	823	799	536	12.0	0.00	0.00	0.00	7.62	0.00	9.47
c.f.[d]	0.742	0.740	0.696	0.705	0.697	(0.687)	(0.689)	(0.695)	(0.696)	0.735	(0.700)	(0.692)

[a] Months with closure of fishery *(veda)*; catches mainly from surveys (June).
[b] Catch and % frequencies refer to northern region only (*veda* in central region).
[c] % frequencies refer to northern region only.
[d] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 24. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1976.

Midlength (TL, cm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug[a, b]	Sep[b]	Oct	Nov	Dec
4.25												
5.25												
6.25												0.017
7.25	0.025		0.027	0.004		0.002	0.025					0.227
8.25	0.311	0.116	1.385	1.343	0.269	0.822	0.431	0.001				0.796
9.25	2.612	2.214	15.080	17.450	7.676	14.470	7.705	1.886		0.537		0.414
10.25	9.523	15.030	29.680	34.210	22.980	31.900	29.350	8.050		6.759		2.697
11.25	23.590	18.450	24.130	25.530	24.620	22.370	30.200	26.670		13.040	0.541	8.417
12.25	25.640	10.170	17.150	12.550	17.110	10.340	14.270	34.600		16.360	8.033	9.544
13.25	11.820	3.534	6.995	4.556	11.330	8.599	8.684	17.910		23.820	15.850	15.390
14.25	2.252	0.971	1.371	1.030	7.062	6.292	5.229	6.256		22.980	32.370	22.530
15.25	1.032	1.942	0.297	0.292	2.121	1.925	1.915	1.196		12.540	33.530	28.080
16.25	6.127	16.500	0.499	0.401	1.436	0.751	0.616	0.006		2.207	7.481	9.726
17.25	13.180	25.160	2.085	1.589	3.509	1.684	1.102	0.562		1.093	1.706	1.652
18.25	3.695	5.825	1.210	0.979	1.770	0.790	0.462	2.856		0.616	0.470	0.475
19.25	0.187	0.078	0.091	0.061	0.116	0.056	0.012	0.007		0.040	0.011	0.033
20.25			0.086	0.001								
Catch	263	50.9	348	573	318	515	144	0.00	0.00	77.9	390	353
c.f.[c]	0.656	0.622	(0.643)	0.548	0.576	0.542	0.548	(0.665)	(0.680)	0.638	0.688	0.677

[a] Percent catch-composition data obtained from EUREKA surveys.
[b] Months with closure of fishery *(veda)*.
[c] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 25. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1977.

Midlength (TL, cm)	Jan	Feb[b]	Mar[a, b]	Apr	May	Jun[b]	Jul[b]	Aug[b]	Sep[b]	Oct[a, b]	Nov[a, b]	Dec[b]
4.25											6.134	
5.25			0.011								44.800	
6.25	0.013		0.127								23.110	
7.25	1.564		0.325	0.007	0.012						16.680	
8.25	8.791		0.005	0.042	0.021						5.925	
9.25	13.050		0.032	0.430	0.280						1.753	
10.25	14.510		1.488	2.206	1.936						0.560	
11.25	15.340		22.880	6.487	5.132						0.136	
12.25	7.424		49.860	15.060	11.570						0.001	
13.25	8.643		20.120	24.570	19.190						0.001	
14.25	11.600		3.848	31.620	40.170						0.117	
15.25	13.110		1.053	15.530	17.420					22.590	0.222	
16.25	4.895		0.140	3.673	3.608					56.980	0.276	
17.25	0.897		0.000	0.301	0.593					19.340	0.257	
18.25	0.154		0.012	0.059	0.060					1.093	0.015	
19.25			0.103	0.014	0.012							
20.25												
Catch	184	0.00	0.80	265	130	0.00	0.00	0.00	0.00	0.00	0.00	0.00
c.f.[c]	0.531	(0.651)	(0.650)	0.650	0.668	(0.674)	(0.680)	(0.686)	(0.690)	(0.690)	(0.684)	(0.678)

[a] Percent catch-composition data obtained from EUREKA (October), CRUCERO 7703 (March) and CRUCERO SNP-1-ICANE (November).
[b] Months with closure of fishery (*veda*); catch for March mainly from surveys.
[c] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 26. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1978.

Midlength (TL, cm)	Jan[a]	Feb	Mar[a]	Apr	May	Jun	Jul	Aug[a]	Sep	Oct[b]	Nov	Dec
4.25												
5.25												
6.25		0.002										
7.25		–			0.004							
8.25		0.058		0.008	0.144							
9.25		0.529		1.039	1.475	0.010						
10.25		8.119		10.330	5.303	1.110	0.330		2.621			
11.25		32.820		27.050	18.740	7.845	17.810		27.080			
12.25		41.540		34.440	33.390	31.380	44.180		36.000	5.767	0.069	
13.25		15.440		20.550	26.350	44.180	28.010		16.280	23.100	4.972	2.869
14.25		0.383		5.654	10.790	13.560	8.021		14.520	49.430	29.590	33.070
15.25		0.134		0.509	2.380	1.693	1.322		2.474	19.130	42.240	45.790
16.25		0.523		0.274	1.048	0.206	0.333		0.906	2.576	20.040	15.960
17.25		0.454		0.143	0.313	0.011			0.122		2.926	2.132
18.25				0.000	0.008	0.002					0.150	0.185
19.25												
20.25												
Catch	0.00	49.7	0.00	81.0	84.4	91.4	45.7	0.00	0.52	0.26	20.2	207
c.f.[c]	(0.676)	0.521	(0.657)	0.588	0.574	0.503	0.569	(0.697)	0.633	0.630	0.643	0.656

[a] Months with closure of fishery (*veda*).
[b] Catch and % frequencies refer only to central region; fishery was closed further north (*veda*).
[c] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 27. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1979.

Midlength (TL, cm)	Jan[b]	Feb[b]	Mar	Apr	May[b]	Jun[b]	Jul[b]	Aug[b]	Sep[a, b]	Oct	Nov	Dec[b]
4.25												
5.25												
6.25			0.006							0.017		
7.25			0.067							0.866		
8.25			1.537	0.069						–		
9.25			2.128	2.252						–		
10.25			3.878	9.997						0.356		
11.25			5.430	16.870						6.088		
12.25			5.394	16.360					4.625	20.720	0.580	
13.25			10.150	11.250					21.850	11.460	1.534	
14.25			29.500	17.700					26.300	15.850	8.375	
15.25			30.180	17.120					14.590	26.190	38.560	
16.25			10.000	6.688					26.920	15.590	44.910	
17.25			1.635	1.614					4.104	2.557	5.489	
18.25			0.094	0.083					1.614	0.237	0.544	
19.25									0.000			
20.25												
Catch	0.00	0.00	258	603	0.00	0.00	0.00	0.00	0.00	66.1	26.8	0.00
c.f.[c]	(0.671)	(0.671)	0.620	0.583	(0.673)	(0.683)	(0.682)	(0.682)	(0.686)	0.581	0.595	0.673

[a] Percent catch-composition data obtained from EUREKA surveys for northern region only (*veda* in central region).

[b] Months with closure of fishery (*veda*).

[c] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 28. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1980.

Midlength (TL, cm)	Jan[a]	Feb[a]	Mar[a]	Apr[b]	May	Jun	Jul[a]	Aug[a]	Sep[a]	Oct[a]	Nov[a]	Dec
4.25												
5.25												
6.25												0.007
7.25												0.219
8.25												1.547
9.25												2.664
10.25					0.173							2.737
11.25				1.247	4.596	0.438						2.511
12.25				3.582	22.530	12.084						2.102
13.25				15.870	28.580	26.370						3.410
14.25				25.300	17.330	24.320						11.590
15.25				19.970	14.500	18.520						31.070
16.25				28.490	11.320	17.010						30.610
17.25				5.544	0.950	1.035						10.510
18.25					0.020	0.224						1.010
19.25												0.007
20.25												
Catch	0.00	0.00	0.00	0.33	123	26.6	0.00	0.00	0.00	0.00	0.00	45.0
c.f.[c]	(0.670)	(0.668)	(0.662)	0.463	0.610	0.561	(0.681)	(0.688)	(0.690)	(0.690)	(0.687)	0.766

[a] Months with closure of fishery (*veda*).

[b] Catch and % frequency refer to central region only; fishery was closed further north (*veda*).

[c] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 29. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1981.

Midlength (TL, cm)	Jan[a]	Feb[a]	Mar[a]	Apr	May	Jun	Jul[a]	Aug[a]	Sep[a]	Oct[a]	Nov	Dec
4.25												
5.25												
6.25												
7.25												0.006
8.25												0.024
9.25				0.326	0.023							0.022
10.25				0.268	0.025							0.017
11.25				0.400	0.068	0.034						0.006
12.25				10.400	4.034	1.683						0.004
13.25				35.530	20.240	17.440						0.011
14.25				24.510	25.090	27.280					1.036	0.231
15.25				9.191	12.990	17.230					19.690	6.980
16.25				11.300	22.900	22.580					51.800	51.330
17.25				7.551	14.020	13.240					25.550	38.150
18.25				0.528	0.612	0.522					1.917	3.173
19.25					0.001							0.048
20.25												
Catch	0.00	0.00	0.00	27.6	53.2	51.2	0.00	0.00	0.00	24.8	9.15	118
c.f.[b]	(0.682)	(0.668)	(0.671)	0.649	0.656	0.613	(0.688)	(0.688)	(0.694)	(0.686)	(0.687)	0.763

[a] Months with closure of fishery *(veda)*; catch in October mainly from surveys.

[b] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Table 30. Monthly catch and percent catch composition of Peruvian anchoveta (*E. ringens*, northern/central stock, 4-14°S) based on data collected by IMARPE staff in 1982.

Midlength (TL, cm)	Jan[a]	Feb	Mar	Apr	May	Jun	Jul	Aug[a]	Sep[b]	Oct[c]	Nov	Dec[b]
4.25												
5.25												
6.25												
7.25											0.468	
8.25											3.490	
9.25											4.335	
10.25											0.582	
11.25		0.195									0.118	
12.25		0.069	0.070		0.046	0.735	0.534				–	
13.25		0.023	0.758	0.039	0.791	5.164	0.952			0.075	–	
14.25		0.401	3.166	0.772	3.473	7.313	4.931			2.146	1.223	
15.25		5.922	4.422	4.651	9.208	9.181	38.380			3.604	5.298	
16.25		35.690	29.900	21.790	18.160	16.260	42.260			11.570	19.720	
17.25		50.510	52.940	59.090	62.730	46.910	11.000			51.130	43.240	
18.25		7.354	8.656	13.520	5.462	14.140	1.897			29.990	20.990	
19.25		0.102	0.091	0.136	0.136	0.300	0.054			1.483	0.536	
20.25												
Catch	0.00	48.8	146	185	208	196	279	0.00	2.62	16.4	54.0	72.0
c.f.[d]	(0.680)	0.675	0.738	0.720	0.810	0.673	0.846	(0.680)	(0.681)	(0.663)	(0.637)	(0.619)

[a] Months with closure of fishery *(veda)*.

[b] Months without samples *(sin muestreo)*; catches mainly from surveys.

[c] % frequencies refer to northern region only (*sin muestreo* for central region).

[d] Condition factors in brackets estimated from the linear relationship between temperature and condition factor in Palomares et al. (this vol.).

Estimation of Unregistered Peruvian Anchoveta *(Engraulis ringens)* in Official Catch Statistics, 1951 to 1982*

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CASTILLO, S. and J. MENDO. 1987. Estimation of unregistered Peruvian anchoveta *(Engraulis ringens)* in official catch statistics, 1951 to 1982, p. 109-116. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

The causes of underreporting in the Peruvian fishery for anchoveta *(Engraulis ringens)* are discussed. Estimates of this underreporting were obtained for each step in the catch-landing-processing chain from standardized interviews of 40 informants with professional experience in that fishery ranging from deckhand to fleet manager, and from worker in processing plant to plant manager. The interviews led to an aggregate figure of over 20% of fish caught in excess of official catch statistics, much more than previously assessed. This figure is confirmed by an analysis of production figures from processing plants which contrasts reported, low reduction coefficients (i.e., fish meal/fish processed) with their actual, high values.

Introduction

The Peruvian coast is characterized by a high primary production and by high fishery catches and indeed, during the 1960s and early 1970s, the Peruvian upwelling system supported the largest fishery in the world. At the peak of the fishery landings, anchoveta *(Engraulis ringens)* contributed one-sixth of all fish caught in the world and in 1970 Peru became, as far as bulk catches are concerned, the leading fishing nation in the world.

Before, during and after these peak landings, numerous irregularities occurred which contributed to the catches and landings being underestimated (Fig. 1).

IMARPE (1970) reported on this as follows:

> "There are [...] several ways in which those reported statistics may be misleading.
>
> The reported landings are less than the true catches for several reasons, e.g.:
>
> a) losses at sea, including dumping of excess catch
>
> b) losses at unloading
>
> c) underreporting of actual quantities landed (especially during the peladilla season when meal yield is low).
>
> Information presented suggested that occasionally these losses could be large, perhaps 40% of the reported landings. There are no data on how this proportion has changed during the history of the fishery, although [there are indications] that it has probably been rather constant, at least in

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*PROCOPA Contribution No. 36.

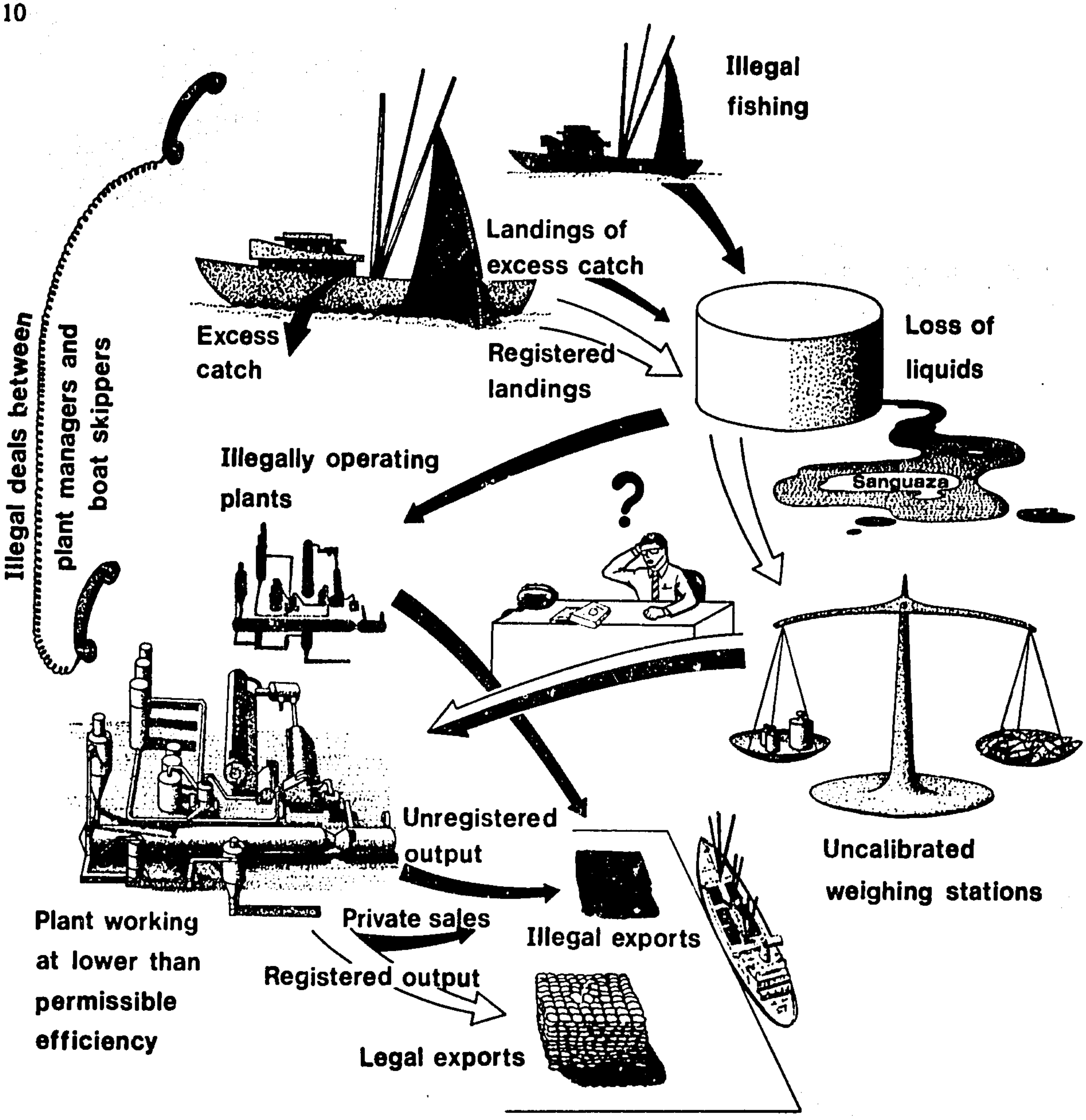

Fig. 1. Schematic representation of major causes of anchoveta catch underreporting in the Peruvian reduction fishery, with emphasis on the *pesca negra* (arrows not to scale; see text for quantitative information).

> recent years. Type (a) losses may likely have decreased, but types (b) and (c) most probably have increased as more peladilla are now being taken.
>
> If the ratio of actual to reported catch has remained constant the analysis of sustainable yield, etc., will be little affected, except that all figures of catch, etc. are underestimated by a constant factor. The estimates of maximum sustained yield and permissible quota, etc., will then be correct guides for management provided that the future catches are also underestimated by the same amount. However, it is most desirable that records could be made of the true removals from the stocks by the fishery."

Vasquez and Lam (1977) attempted to estimate the percentage of anchoveta caught that was not reported in official catch statistics and obtained a value of 12%. They also mentioned that "some people" believed a figure of 20-30% to be more realistic.

The objective of this work is to provide a reassessment of these figures, and thus to contribute to the estimation of actual catches of anchoveta, for the period 1953-1982.

Brief Historical Review of Anchoveta Fishery Management

Although the anchoveta fishery began in the early 1950s, the anchoveta "boom" began in the mid-1960s. In 1968, the number of boats reached a total of 1,500, with an estimated fishing capacity of 26 million tonnes per annum (see Aguero, this vol.). These metal boats were more effective than their smaller wooden predecessor because of the use of new, superior purse seines, hydraulic and/or mechanized winches, power blocks, etc.

The rapid growth of the fishery led, in the 1960s to the first management interventions by the Ministry of Agriculture and Fisheries (later Ministry of Fisheries), based on recommendations from IMARPE. Chronologically, these interventions may be summarized as follows:

- 1950s: totally uncontrolled fishery, start of research,
- 1960s: intensification of research, first recommendations by IMARPE regarding the need to control effort,
- 1965: prohibition to land catches if 50% or more of the catch consists of fish of 12 cm or less. Also, boats are prohibited to utilize more than 70% of their hull capacity. Introduction of a fishing week of 5 days (Monday to Friday), with the intention of reducing catches by 8%,
- 1966: introduction of closed seasons (see Tsukayama and Palomares, this vol.),
- 1971: imposition of production guidelines for processing plants,
- 1973: creation of the state-owned firm PESCAPERU through nationalization of assets previously held privately.

The creation of PESCAPERU followed the collapse of the fishery in 1972 (Tsukayama 1982 and see other contributions in this vol.) and a major decline of the world market for fish meal (see Aguero, this vol.). Also, large quantities of sardines *(Sardinops sagax)*, mackerels *(Scomber japonicus)* and horse mackerels *(Trachurus murphyi)* appeared off Peru, partly replacing the anchoveta.

At this time, a piece of legislation was passed which separated the fishing industry into two subsectors: the industrial fishery, based exclusively on the anchoveta, which was to continue producing fish meal, and the fishery for human consumption, based on sardine, mackerel and horse mackerel. The latter fishery, which was to produce fish for the canning industry, was to be conducted with assets (boats, nets, etc) originally used for catching anchoveta.

What happened, however, is that the reduction plants processed large quantities of sardines into fish meal. Some reduction plants, on the other hand labelled themselves "canning plants", and continued to process anchoveta into fish meal.

Material and Methods

The structured interviews which form the basis of the present contribution were conducted between March and April 1985. The persons interviewed were former crew members and captain of the purse seiners fleet, administrative personnel and employees of reduction plants (see Table 1). Overall, 40 persons were interviewed, all in the area between Puerto Chicama (7°S) and Callao (12°S). All interviewees had a good educational level and a long experience in the anchoveta fishery. The interviewees were assured they would remain anonymous. The first author, who conducted the interviews, has himself a long professional experience in the fishery, and hence felt he could elicit truthful answers even to "difficult" questions.

The questions asked pertained to the following items:

1) Week-end fishing and respect of seasonal bans,
2) Excess fishing with regard to (actual and/or legal) boat capacity,
3) Weight loss of anchoveta as blood (*sanguaza*),
4) Anchoveta weighed without control in the containers of the factory; use of clandestine pipelines and/or illegal weights and measures,
5) Deals between boat owners and plant managers,
6) Irregular sales of anchoveta.

The mean figures obtained from the interviews were used to correct nominal catches. These

Table 1. Basic information on age and career development of 40 informants on the Peruvian anchoveta fishery, 1953 to 1982.

INFORMANT #	A	B	C	D	E	F	G	H	I	J	K	L	M
1	O	O	P								52	33	27
2	O	O	O		P						51	38	25
3	O	O	P								50	32	20
4	O	O	P								44	27	24
5	O			P							55	32	8
6	O	O	P								48	36	25
7	O	O	P								46	35	25
8	O			P							47	24	22
9	P			O							40	21	21
10				P							50	19	10
11	O	O	O		P						51	34	14
12	O	P	O			P					47	28	25
13	O	O	O								49	25	6
14	O	O	P								34	22	6
15	O	O	P								44	27	20
16	O	O	P								43	25	12
17	O	O	O								64	26	20
18	P										50	21	9
19	P			O							41	23	15
20	O	O	O		O	P	P				43	25	14
21						P	O				61	38	20
22	O	O	P								40	25	15
23	O	O		O							51	34	20
24	O	O	P								53	29	15
25	P	O	O								51	34	27
26	O	R									69	40	25
27	P	O									55	29	23
28	P										42	25	16
29	O	P		O							48	24	17
30	O	O	O		P						44	31	25
31	O	O	P								49	24	18
32	O	O	R								42	22	15
33	P										50	25	23
34	P										45	20	18
35	O	P									57	30	20
36										P	44	25	19
37									O	P	53	30	22
38						P	P	O	O		48	22	15
39								O	O	P	51	24	16
40										P	48	24	17

Legend:

O - former occupation *(cargos desempenados)*
P - present occupation *(ocupacion actual)*
R - Occupation just prior to retirement *(juvilado)*

Column

A - crew member on purse seiner *(delegado y/o tripulante)*
B - assistant of captain *(segundo patron)*
C - captain of purse seiner *(patron)*
D - mechanic in purse seiner *(motorista)*
E - assistant of fleet manager, or fleet manager *(asistente y/o jefe de flota)*.
F - owner of purse seiner (fleet) *(armador)*
G - middleman *(comercializador)*
H - worker in processing plant *(obrero de planta)*
I - clerk in processing plant *(empleado de planta)*
J - processing plant manager *(jefe de planta)*
K - age of informant *(edad del encuestado)*
L - years in the fishing sector *(tiempo de actividad en el sector pesquero)*
M - years in the anchoveta fishery *(tiempo de actividad en la pesca de anchoveta)*

corrected catches were used to re-estimate reduction coefficients (landed catch/fish meal produced) and conversion efficiency (fish meal produced/total catch) for the anchoveta fishery as a whole.

Results

Table 1 summarizes basic information on the 40 interviewees. As might be seen, their ages ranged between 34 to 69 years, with a professional experience in the fishery sector of 19 to 40 years, of which 6 to 27 years were in the anchoveta fishery. A high percentage of the informants were crewmen, assistant of captains, or captain of purse seiners. The following summarizes the available information, by item as in the text above and in Table 2.

1) Twenty-three (58%) informants stated that they had respected the ban on weekend fishing enforced since 1965. All informants appeared to have more or less respected seasonal fishing bans (*vedas*), whether long or short (this item is not included in Table 2).

2) Estimates of discard of fish at sea that had been caught in excess of hold capacity ranged from 5 to 15% with an average of 9.13%. Several boats sank because they were overloaded.

3) The estimates of loss of fish as liquid (blood, liquified muscle protein, etc) during transport from fishing to processing plant ranged from 4 to 10% with a mean of 4.91%.

4) Underestimation through misreporting after weighing in processing plants, the use of fraudulent weights and measures and related irregularities were assessed as ranging from 5 to 20%, with a mean of 16.13%. We believe that our respondents overestimated this effect, which Vasquez and Lam (1977), on the other hand, considered to result in an underreporting of 5%. In this contribution, an intermediate value of 10% will be assumed for this step in the processing chain.

5) Deals between boat owner and plant manager refer especially to the illegal landing of *peladilla* (i.e., fish under 12 cm) and/or catches in excess of 70% boat capacity (see above). Such deals also refer, however, to discounting of landed weight of fish because of their bad quality. The estimates of the effect of such deals on catch estimation ranged between 1 and 10% with a mean of 4.38%.

6) Irregular sale of anchoveta refer according to Vasquez and Lam (1977) to sales made by the crew of a boat, without the boat owner being aware of the transaction. We consider here, however, the far more important aspect of irregular sale, called *pesca negra*, i.e., the reporting of anchoveta catches under another species name (i.e., as sardines, mackerel or horse mackerel). Irregular sale as defined here is reported to have involved 2-10% of the catch, with a mean of 4.11% before and 6.23% since 1975. A mean of 5% is used for the period 1951 to 1982.

The percentages presented above were then used to estimate actual from nominal catches, as shown on Table 3 (columns A and D).

Discussion

The first question to be discussed here relates obviously to the trustworthiness of our informants and to the precision of their estimates. All we can suggest here is that these informants as a group appears to be broadly representative of the fishery, and that we have no reason to assume they would have lied to us. However, not being trained in interviewing techniques, we cannot exclude the possibility of having posed some "leading" questions, or unwittingly nudged our respondent toward values within a range we considered reasonable. More important however might be the possibility of personal biases affecting our respondents' recollections, as was probably the case with regard to item #4.

Moreover, it is important to realize that the mean percentages presented here cannot really be generalized for all the years, seasons or months because they varied depending on factors only some of which were considered here (e.g., fishing regulations, see above) while some are not explicitly considered (e.g., the absolute and relative abundance of sardines and anchoveta).

Throughout the period 1951 to 1982, however, all irregularities discussed and quantified here did occur (as they presently do in the sardine fishery) although not all at the same time.

Table 2. Estimate by our informants of "losses" in the Peruvian anchoveta reduction fishery, by source of "loss". The corresponding estimates presented by Vasquez and Lam (1977) are given for comparison.

INFORMANT #	(1)	(2)	(3)	(4)	(5)	(6)	
						BEFORE 1975	SINCE 1975
1	no	10	4	15-20	5		5-10
2	yes	10	4	20	5	5	2
3	yes	5	4	15-20	5-10		
4	yes	5	4	20		5-10	3
5	no	5	6	20	5	6	
6	no	10	5-6	15	5		
7	no	10	5-6	10-15	5		
8	yes	10	7	15-20	3	3	5-10
9	yes	10	5	15-20	4	3	5-10
10	yes	10-15	3	10-15	5-10		
11	no	10	5	20	4		
12	yes	5	5	15-20	5-10		
13	no	15	4	20	2		
14	yes	10	5	15-20	5		
15	yes	10	4	15	5		
16	no	5-10	5	15-20	3		
17	no	10-15	4	15-20	5		
18	yes	5	4	15-20			
19	no	10	3	15	3		
20	no	15	4	15-20	5		
21	yes	10-15	3	20	5		10
22	yes	10	8	10-15	3		15
23	no	10	6	20	1-2		
24	yes	10-15	5	10-15	3		
25	no	10	4	10	3	2	
26	yes	5	4	20-25	5		
27	yes	5	8	20	5		3
28	no	7	4	10-15	5	2	
29	yes	5	4	10-15	3		
30	yes	5-10	5-10	0	5	5	3
31	yes	10	5	10-15	5	5	
32	yes	10	5	20		2-5	
33	no	10-15	5-6	5-6	3		
34	no	10	6	10	3		
35	no	5	6	10-15	5	2-3	
36	yes			15	4	2	5
37	yes			15	3		
38	yes			15-20	6	3	
39	yes			15	2-3		
40	yes			10-15	5-6	8	5
Mean		9.13	4.91	16.13	4.38	4.1	6.23
95% confidence interval		8.1- 10.1	4.5- 5.5	15.0- 17.2	3.9- 4.9	3.5- 4.7	3.9- 8.5
Estimates of Vasquez and Lam (1977)		5	4-5	5	0.5	0.5	0.5

1) Answers to question "did you respect the regulation stating that you should not fish on Saturdays and Fridays? (since 1965).
2) % catch in excess of storage room capacity (released dead or dying after capture by purse seine).
3) % loss of catch due to losses of "blood" (incl. liquefaction of entire fish) during storage and transport.
4) % "losses" due to misreporting after weighting in processing plants to illegal pipelines tapping the plant fish transport system and to use of fraudulent weights and measures.
5) % "losses" due to illegal deals between plant managers and fleet owners.
6) % "losses" due to illegal and unregistered sales of fish (in part to clandestine processing plants).

Thus, excessive fishing - in relation to storage capacity - occurred in the 1950s because the boats did not have echo sounders, hence the likely catch from a given purse seine set could not be estimated ahead of time.

On the other hand, the abundance of anchoveta and the fact that the boats could land their catch without having to wait at the harbor allowed fishing to proceed systematically, without undue haste. We believe therefore that in the early 1950s, excessive fishing (item #2 in our list) may have been less prevalent than in the period from 1961 to 1973, because when the number of vessels increased, port waiting time also increased, leading to a reduced willingness to spend

Table 3. Basic statistics on the Peruvian reduction fishery for anchoveta 1953-1982. Based on nominal landings and fish meal production figures in Tilic (1963a) in MIPE (1977-1979) and unpublished data held at IMARPE. Corrected fish landings and estimated catch were computed using the raising factors given in the text. Also see text for discussion of reduction coefficients (columns F and G) and of gross conversion efficiency (column H). Column A to E are t x 10^3/year.

Year	Estimated catch A	Corrected landings (= landings + "blood" losses) B	Corrected fish landings C	Nominal landing D	Fish meal production E[a]	Reduction (D/E) F[a]	Coefficients (C/E) G	Conversion efficiency (E/A) H
1953	51	46	44	37	6.8	5.46	6.47	0.13
1954	59	54	51	43	8.6	5.02	5.93	0.15
1955	80	74	70	59	11.2	5.23	6.25	0.14
1956	163	149	142	119	23.0	5.16	6.16	0.14
1957	446	408	389	326	59.2	5.50	6.57	0.13
1958	1,009	923	880	737	121.0	6.09	7.27	0.12
1959	2,659	2,433	2,319	1,942	326.2	5.95	7.11	0.12
1960	4,532	4,146	3,952	3,310	551.7	5.74	7.16	0.12
1961	6,860	6,276	5,982	5,011	835.2	5.27	7.16	0.12
1962	9,161	8,381	7,988	6,692	1,100.0	5.70	7.26	0.12
1963	8,794	8,045	7,668	6,423	1,158.4	5.54	6.62	0.13
1964	12,134	11,111	10,581	8,863	1,547.7	5.72	6.84	0.13
1965	9,915	9,070	8,646	7,242	1,279.4	5.66	6.76	0.13
1966	11,207	10,683	10,183	8,530	1,466.4	5.82	6.94	0.13
1967	13,450	12,305	11,729	9,825	1,804.7	5.44	6.50	0.13
1968	14,076	12,877	12,274	10,282	1,913.2	5.36	6.42	0.14
1969	12,267	11,222	10,697	8,960	1,605.0	5.58	6.66	0.13
1970	16,807	15,376	14,656	12,277	2,246.5	5.46	6.52	0.13
1971	14,076	12,877	12,274	10,282	1,926.8	5.33	6.37	0.14
1972	6,088	5,570	5,309	4,447	885.3	5.02	6.00	0.15
1973	2,071	1,895	1,806	1,513	361.8	4.18	4.99	0.17
1974	4,906	4,488	4,278	3,583	835.6	4.28	5.12	0.17
1975	4,215	3,856	3,675	3,079	682.1	4.51	5.39	0.16
1976	5,289	4,838	4,612	3,863	836.7	4.62	5.51	0.16
1977	1,084	992	946	792	181.5	4.37	5.21	0.17
1978	1,618	1,483	1,413	1,187	203.0	5.85	6.96	0.13
1979	1,858	1,703	1,622	1,363	344.5	3.96	4.71	0.19
1980	982	900	857	720	(164.0)	(4.39)	5.23	0.17
1981	1,670	1,531	1,458	1,225	(279.0)	(4.39)	5.23	0.17
1982	2,352	2,156	2,054	1,726	(393.9)	(4.39)	5.21	0.17
$\bar{X}$:						5.17	6.25	0.143
95% confidence interval :						5.0-5.4	5.9-6.6	0.137-0.149

[a] values in brackets based on mean value of reduction coefficient (D/E) for the years 1973 to 1977.

time transporting to other boats fish caught in excess of hold capacity.

Similarly, when the decree to prevent the landing (and presumably the catch) of small fish came in force, vessels that caught such fish discarded them at sea (dead, obviously) in order to avoid payment of a fine. Later, when enforcement became lax, fishermen began again to land small fish, which however, remained unregistered.

In the period 1974 to 1982, finally, restrictions of fishing areas, fishing time and catch quotas led to increased duration of fishing trips, and excess catch increased again, along with other irregularities in recording landings. These historical facts lead to consider the 5% reported by Vasquez and Lam (1977) as an estimate of item (#2) as too low. On the other hand, our estimate of the losses of anchoveta in the form of blood and other liquids is similar to those obtained by Vasquez and Lam (1977) and Sanchez and Icochea (1968).

With reference to deals between vessel owners and plant managers (item #5 in our list above), it must be noted that Vasquez and Lam (1977) included here only illegal sales of (illegally caught) small fish. For these, the plant managers would pay only 40-50% of the price of legally caught anchoveta. However, there were additional deals involving the sale of fish caught in excess of 70% boat storage capacity. Such fish were "given" to the factory, in return for preferential treatment upon landing regularly caught fish. This type of deal occurred from 1965 to 1975, when the pertinent decree was being enforced. Therefore, we believe that our estimate of losses in connection with item #5 (i.e., 4.38%) is more realistic - for 1965-1975 at least - than the estimate of 0.5% in Vasquez and Lam (1977).

Our value of 5% for item #6, i.e., the irregular sale of anchoveta also appears more realistic than the 0.5% value of Vasquez and Lam (1977), who, here also, considered only a small aspect of the overall problem.

This brings us, finally, to the question as to how realistic the combined effect of our various estimates are, when compared with independent, albeit indirect evidence. Such evidence is provided by "reduction coefficients" i.e., the quantity of raw material (anchoveta, wet weight) needed to produce one unit weight of fish meal. This coefficient was estimated on the basis of on-the-spot analyses by Tilic (1963a, 1963b) in 1960-1961 for factories from Chimbote to Callao, and by Arnesen and Sanchez (1963) for 23 different factories along the Peru coast, as 5.1-6.5 and 5.85, respectively. Data pertaining to the fishery as a whole, for 1968-1977 lead to an overall mean reduction factor of 6.0 (MIPE 1979), a relatively high value which we consider realistic, and which is close to the values cited above.

On the other hand, if we compute the reduction factor using columns D and E of Table 3, we obtain rather low values, ranging between 4.18 and 5.82, with a marked decrease in the 1970s, notwithstanding the increased use of low yielding small fish in that period.

If, however, we assume, as indeed empirical investigations demonstrate, that the industry never operated with reduction coefficients below 5, and that a value of 6 is nearer to the mark, then we obtain corrected fish landings markedly higher than nominal catch: by 8.7% in the 1950s, 7.5% in the 1960s and 22% in the 1970s. Thus using realistic reduction factors, and reported fish meal production (which, incidentally, may also be underestimated) leads to catch corrections roughly similar to those derived previously, especially as far as the 1970s are concerned, i.e., the important period during which peak landings were achieved, and the fishery subsequently collapsed.

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Growth of the Peruvian Anchoveta (*Engraulis ringens*), 1953 to 1982*

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Abstract

Growth parameters were estimated, using the ELEFAN I method of D. Pauly and N. David, from length-frequency data covering the years 1953 to 1982 and pertaining to the northern/central stock (4 to 14°S) of the Peruvian anchoveta *(Engraulis ringens)* and, for larvae and young juveniles, from daily otolith rings. Growth was found to oscillate seasonally with an annual minimum in August when temperatures are usually lowest. The dynamics of "condition" and fat content are discussed with emphasis to their relation to water temperature. A marked increase in the 30-year period covered of anchoveta maximum length and growth performance is documented along with a simulation model used to identify some density-dependent factors capable of explaining the changes in growth that have occurred.

Introduction

Growth studies of the anchoveta (*Engraulis ringens* Jenyns) inclusive of growth parameter estimates such as needed for population modelling have been few, especially in view of the fact that this species once supported the largest fishery of the world.

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We shall first review, in this contribution, what is known of the growth of the Peruvian anchoveta, then proceed to present new information, based on daily rings, on the growth of larvae and growth parameter estimates for each year during the period 1954 to 1982, based on detailed analysis of length-frequency data. These growth parameters describe curves that oscillate seasonally, and we shall thus discuss seasonal oscillations as a feature of the biology of anchoveta.

We shall also demonstrate that the overall growth performance of anchoveta increased from the early 1950s to the early 1980s and recent evidence of this being due to density-related effects will be presented. Also, we shall present a model developed to simulate the growth of anchoveta and use its results to identify and quantify some of these density-related effects.

Overall, our goals shall be both to consolidate the present knowledge of the growth of the Peruvian anchoveta and to provide a basis for other investigations, notably population studies involving length-based Virtual Population Analyses (see, e.g., Pauly, Palomares and Gayanilo, this vol.). For the latter we shall use the seasonally oscillating growth equation of Pauly and Gaschütz (1979)

$$L_t = L_\infty \left(1 - \exp\left(-K (t-t_0) + CK/2\pi \sin 2\pi (t - t_s)\right)\right) \qquad \text{...1)}$$

where L_t is the length at age t, L_∞ the asymptotic length, K a growth coefficient with dimension t^{-1}, t_0 the (hypothetical) age at which length would be zero *if* the adult and subadult growth curve could be extrapolated back to the origin, t_s the age at onset (with reference to $t = 0$) of a growth oscillation of period 1 year and C is a dimensionless constant expressing the amplitude of a growth oscillation, with dl/dt reaching zero once a year when $C = 1$. Equation (1) reverts, when $C = 0$, to the standard von Bertalanffy growth function (VBGF), i.e.,

$$L_t = L_\infty \left(1 - \exp\left(-K (t - t_0)\right)\right) \qquad \text{...2)}$$

(Bertalanffy 1938; Beverton and Holt 1957; Pauly 1984a).

Growth of Larvae and Early Juveniles

Anchoveta growth, as reviewed here, relates only to posthatch growth (see Santander and Castillo 1973 for an account of embryonic growth). Little work has been done on the growth of anchoveta larvae, and even less was formally published. We have thus complemented this part of our review with some original data (see Table 1, Figs. 1 and 2) both to assess the validity of previous results and to expand on these.

Table 1 summarizes some of the available information on growth and age of larvae anchoveta; these data suggest that anchoveta reach a length of about 1.5 cm at the end of their first month of life, and then continue growing at a rate of about 1.4 cm per month (see Fig. 2).

This inference confirms earlier results of Pastor and Malaga (1966), based on tetracycline marking of fish of 2.58 cm mean length, which reached 3.90 and 4.30 cm after 23 and 49 days, respectively, and also leading to a mean monthly growth rate of 1.4 cm.

"Recruits" in the contributions included in the present volume are defined as fish of total length of 4.25 cm, corresponding to the median of the smallest length class frequently represented in catch samples (see Tsukayama and Palomares, this vol.). Estimates of the age of such recruits can be obtained using two independent approaches:

i) forward projection of larval growth rate, or

ii) backward projection of growth curves describing the growth of subadults and adults

The first of these approaches, using 1.4 cm/month and a length at hatching of 2 mm (Einarsson and Mendiola 1963) yields an age of 2.89 month for 4.25 cm fish.

The second approach assumes that growth is described by the VBGF (without seasonal growth oscillations). Using the values of L_∞ and K in Table 2 to estimate Δt for fish of 1.5 to 4.25 cm from the equation

Table 1. Age in days in anchoveta larvae of different lengths, based on different authors.

Total length (mm)[a]	Kramer and Zweifel (1970)[b]	Mendiola and Gomez (1981)[c]	Herrera et al. (1985)	This study[d]
12.5	22	25	15.9	18.4
13.6	24	26	18.7	20.8
14.8	28	32	21.9	23.5
15.6	31	35	24.2	25.20

[a] Mean length of fish in study of Mendiola and Gomez (1981), with n = 8,7, 10 and 10, respectively.

[b] Using age-length relationship (Gompertz curve) for *E. mordax* and assuming similar growth for *E. ringens* (from Mendiola and Gomez 1981).

[c] Assuming that absolute age in days is equal to number of daily rings counted + 3 (note that addition of 3 days may not have been appropriate).

[d] From linear regression in Fig. 2.

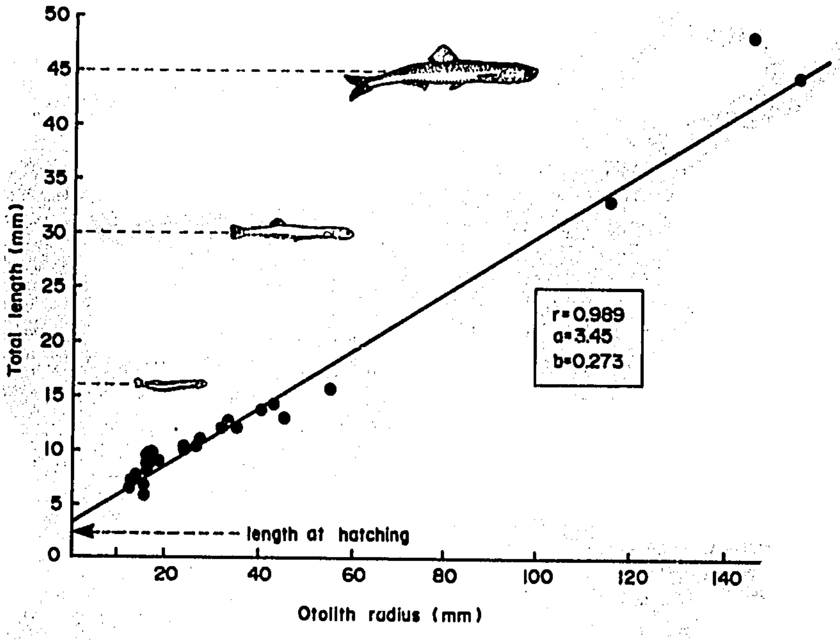

Fig. 1. Relationship between the total length and the otolith radius of anchoveta (*Engraulis ringens*) larvae and early juveniles. The drawings of anchoveta larvae and early juveniles are adapted from Einarsson and Mendiola (1963).

$$\Delta t = (1/K)\,\log_e((L_\infty - 1.5)/(L_\infty - 4.25)) \qquad \ldots 3$$

leads to Δt - values ranging from 1.24 to 2.81 month, with a mean of 1.84 to which one month must be added to account for the time needed to grow to 1.5 cm. Thus, fish of 4.25 cm would have an age of 2.84 months, extremely close to the value obtained using the first approach, and in fact matching quite precisely the age at recruitment estimated on the basis of the original data in Fig. 2.

Growth of Subadult and Adult Anchovies

The studies on the growth of subadult and adult anchoveta conducted to date can be subdivided into two, very unequal groups:

(i) growth inferences based on the study of hard parts, i.e., scales (Barreda 1953; Simpson and Buzeta 1967) and otoliths (see Table 2), and

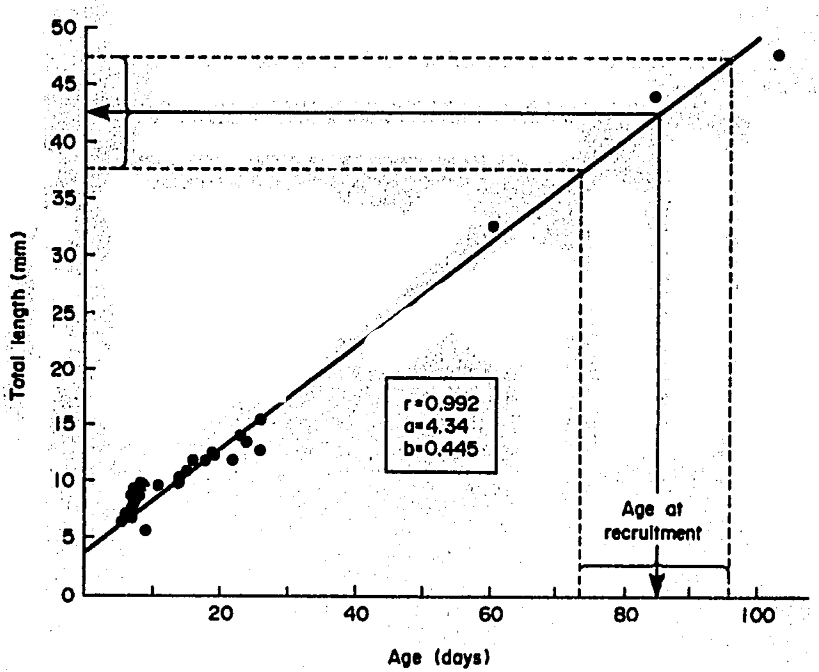

Fig. 2. Relationship between the total length and the estimated age in days of anchoveta (*Engraulis ringens*) larvae and early juveniles. Note that "recruits", as defined in this volume (i.e., fish of 37.5-47.5 mm) have an estimated age of slightly less than 3 months.

(ii) detailed analysis of length-frequency data using either Modal Progression Analysis (MPA, see Table 2) or the ELEFAN I program of Pauly and David (1981 and see below).

Overall, the results obtained by these two groups of methods tend to agree, although some of the "annuli" reported earlier (e.g. Barreda 1953) now quite clearly appear to have been artefacts.

Thus, while studies of hard parts (especially otoliths) usually provide the crucial evidence in controversies about the growth of fish, it is apparent that the studies of hard parts of anchoveta have not (to date) progressed far enough to help settle controversies involving *E. ringens*. Therefore, all following considerations will have to be based on the results of length-frequency analyses and consequently on the problems occurring when performing such analyses.

Three of the sets of growth parameters in Table 2 were estimated using MPA, while one set was obtained using the computer-based ELEFAN I method of Pauly and David (1981). A number of problems occur when performing MPA "by eye" (George and Banerji 1964). The most important are:

(i) the linking of modes thought to belong to the same cohort is entirely subjective (Pauly et al. 1984),

(ii) seasonal growth oscillations can usually not be identified, let alone taken explicitly into account, and

(iii) incomplete selection to the gear and incomplete recruitment cannot be accounted for and hence modes pertaining to small fish, being shifted toward larger sizes, tend to lead to underestimation of the parameter K of the VBGF. (Pauly 1986b).

The first study providing estimates of growth parameters in *E. ringens* appears to be that of Saetersdal and Valdivia (1964). Although their estimate of L_∞ is much lower and their value of K consequently higher than those of their successor (see Table 2), the value of the growth performance index

$$\phi' = \log_{10}K + 2\log_{10}L_\infty \qquad \ldots 4)$$

(Pauly and Munro 1984; Moreau et al. 1986) is roughly similar to the other, later values, with differences being explainable through density-related changes (see below).

Table 2. Growth parameters of subadult and adult anchoveta *Engraulis ringens* off Peru and Chile, as reported from various authors.

Sampling area (and period)	Method	L_∞(TL cm)	K (y^{-1})	ϕ'^{a}	Source
Chimbote-Callao (1961-63)	MPA[b]	15.0	1.70	2.58	Saetersdal and Valdivia (1964)
Chimbote, Callao, Ilo (1961-64)	MPA	16.0	2.04	2.72	Robles (MS)
Arica, Iquique (1970-72)	Otoliths	16.9	1.60	2.60	Simpson and Buzeta (1967)
Arica, Iquique (1970-72)	Otoliths	19.0	1.11	2.60	Simpson and Buzeta (1967)
Chimbote, Callao (1962-66)	Otoliths	16.8	1.08	2.48	Vildoso and Chuman (MSS),
		16.0	1.40	2.55	Chuman (MSS)
Peruvian Coast	MPA	18.5	1.10	2.58	Tsukayama and Zuzunaga (MS)
Arica, Iquique (1970-72)	Otoliths	19.0	0.73	2.42	Aguayo (1976)
Northern Peru (1961-1979)	ELEFAN I	20.6	1.26	2.70	Pauly and Tsukayama (1983)[c]

[a] $\phi' = \log_{10} K + 2 \log_{10} TL_\infty$.

[b] = Modal Progression Analysis, see text.

[c] Parameters presented here are means of 19 values in original paper, each of which pertained to a different year, from 1961 to 1979 (see text).

Changes in Anchoveta Growth Rates

Three types of growth rate changes have been discussed by previous authors in relation to the Peruvian anchoveta:

(i) changes of growth rates related to the influence of El Niño,

(ii) density-dependent changes in anchoveta growth, due to the decline of stock biomass in the last decades, and

(iii) seasonal growth oscillations.

With regard to the first of these three items, the only information available is by Tsukayama and Alvarez (1981), who stated (without presenting evidence) that the growth rate of anchoveta declined in 1976, an El Niño year. However, it is doubtful, given the low overall reliability of length-frequency analyses "by-eye" that such effect could be convincingly demonstrated. Rather, indirect evidence should be sought, e.g., the reduction of the "condition" of the anchoveta during El Niño, a phenomenon pointed out previously by various authors (e.g., Valdivia 1978, Fig. 7) and which will be elaborated upon further below.

At least three papers relate, albeit indirectly, to density-dependent changes of anchoveta growth:

i) Jordan (1980) points out that "recent information for the Peruvian coast [...] indicated an evident shift of L_{max} up to 20.5 cm [... which] may be the result of a changing growth rate",

ii) Cushing (1981) *assumed* density-dependent growth (no evidence is given, however), and

iii) Pauly and Tsukayama (1983, Table 1) presented a series of growth parameter estimates (L_∞ and K) which lead to estimates of ϕ' (see equation 4) that show a weak, positive correlation with time (r = 0.396, df = 17), a fact which they missed and which tends to contradict their statement that "the growth parameters describing the growth in length of the northern stock of the Peruvian anchoveta have been more or less constant for the period 1961 to 1979".

As will be shown below, we have now found strong evidence for density-dependent growth in the Peruvian anchoveta, confirming Jordan's observations.

Seasonal growth oscillations have been previously discussed by Cushing (1981) who suggested, with regard to newly recruited, small anchoveta that "the first group arises from the spawning in August, September, and October and the second from that in January; the latter grows somewhat more slowly because its initial growth occurs outside the period of major upwelling". Evidence for this statement - which implies that (cold!) upwelled water accelerates growth - was not presented, however.

Pauly and Tsukayama (1983), on the other hand, estimated for the period of 1961 to 1979 a mean value of 0.3 for the parameter C of equation (1). This implies that growth rate diminishes by 30% below normal during that part of the year when growth is most strongly reduced. They also showed that this 30% reduction occurs in September, i.e., in (southern) winter, when mean monthly water temperatures off Peru are lowest (Zuta and Urquizo 1972; Bakun, this vol.; Brainard and McLain, this vol.)

With this, we conclude this brief review of anchoveta growth, since enough of a stage has been set for the new results which follow.

Reassessing the Growth of Anchoveta

Material

The length-frequency data used for this analysis and pertaining to the northern/central stock are given in Tsukayama and Palomares (this vol.). The following important points should be noted:

i) interpolations of the length-frequency data, such as used in Pauly, Palomares and Gayanilo (this vol.) for the Virtual Population Analyses were *not* used for the growth analysis,

ii) the available data were grouped in files covering the entire "life" of cohorts, from their entry into the fishery to their disappearance therefrom, or at least to the time when their modes merged with those of other cohorts.

The second point implies that the procedure used by Pauly and Tsukayama (1983) for estimating growth parameters from data set covering at most the 12 months of a calendar year was avoided, and that the "year" used here to label a given cohort does not refer to the time when the data were collected, but to the time when the cohort in question had its peak biomass.

Methods

The ELEFAN I method, used here to perform all growth analyses, essentially consists of three main routines:

i) a routine to transform the available length-frequency data such that peaks on the data are expressed as positive points, and troughs as negative points,

ii) a routine to "trace" growth curves through the transformed data, to score the positive and negative points "hit" by the curve ("Explained Sum of Peak", or ESP, analogous to explained variance in parametric statistics) and to relate this ESP to the sum of positive peaks ("Available Sum of Peaks" or ASP, analogous to total variance) in the data set,

iii) a routine that changes, in small steps, seeded values of the parameters of equation (1) until a curve is found which maximizes the ratio ESP/ASP.

This algorithm assumes that the single, consistent growth curve which passes through most peaks, while avoiding troughs as far as possible, is the mean population growth curve.

An extensive literature now exists on the ELEFAN I program, its assumption and sources of bias (see Pauly 1985a, 1985b, 1986a, 1986b, 1986c).

For the actual fitting, we have used the graphics-oriented version of ELEFAN I developed by Saeger and Gayanilo (1986); this version incorporates several improvements suggested by early users of ELEFAN programs (see Pauly 1985a). Moreover, we have estimated growth parameters in a cohort-specific basis (as was not done in earlier applications of the programs) and largely compensated for the bias due to incomplete recruitment and gear selection (Pauly 1986b), as follows:

i) preliminary estimate of growth parameters (L_∞ and K) were obtained using the original length-frequency data; these parameters were then averaged over the period 1953 to 1984,

ii) a file was created from the original data set in (i) which included the month(s) from each year (for the period 1953 to 1982) that contained the smallest fish,

iii) using the values of L_∞ and K obtained in (i) and the file derived in (ii), a length-converted catch curve (Pauly 1984c) was derived; from this, the number of fish that would have been caught, had it not been for incomplete selection and recruitment, was estimated using the method described in Pauly 1984a, Table 5.6),

iv) the number of fish actually caught for each length class was divided by the number estimated in (iii) thus providing estimates of the probabilities of capture, and finally

v) the probabilities of capture estimated in (iv) were used to correct all available length-frequency data files, and the corrected files were then used to re-estimate growth parameters (see Fig. 3).

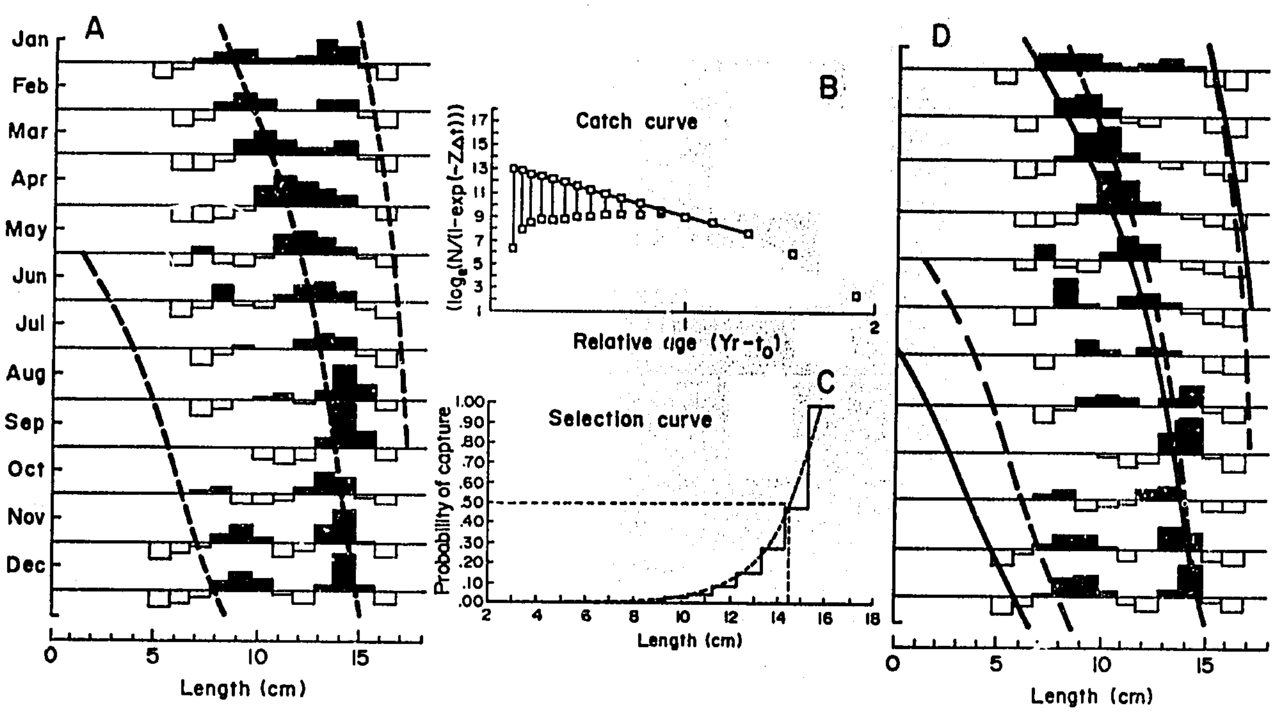

Fig. 3. Steps used to correct ELEFAN I estimates of growth parameters in Peruvian anchoveta, using the method of Pauly (1986b). A) Estimation of a preliminary set of growth parameters for each cohort from 1954 to 1982 and averaging of the same; B) Derivation of a length-converted catch curve based on growth parameters estimated in (A) and an accumulated length-frequency file composed of data from the two months of each year containing the smallest fish (such as to obtain a correction for gear selection covering a size range as wide as possible); backward projection of catch curve to estimate number of fish that would have been caught, had it not been for gear selection and/or incomplete recruitment; C) Estimation of probabilities of capture from the ratio of fish caught to virtual fish, by length, and division of all original length-frequency data by the appropriate probabilities of capture, and D) Re-estimation of growth parameters (solid line). The correction leads to much improved estimates of the von Bertalanffy parameter K (see text).

Growth Parameter Estimation of Anchoveta Cohorts, 1954 to 1982

Table 3 gives the growth parameter estimates obtained using the ELEFAN I program. These estimates are, on the average, similar to those obtained, for the northern substock, for the years 1961 to 1982 by Pauly and Tsukayama (1983).

Fig. 4 gives a graphic representation of the growth of several cohorts, and of the transformed length-frequency data from which the growth curves were estimated. Faint seasonal growth oscillations will be noted: they would probably not have been picked up by anyone performing the same analysis by tracing growth curves "by eye" only. The mean value of C is 0.27, which is very near the 0.3 value estimated earlier by Pauly and Tsukayama (1983); the greatest reduction of growth rate occurred, on the average, in mid-August, i.e., the mean winter point value is 0.62, against 0.7 cm estimated earlier (see Table 3).

Note, finally, that the shaded histograms corresponding to very small fish tend to be to the right of the estimated growth curve: this is due to the fact that the correction for gear selection and/or incomplete recruitment did not suffice for entirely de-biasing the original length-frequency data. Still, we see that the growth curves so obtained start at the appropriate time after the spawning seasons and follow the cohorts throughout most of their passage through the fishery, up to their complete disappearance therefrom.

Evidence for Density-Dependent Growth, 1953 to 1982

The available evidences for density-dependent growth in anchoveta are:

i) the strong positive correlation between time and the maximum length in catch samples, from 1953 to 1982 (Table 3, Fig. 5);

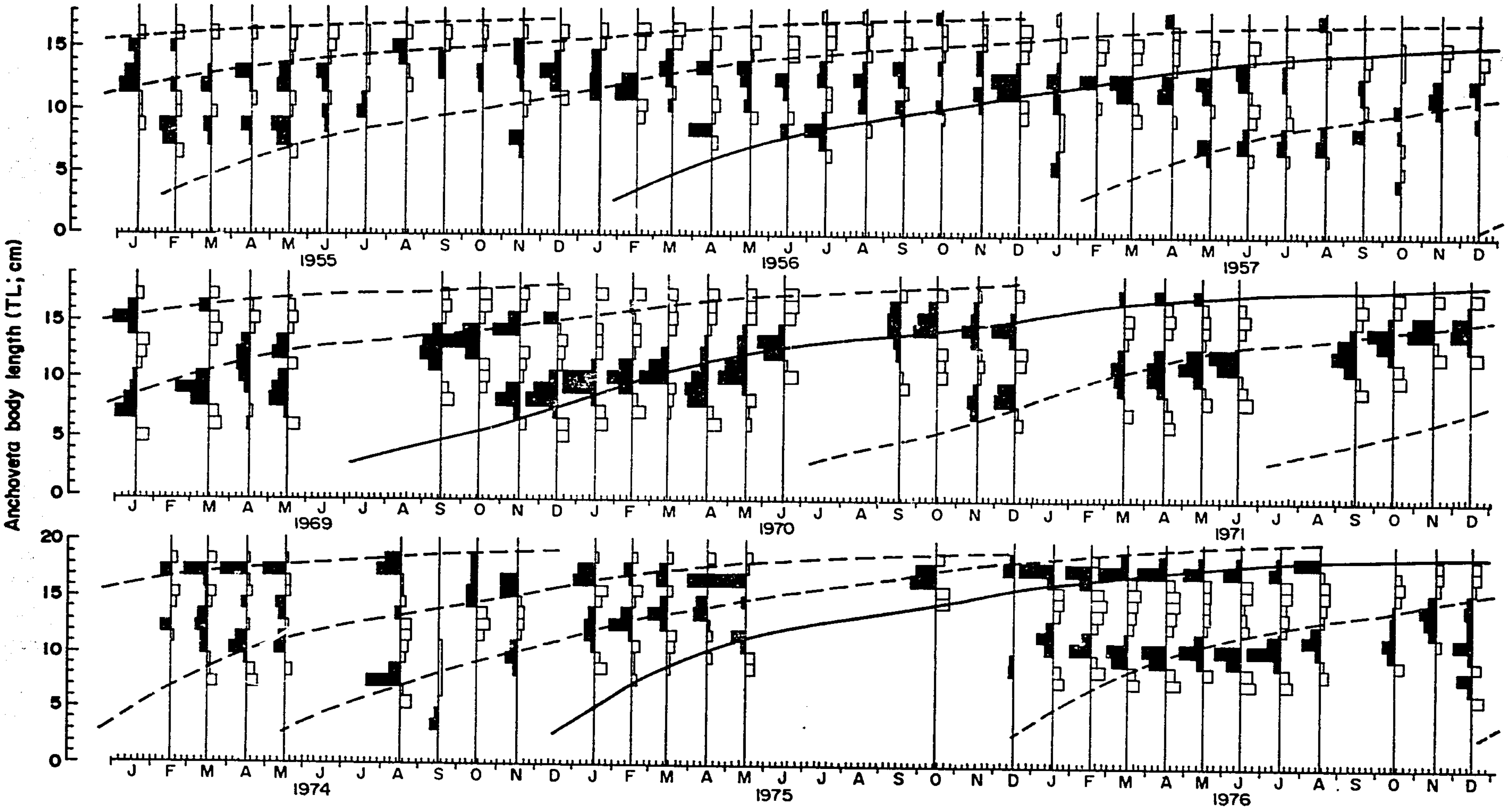

Fig. 4. Example of cohort-specific growth curves identified using the ELEFAN I program. Black histograms refer to what were peaks in the original length-frequency data, open histograms refer to what were the troughs separating peaks. Note faint seasonal growth oscillations, and the fact that growth curve originate at spawning seasons (Sept.-Nov. and Feb.-April). See text for details on the ELEFAN I program.

Table 3. Growth parameters of anchoveta 1954 to 1982, as estimated using ELEFAN I; WP and C relate to seasonal oscillations (see text).

Year	L_{max}[a] (TL; cm)	L_∞ (TL; cm)	K (1/yr)	ϕ'[b] ($\log_{10}$ cm^2/yr)	WP[c] –	C[c] –
1953	16.25	–	–	–	–	–
1954	17.25	21.50	0.76	2.54	0.60	0.24
1955	16.25	20.00	0.63	2.40	0.53	0.36
1956	17.25	18.50	0.87	2.47	0.67	0.28
1957	17.25	19.00	0.62	2.35	0.60	0.30
1958	17.25	19.80	0.90	2.55	0.67	0.32
1959	15.25	18.25	0.75	2.40	0.70	0.30
1960	17.25	22.50	0.60	2.48	0.60	0.35
1961	18.25	20.00	0.79	2.50	0.56	0.30
1962	18.25	19.50	0.85	2.51	0.67	0.30
1963	17.25	20.50	0.95	2.60	0.52	0.20
1964	17.25	19.75	0.71	2.44	0.70	0.31
1965	18.25	19.25	0.75	2.44	0.60	0.17
1966	17.25	20.60	0.79	2.52	0.61	0.20
1967	18.25	20.50	0.82	2.54	0.57	0.20
1968	19.25	21.00	0.90	2.60	0.60	0.20
1969	18.25	21.00	0.85	2.57	0.60	0.20
1970	18.25	20.50	0.86	2.56	0.62	0.36
1971	18.25	22.50	0.90	2.66	0.60	0.20
1972	19.25	20.50	1.00	2.62	0.61	0.25
1973	18.25	21.30	0.80	2.56	0.54	0.23
1974	20.25	20.70	0.84	2.56	0.66	0.30
1975	20.25	20.50	1.28	2.73	0.60	0.30
1976	20.25	21.30	0.82	2.57	0.50	0.28
1977	19.25	21.00	1.05	2.66	0.55	0.20
1978	18.25	20.70	1.11	2.68	0.67	0.27
1979	19.25	21.50	1.20	2.74	0.74	0.30
1980	19.25	21.50	1.20	2.74	0.74	0.30
1981	19.25	20.25	0.95	2.59	0.71	0.30
1982	19.25	20.25	0.95	2.60	0.58	0.25

[a] Extracted from Tables 1 to 30 in Tsukayama and Palomares (this vol.).
[b] $\phi' = \log_{10} K + 21 \log TL_\infty$ (y^{-1} and cm, resp., see text).
[c] Mean WP and C values are 0.62 and 0.27, respectively.

ii) the extremely tight positive correlation between time and the values of the growth performance index ϕ' from 1954 to 1982 (see Table 3, Fig. 5) and;

iii) the significant ($P = 0.05$) negative correlation between ϕ' and anchoveta biomass for 1954 to 1982 (Fig. 6).

These three lines of evidence, both separately and considered together, strongly confirm the earlier suggestions of a change in the growth patterns of anchoveta summarized in Fig. 7.

A possible explanation for density-dependent growth in the Peruvian anchoveta might be provided by the fact that the surface area of fish gills (G) and hence fish metabolism increase in proportion to a power $d < 1$ of body weight (W), i.e.,

$$G = a \cdot W^d \qquad \text{...5)}$$

Thus, relative gill areas and metabolism must decrease with increasing body weight, down to a metabolic level (at W_∞, the asymptotic weight) at which average oxygen supply meets average oxygen requirements (Fig. 8). Therefore, an increase in asymptotic size as demonstrated above implies - given no change in gill structure - a decrease of average oxygen requirements. The magnitude of this decrease can be estimated, from predicted values of W_∞ for 1950 and 1980 of 40 and 80 g, respectively (see Fig. 8) because in small fish such as anchoveta, the value of d (in equation 5) usually ranges between 0.7 and 0.8 (Winberg 1960; Pauly 1981). Thus, using the midrange of the two latter values we have

$$(80/40)^{-(1-0.25)} = 0.84 \qquad ...6)$$

which express the average oxygen consumption of anchoveta in 1980 as a fraction of their consumption in 1950. Or put differently the model in Fig. 8 and equation (6) suggest that the "cost of living" of an anchoveta may have dropped, for 1950 to 1980 by approximately 16%. We shall present further below a simulation model developed to test this estimate and explore some possible scenarios for density dependence in the Peruvian anchoveta.

Before we turn to this model, however, three more aspects of anchoveta growth, not considered in this model, should be discussed.

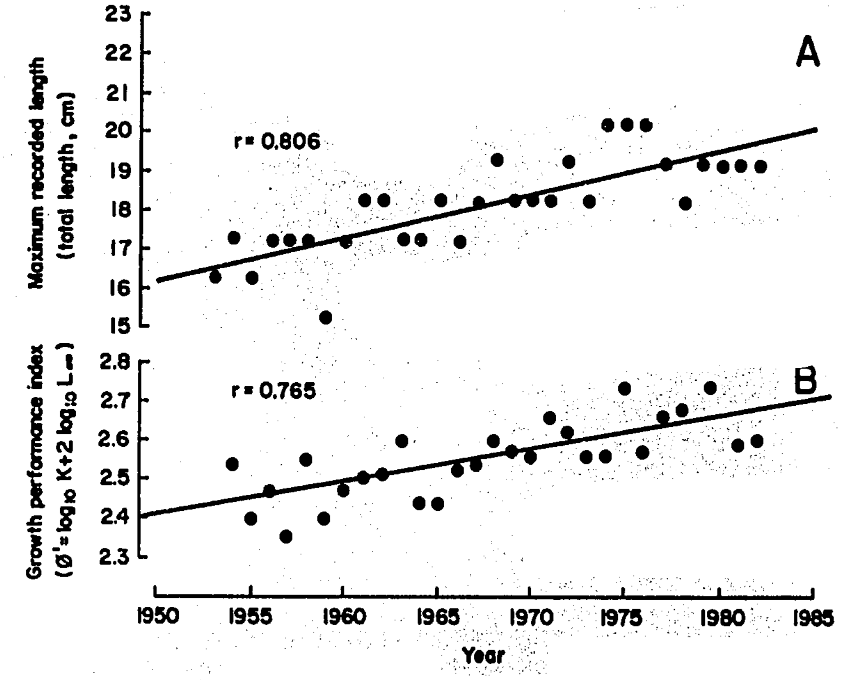

Fig. 5. A: time series of maximum recorded length in Peruvian anchoveta catch samples (from Table 3). B: time series of the growth performance index ϕ' suggesting that anchoveta presently grow faster, toward a larger asymptotic size than in the 1950s (see text).

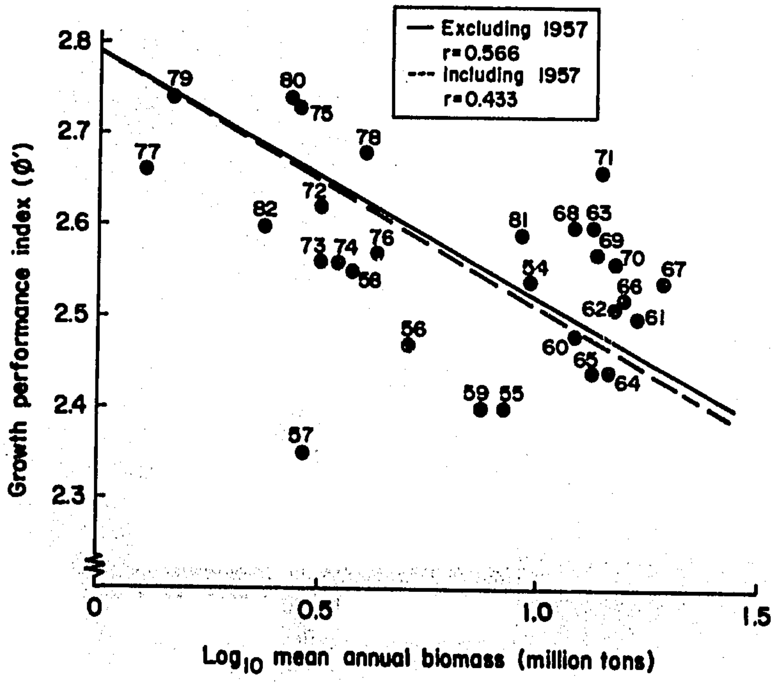

Fig. 6. Relationship between the growth performance index ϕ' of anchoveta (1954 to 1982) and the mean annual biomass of *E. ringens* off Peru (4-14°S). The ϕ' values are from Table 3; the biomass were obtained using Virtual Population Analysis (see Pauly, Palomares and Gayanilo, this vol.).

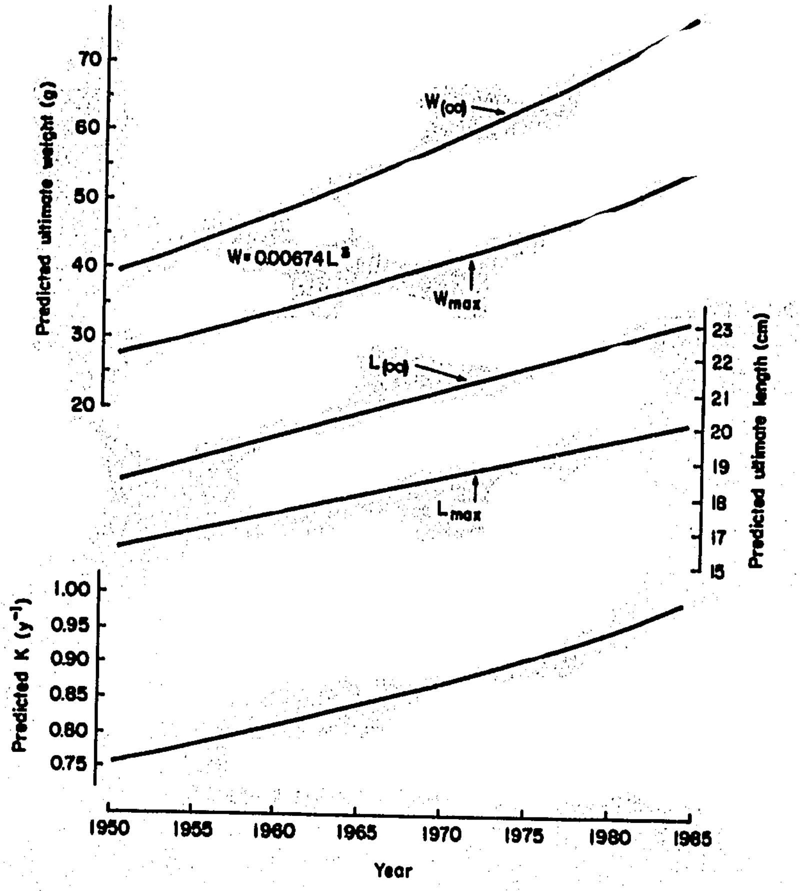

Fig. 7. Change in growth parameters of Peruvian anchoveta, 1950 to 1985 (based on Fig. 5 and data in Table 3). $W_{(\infty)}$ and $L_{(\infty)}$ refer to predicted ultimate sizes, as opposed to estimated values of asymptotic weight (W_∞) and length (L_∞).

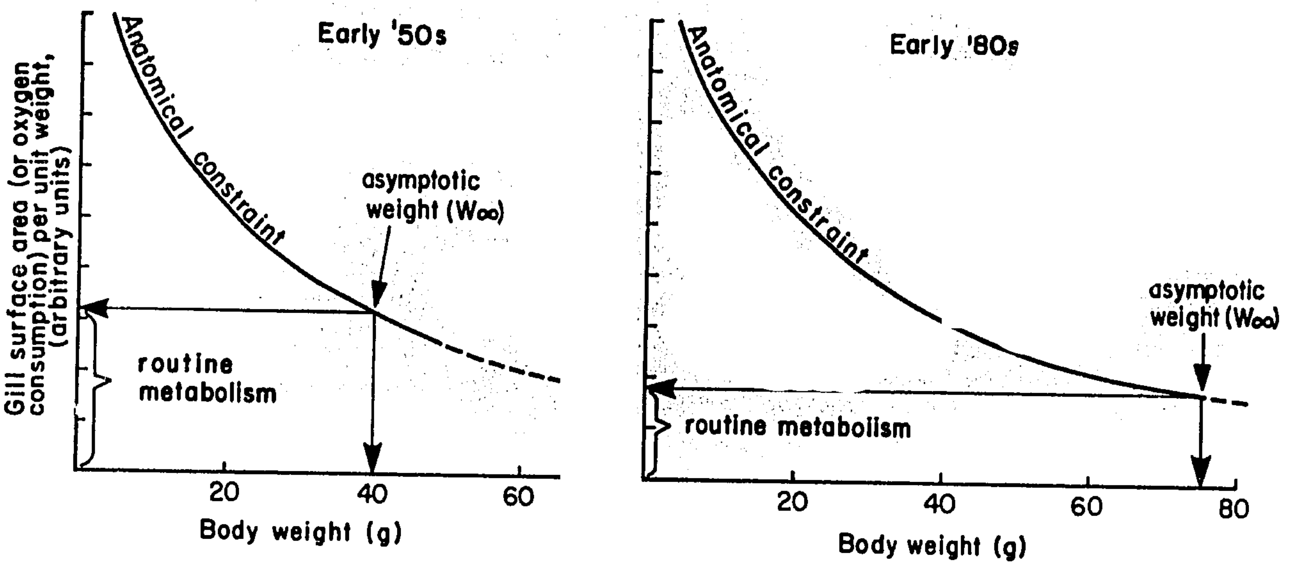

Fig. 8. Schematic representation of the mechanism leading, via density-dependent reduction of routine metabolism, to an increase of maximum and asymptotic sizes in anchoveta, from the early 1950s (high anchoveta biomass) to the early 1980s (low biomass). This scheme is structured around the feature that all fish have gills growing in proportion to a power d <1 of body weight (adapted from Fig. 5, Table 3, a mean condition factor of 0.7 and Fig. 1 in Pauly 1984b).

Latitudinal Differences in the Growth of Anchoveta

Fish stocks belonging to the same species, but occurring along a latitudinal gradient usually display trends in their growth parameters, with higher asymptotic sizes (and consequently lower K values) at the "cold" poleward ends of their distributions (see Pauly 1984a; Longhurst and Pauly 1987). The anchoveta is no exception to this rule as documented by Brandhorst (1966) who, based on a survey conducted in 1961, wrote that "while [the anchoveta] has a maximal size of about 17 cm in the Arica-Iquique area [19°S], fish of 18 cm were measured in Valparaiso [33°S] and of up to 21 cm in Talcahuano [37°S]" (our translation from German). Note that in 1961, the anchoveta off northern/central Peru reached a length of about 17 cm, similar to the one in northern Chile, but markedly less that off southern Chile.

Temperature and the "Condition Factor" and Fat Content of Anchoveta

The condition factor (c.f.) of fish is defined by

$$W = (c.f./100)\, L^3 \qquad ...7)$$

in which c.f. is divided by 100, when length (L) is expressed in cm and weight (W) in g to have c.f. values near unity in fish with "normal" shapes. Changes in the length-weight relationship of fish can be directly related by comparing their c.f. values because the exponent of the length-weight relationship (equation 7) is here fixed at a value of 3, corresponding to isometric growth. Tables 1 to 30 of Tsukayama and Palomares (this vol.) include actual values of c.f., computed from anchoveta samples that had been weighed, measured and counted, as well as values (in brackets) that have been estimated using the plot of actual c.f. values on the mean monthly sea surface temperatures in Fig. 9. As might be seen, Fig. 9 suggests a rather strong negative correlation between c.f. and temperature, confirming previous reports of anchoveta looking emaciated at the high temperature occurring during El Niño conditions.

A plot of water temperature against the coefficient of variation of c.f. values (see Fig. 10) is presented here to show that c.f. values become more variable at high water temperatures.

Fig. 11 shows plots of the monthly means of actual c.f. values (i.e., excluding the bracketed values in Tables 1 to 30 of Tsukayama and Palomares, this vol.) against month and sea surface temperature against month, showing in different form the strong inverse relationship between c.f. and sea surface temperature.

Fig. 11 also shows the seasonal changes in growth rate (in length, i.e. dl/dt) of anchoveta, as implied by a value of C = 0.3 and a "winter point" of 0.7 (WP = period of the year when growth is slowest; a parameter estimated by ELEFAN I, see Table 3).

As might be seen, dl/dt in anchoveta varies inversely with condition (and hence relative weight). This relationship can be understood, however, only when simultaneously considering the seasonal dynamics of anchoveta fat content, as briefly sketched below.

In anchovies from temperate waters, as in most other fish from higher latitudes, the fat content fluctuates seasonally, being highest at the end of the "growth season" (summer/autumn) and lowest just after spawning. This cycle is here illustrated by Fig. 12A, which pertains to *Engraulis encrasicholus* and is adapted from Shul'man (1974).

In *Engraulis ringens* from northern Chile where strong seasonal temperature oscillations occur, the fat content also varies seasonally in sinusoidal fashion. This is illustrated here by Fig. 12B based on Brandhorst (1966).

Further toward the equator, however, the dynamics of fat content become more complex, with the available data suggesting that fat content peaks *twice* a year, i.e., before the August-October and January-February spawning seasons. This is illustrated here by Fig. 12C and 12D based on Einarsson et al. (1966).

In this context, it was also observed that anchoveta, during positive temperature anomalies (i.e., El Niño events), have a higher than average fat content. Thus, IMARPE (1972) wrote:

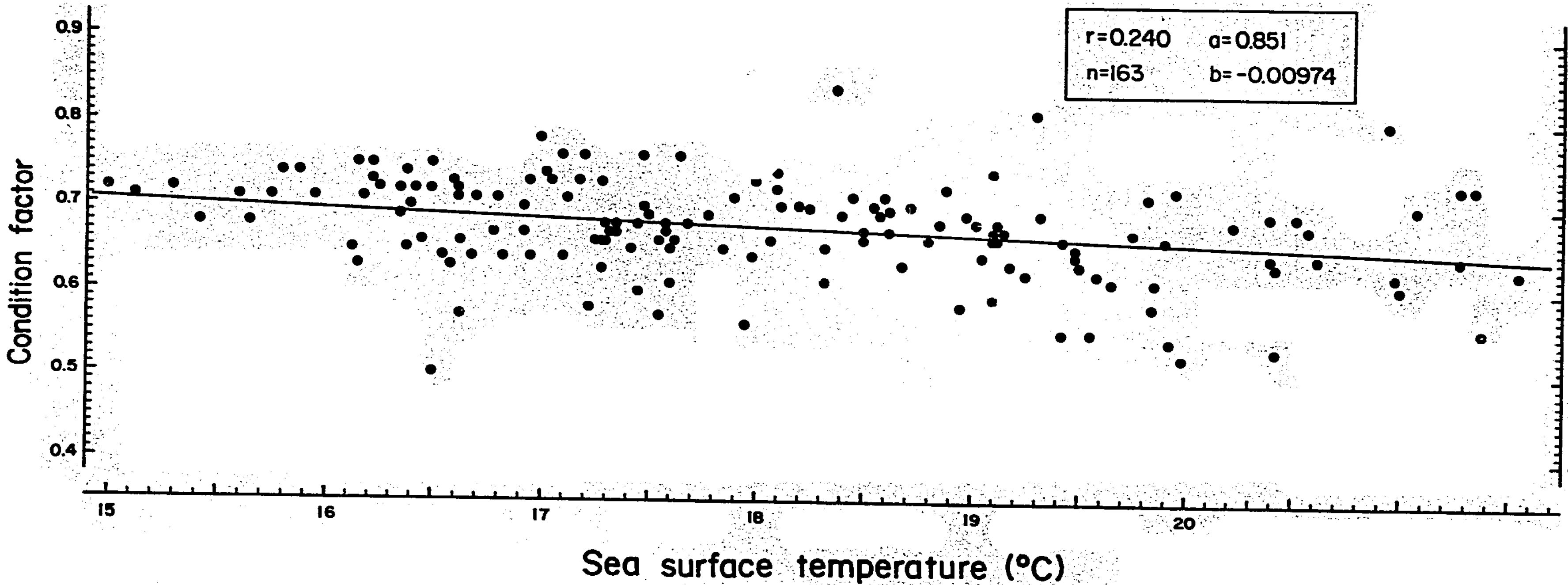

Fig. 9. Relationship between condition factor and sea surface temperature in anchoveta *Engraulis ringens* off Peru (4-14°S). Based on original c.f. data in Tsukayama and Palomares (this vol.) and temperature data in Pauly and Tsukayama (this vol.). See text for discussion.

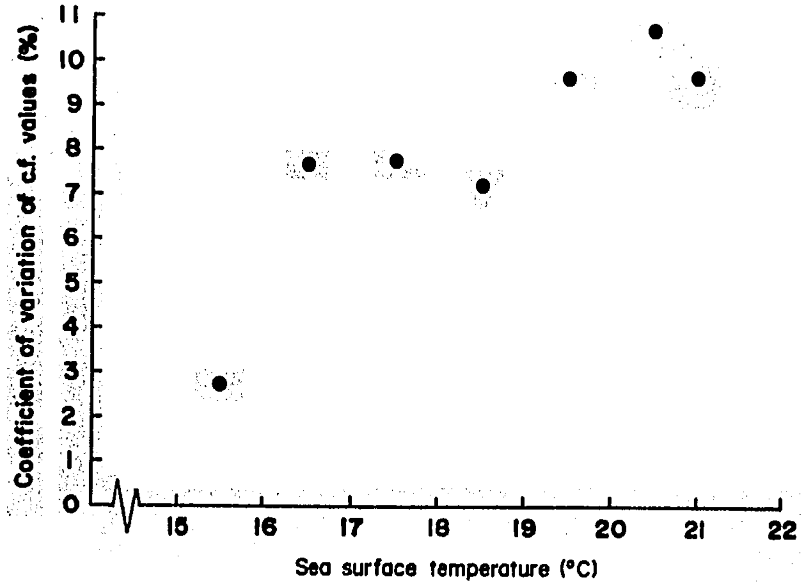

Fig. 10. Relationship between the variability of anchoveta condition factor (c.f.) estimates and mean monthly sea surface temperature (based on data in Tables 1-30 in Tsukayama and Palomares, this vol.). At low temperatures, anchoveta have high c.f. values that vary little between different months. At high temperatures, wide fluctuations between adjacent months and between the same months of different years may be observed.

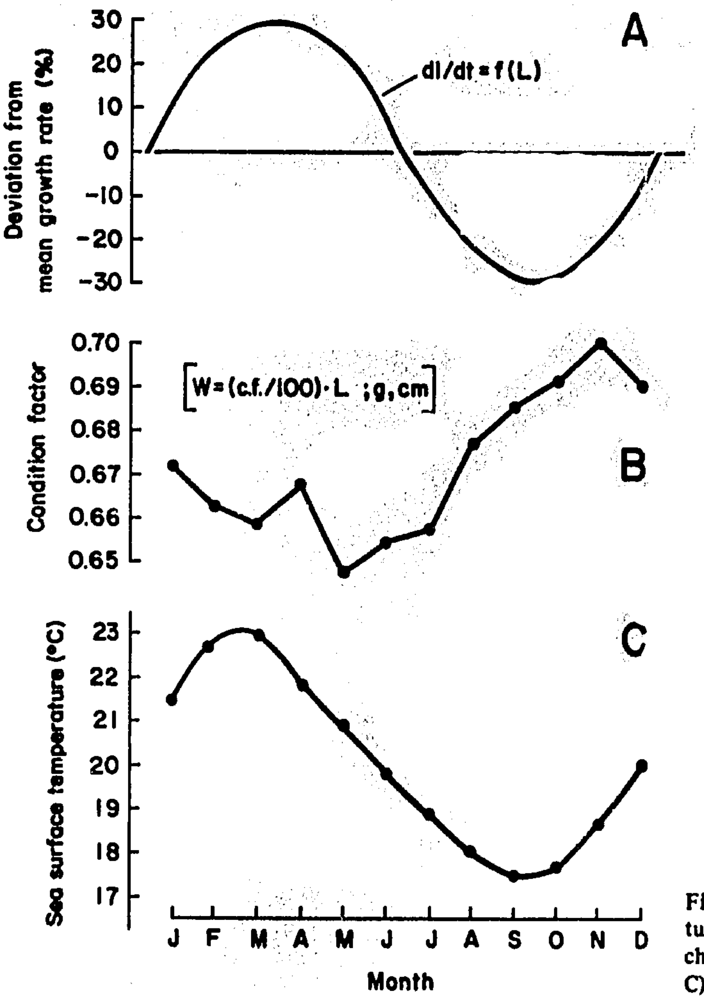

Fig. 11. Seasonal changes of some growth-related features of the Peruvian anchoveta and its ecosystem. A) changes in length growth rate; B) changes in condition; C) changes in sea surface temperature (see text).

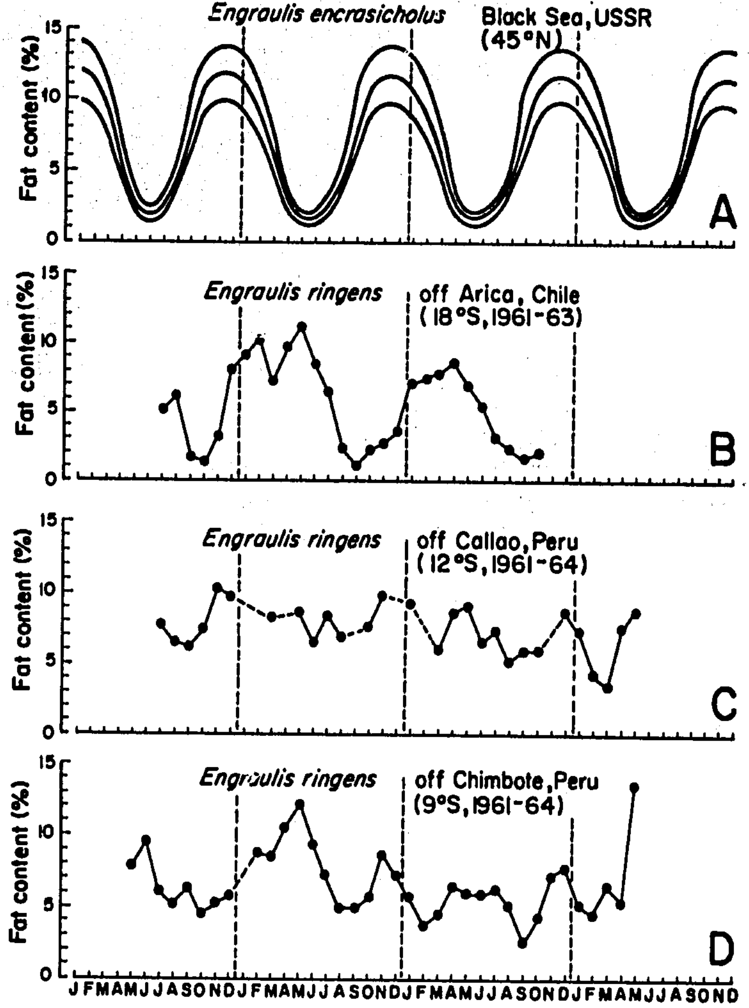

Fig. 12. Time series of fat content in Black Sea anchovy (A) and Peruvian anchoveta (B-D): note tendency for fat content to peak before spawning season(s).

An indirect indication of a low level of spawning is given by the fat content of the fish, which is fairly high before spawning and normally decreases during the spawning period from a level which is on the average around 12 or 13% in June to one of about 5% in September for fish of over 14 cm. In 1971 the fat content in March-June was in general somewhat below the average for these months, but in September-October the values were some 2% higher than average, and increased to very high levels in December (18.8% in Chimbote, 14.1% in Callao and 11% in Ilo).

This behavior may be an adaptive response which enables anchoveta to store energy in a form which does not increase oxygen requirements (as an energy storage in the form of protein would (see Pauly 1981).

The time-series data in the various contributions in this volume, the fat content data in Lam (1968) and other unpublished fat content data presently on file at IMARPE will allow a test of this hypothesis.

In the meantime, it suffices to recall here that:

i) anchoveta show seasonal oscillations of their growth rate (in length) which correlate with temperature, and

ii) fat content and condition tend to be inversely related, with fat content usually being higher during periods when oxygen requirements are high.

A Simulation Model of Anchoveta Growth

Basic Concepts and Assumptions

The remarkable increase of growth performance in the anchoveta, for the early 1950s (here "1950" for simplicity's sake) to the early 1980s (here "1980") could be the result of changes in availability and/or composition of anchoveta food resources as a consequence of the decline of the anchoveta's own biomass during the last decades.

This hypothesis, suggesting that anchoveta growth is density-dependent, cannot be tested using empirical data as the detailed time series data on file at IMARPE on anchoveta stomach contents are presently being processed, and will not be available early enough for consideration in the present volume. Therefore we have tested the hypothesis of density-dependent growth in anchoveta using a relatively simple deterministic simulation model based on the results of experiments and simulation conducted and reported upon earlier by Villavicencio (1981), and Villavicencio and Muck (1983a, 1983b). This model does not consider the seasonaly oscillating factors discussed in the preceding section, but does include a term for spawning (see Table 4). The model is based on the terms

$$\text{Growth} = [\text{food ingested}]-[\text{food used for purposes other than growth}] \qquad ...8$$

or put differently

$$G = (R \cdot A)-(Ml_r + ML_a) \qquad ...9)$$

where G = growth rate, R = ration, A = assimilation, ML_r= losses associated with resting metabolism and ML_a = losses associated with active (feeding) metabolism.

Three different types of changes are here considered explicitly with regard to their potential impact on growth rate:

i) *competition for food within the anchoveta stock*: reduced biomasses of anchoveta imply, given constant production of anchoveta food, an increased availability of food per surviving anchoveta. Thus, if R·A in equation (9) remains constant, G should increase because ML_a (expressing the metabolic losses associated with feeding) should decline.

ii) *food quality*: here, it is assumed that the decline of anchoveta biomass has reduced the grazing pressure on phyto- and zooplankton, resulting in (a) reduced competition for filter-feeding zooplankters and (b) reduced zooplankton mortality through anchoveta predation. Both items (a) and (b) should result in a relative increase of zooplankton *vis à vis* phytoplankton and hence in an increase of zooplankton in the diet of the anchoveta, an opportunistic feeder. Such shift in diet composition would entail (a) an increase of caloric content per unit weight of anchoveta stomach content and/or (b) an increased assimilation of the ingested food.

iii) *feeding mode*: a shift from feeding predominantly on phytoplankton to feeding predominantly on zooplankton would not only entail a shift in food quality, however. Rather, this would result in a shift of feeding mode, from filter to particulate feeding, and hence from a less to a more efficient (in terms of net energy gain) mode of feeding. This would result in G increasing because ML_a would decrease.

Fig. 13 summarizes the assumption listed above and the overall structure of the model presented here.

Implementation of the Model

Table 4 lists the equations used to implement the model in Fig. 13 along with their sources.

Anchoveta growth was integrated in steps of one day, starting from an assumed length of 10 cm and a weight of 9 g at age 1 year up to an age of 4 years for all simulations.

"1950" was simulated by calibrating the model such that 16 cm was reached at 4 years. Then, the sensitivity of the model was tested by changing one at a time the value of four parameters, related to the three factors discussed above.

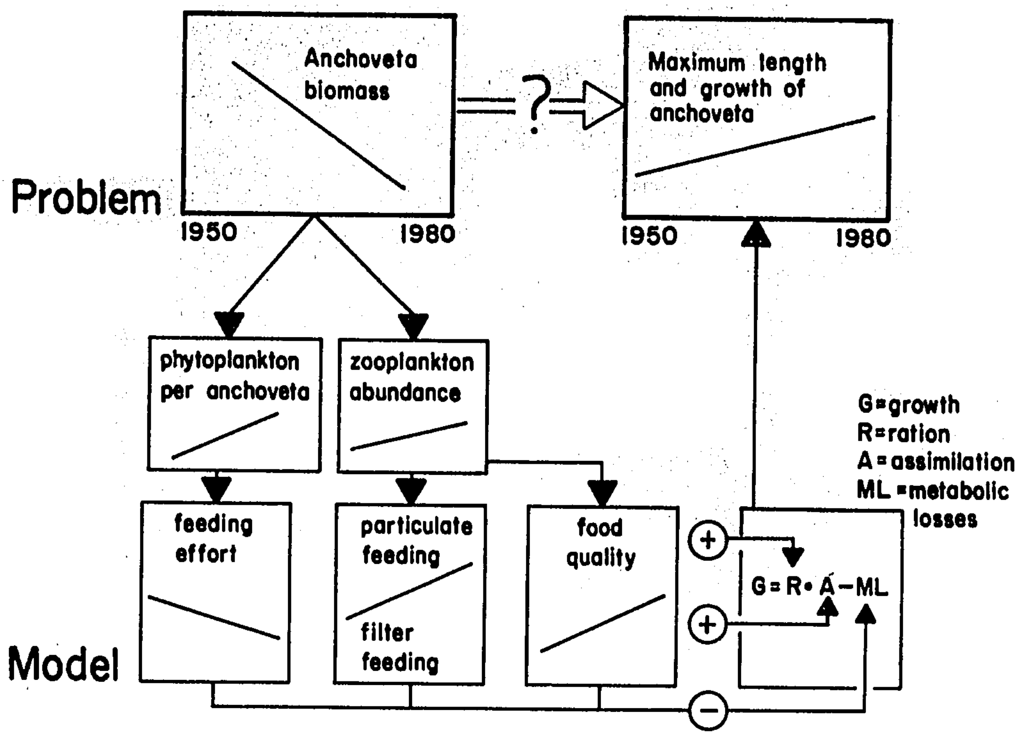

Fig. 13. Basic elements of a model for indentifying possible causes for a change in the growth performance of anchoveta. The "Problem" level shows the question to be answered, while the "Model" level shows some of the mechanisms hypothesized to affect growth rate (see text).

Finally, "1980" (when 20 cm is reached at an age of 4 years) was simulated, by assuming alternatively:

(a) only one of the four parameters changed, and
(b) all four parameters changed simultaneously.

The four parameters subjected to change were:

- assimilation coefficient (A);
- caloric food content;
- costs per unit time feeding; and
- duration of feeding period (h_a)

(see also Table 4).

The duration of the feeding period $(0<h_a<24h)$ was made to change by varying food density (in g/liter). When food density is high, the time needed to reach R, the maximum ration is short; conversely, when food density is low, anchoveta may feed for up to 24 hours. [Daily ration (R) is used here as an upper limit which anchoveta try to reach either by increasing their feeding time or by changing their feeding mode.]

Metabolic costs per unit feeding time were changed by multiplying the energy expenditure during filter feeding (ML_a) with a factor (f) and total metabolic losses (ML) computed from

$$ML = (ML_a \cdot h_a \cdot f) + (ML_r \cdot h_r) \qquad ...10)$$

where h_a and h_r are as defined in Table 4, and where f was set = 1 when the fish are filter feeding and 0.3 when the fish had shifted toward particulate feeding. Table 4 shows the ranges within which each parameter were varied.

Thus for each (daily) step, somatic growth in weight, length and gonad growth were computed as follows:

i) filtering rate (liter/hour) is computed from the length-specific swimming speed, area of the open mouth and the frequency by which the mouth is opened;

ii) filtering rate was multiplied by particle density (g/liter) to give ingestion rate (g/hour),

iii) the computed ingestion rate is related to the upper limit of the ration, and the time is computed that is needed to reach this upper limit;

Table 4. Formulas and constants used in anchoveta growth simulation model.

Relationship	Equation(s)	Sources and/or remarks
Length *vs.* weight	$W = 0.0215L^{2.604}$ (g, cm)	Villavicencio and Muck (1983a)
Wet weight vs. caloric content	1 g anchoveta = 1,150 cal 1 g anchoveta food = 1,000-1,450 cal	Villavicencio and Muck (1983a)
Swimming speed during feeding *vs.* anchoveta length	$V = V_l\ 0.05\ T$ (V in body length/s; T = °C) $V_1 = 0.5822L^{0.5262}$ (for $L < 12$ cm) $V_2 = (0.5822L^{0.5262}) + (6.522\text{-}2.645 \log_e L)$ (for $L >= 12$ cm)	adapted from Villavicencio and Muck (1983a, 1983b, 1985)
Metabolic rate *vs.* size of an individual fish	$ML_a = 0.0887\ e^{0.0959T + 0.036V\ L}\ W^{0.9}$ (Ml_a = active metabolish; cal/h) $ML_r = 0.3ML_a$ (ML_r = resting metabolism)	Villavicencio and Muck (1983a) T was set at 18°C throughout 0.3 value from data in Winberg (1960)
Filtering rate *vs.* length	$FR = A \cdot 0.78 \cdot V \cdot L \cdot 3.6$ (FR = filtering rate, in liter/hr; S = frontal area (surface) of open mouth, in cm^2, 0.78 = mouth openings per second, 3.6 = factor for converting cm^2 & body length/s to liter/hr)	Villavicencio and Muck (1985)
Frontal area of open mouth	$S = 15/(1 + e^{6-0.44L})$	Villavicencio and Muck (1985)
Filter feeding rate	$R = FR \cdot D \cdot 0.8$ (R = g/h; D = food density, in g/liter and 0.8 is an empirical retention factor)	
Upper limit of daily ration	$R = 7.57\ T \cdot L^{-1.4}$ (R = % of individual body weight per day)	Villavicencio and Muck (1985)
Daily total production per fish	$P_{tot} = (R \cdot h_a \cdot A) - ((ML_a \cdot h_a) + (ML_r \cdot h_r))$ (P_{tot} = cal/day; h_a = hours of activity, i.e., feeding; h_r = hours resting)	this contribution (see text)
Assimilation coefficient	A = fraction of ingested food available after fecal and excretory losses, as well as Specific Dynamic Action (Jobling 1983) are accounted for.	
Duration of feeding and resting periods	$h_a = R/l$ (for $h_a > 24$, $h_a = 24$; l = food ingestion rate expressed as % of body weight, per day; $h_r = 24 - h_a$).	as defined in text
Ratio of gonad production to total production	$G_o = 1/(1.1 + e^{6-0.5L})$	assumed value (see text)
Spawning	when $G_o = 0.1$ of gonad-free body weight	assumed value (see text)
Batch fecundity	Eggs = 1,104 + 614 W (W = ovary free female wet weight, in g) Batch = Eggs 0.0301 5.8/1,000 (g wet weight) 0.0301 = egg dry weight (mg); 5.8 = dry to wet weight conversion	Hunter et al. (1986); Hunter and Leong (1981)

iv) the filtering time required to obtain the daily ration is subtracted from 24 hours to obtain the resting time;

v) daily metabolic losses are computed as the sum of losses during feeding and losses during resting time;

vi) estimated daily ration is converted into calories, and the fraction of these calories available for growth is computed by multiplication of the (caloric) ration by the assimilation coefficient;

vii) daily total production is computed as the difference between the fraction of the food available and the sum of the metabolic losses;

viii) daily production (i.e., the growth increment) is added to the previous size estimate, i.e., to length, body weight and gonad weight;

ix) the body weight is decreased by the weight of the gonad when gonad weight reaches 10% of body weight;

x) return to (i) until an age of 4 years is reached.

Main Results of the Simulation

Fig. 14 shows anchoveta growth curves obtained for "1950" and "1980" conditions. Table 5 summarizes the results for two runs, while Table 6 shows the main results of the sensitivity analyses of the model. As might be seen, assimilation coefficient and caloric food content, both related to the food quality factor, have the strongest effects on model output. Table 6 also shows that these parameters, considered *alone* must be changed by 45% for anchoveta to change from its "1950" pattern to the "1980" pattern. On the other hand, if all parameters in Table 6 are changed *simultaneously*, a change of only 15% is needed for the "1950" to "1980" transition (see also Fig. 14).

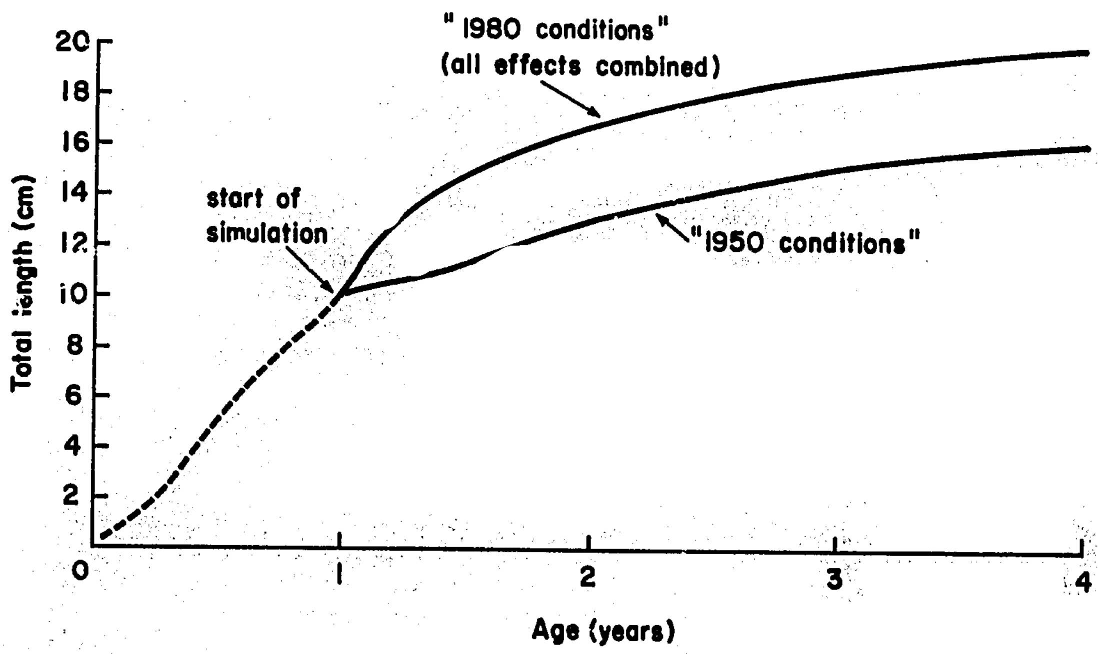

Fig. 14. Growth of Peruvian anchoveta as simulated using model described in text. Note that most of the difference between the "1950" and "1980" growth curves is due to growth rate differences of fish between 1 and 1.5 years.

Table 5. Summary of two runs of the anchoveta growth simulation model, for high ("1950") and low ("1980") anchoveta biomass.

Parameter (units)	1950 conditions		1980 conditions[b]	
	mean	range	mean	range
Weight increment (% BWD)[a]	0.27	0.17-0.41	0.65	0.32-1.49
Length increment (mm•d^{-1})	0.056	0.002-0.1	0.09	0.03-0.4
Metabolic losses (% BWD)	1.5	1.27-2.02	1.16	1.07-1.69
Ration (% BWD)	3.5	2.8-4.6	2.60	2.1-4.6
Growth efficiency (%)	9.3	5.0-12.2	23.76	10.7-22.4
Duration of feeding (h•d^{-1})	15.3	11.3-24.0	12	10.7-22.4

[a] % BWD = percent of body weight per day.

[b] with all factors affecting growth changed by 15% (see text).

Table 6. Sensitivity analysis of anchoveta growth simulation model.

Parameter	Small change (25%) applied to "1950" conditions from	to	Resulting length[a] at 4 yr (in cm)	Changes needed to move from "1950" to "1980" conditions % change	i.e., to
Duration of feeding period	15.3 h	11.4 h	17.2	-76	3.6 h
Metabolic cost per unit time feeding	100%	75%	17.8	-70	30%
Assimilation coefficient	0.60	0.75	18.7	+45	0.87
Energy content of 1 g of food (cal)	1,000	1,250	18.7	+45	1,450

[a] As compared with a length of 16 cm for the initial ("1950") conditions.

Discussion

Overall, our growth estimates match those obtained previously by other authors (Table 7, Fig. 15). However, the key finding presented here is obviously the strong evidence for density-dependent growth in the Peruvian anchoveta, a phenomenon for which only anecdotal evidence existed previously. Our ability to extract evidence for changes in the growth performance of anchoveta depended on two main factors not found elsewhere:

i) the availability of an extremely long time series of length-frequency data, and

ii) the availability of powerful software for the analysis of these time series.

Table 7. Review of some growth-related statistics in adults of *Engraulis* spp.

Parameter	Mean	Range	Species	Source
Daily ration (% body weight)	4.5	4-6	*E. mordax*	Hunter and Leong (1981)
	2.6	1.5-3.7	*E. encrasicholus*	Sirotenko and Danilevsky (1977)
	2.4	1.4-3.4	*E. encrasicholus*	Mikhman and Tomanovich (1977)
	3.5[a]	2.8-4.5	*E. ringens*	this
	2.6[b]	2.1-4.6	*E. ringens*	study
Growth efficiency (%)	12.8	–	*E. mordax*	Hunter and Leong (1981)
	9.3[a]	6-12.2	*E. ringens*	this
	23.9[b]	15-32	*E. ringens*	study
Daily length increment (mm)	0.020[c]	0.015-0.025	*E. mordax*	Parrish et al. (1985)
	0.053[a, d]	0.020-0.106	*E. ringens*	this
	0.056[b, d]	0.020-0.016	*E. ringens*	study
Daily weight increment (% BWD)	0.74[e]	–	*E. ringens*	Walsh (1975)
	0.28[a]	0.17-0.41	*E. ringens*	this
	0.65[b]	0.32-1.50	*E. ringens*	study
Spawning events per year	15.1	5.3-23.5	*E. mordax*	Parrish et al. (1986)
	20.0	–	*E. mordax*	Hunter and Leong (1981)
	[9.6][f]	–	*E. ringens*	Alheit (1986)
	6.0[a]	4.0-9.5	*E. ringens*	this
	17.3[e]	14.0-22.0	*E. ringens*	study
	24.2	–	*E. ringens*	Pauly and Soriano (this vol.)

[a] "1950" condition.

[b] "1980" condition, combined effects.

[c] Computed from Table 2 of Parrish et al. (1985) and referring to the Central (California) stock.

[d] Refers to anchoveta of 1.5 yr and more to allow comparison with data in [c].

[e] Most favorable upwelling conditions.

[f] Refers only to the main spawning months (August & September), and hence, cannot be directly compared to other values.

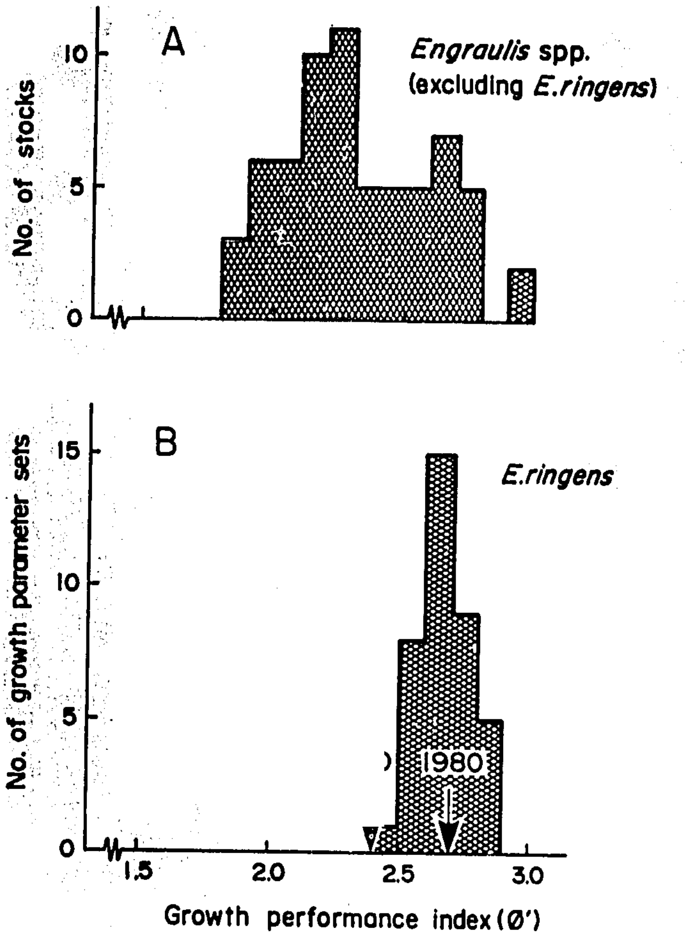

Fig. 15. A. Frequency distribution of growth performance indices in *Engraulis* spp. (excl. *E. ringens*), showing a wide range covered by the genus. Based on data in Pauly (1978), Radovich and MacCall (1979), Volovik and Kozlitina (1983), Melo (1984) and Gallardo-Cabello (1985). B. Frequency distribution of growth performance indices in *E. ringens* showing that the species grows, as a whole, better than other *Engraulis* spp.; the arrows refer to values of ϕ' for 1950 and 1980 on Fig. 5 and express the density-related change of anchoveta growth identified in the present study (see text).

Density dependence, as demonstrated here, is not confined to anchoveta and indeed numerous authors have shown that growth rates are density-dependent in a large number of fishes, especially as far as juveniles are concerned (Cushing 1973; Mathisen et al. 1978). This is confirmed by our simulation model, which generated mean growth rates of about 0.05 mm/day for both "1950" and "1980" conditions in fish of more than about 1.5 years (see Fig. 14 and Tables 6 and 7), suggesting that density-dependent growth affects mainly juveniles and young adults.

The existence of marked seasonal growth oscillations (not considered in the simulation model) in anchoveta also show this fish to behave, with regard to temperature, just as other fish do (see Fig. 16), i.e., length growth rate is reduced when temperature is low even if the cold period corresponds to a major upwelling and hence to increased food availability.

The main problem thus remaining is the identification of the cause(s) for the density-dependent growth changes presented here.

Clearly, the "holistic" model presented here as Fig. 8 and equation (5) cannot be used to distinguish potential causes - all the model can do is roughly quantify their *combined* effect. A "reductionistic" model such as the one presented in Fig. 13 and in the preceding section, on the

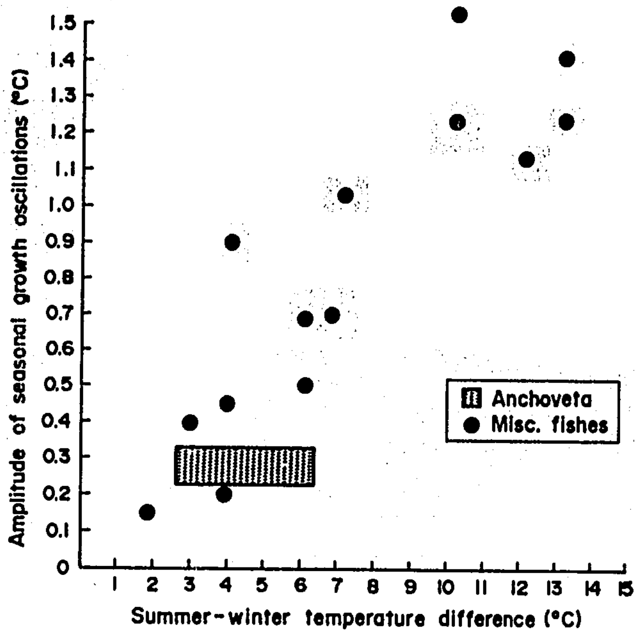

Fig. 16. Relationship between the amplitude of seasonal oscillations in the growth in length of temperate and tropical fishes (= C in equation 1) and the difference between highest and lowest mean monthly water temperature. The shaded area, referring to *E. ringens* off Peru (4-14°S) shows that anchoveta growth is reduced, during the cold season just as one would predict from other fishes. Modified from Pauly and Tsukayama (1983).

other hand, can be used to identify such factors and their effects, both singly and in the aggregate.

However, translating the assumptions and results of a given model into those of another model is not straightforward, and is indeed rather akin to translating puns from one language to the other. Thus, to take the analogy one step further, one could provide a "translation" of the model in Fig. 8 in terms of the model in Fig. 13. This would read as follows:

> Fish stop growing when the metabolic costs of all their activities invoke an oxygen demand which matches the average oxygen supply through their gills. Hence, factors such e.g. as reduced food competition, improved food quality or a shift from filter to particulate feeding, by reducing their overall metabolism, increases the body weight at which oxygen supply per unit weight becomes limiting.

Thus, one should expect the two models to give similar results only in terms of combined effects - and here indeed the agreement is remarkable, as the holistic and reductionistic models give results (i.e., aggregate percent changes of growth-enhancing factors needed for the transition from "1950" to "1980" conditions of 16 and 15%, respectively.

Previous investigations by Tsukayama (1965, 1966) and Mendiola (1979) have shown that the fish of the southern stock of anchoveta which feed on zooplankton more than the mainly planktivorous fish of the northern/central stock, also have coarser gill rakers and shorter guts.

If a major shift by anchovetas of the northern/central stock toward particulate feeding of zooplankton occurred, this should be reflected, therefore, in their now having coarser gill rakers and shorter guts than was previously estimated by the authors cited above, i.e., the fish should have become "southernized", as is also expressed by the increase of their maximum size. It is suggested here that the analysis of the large database presently being standardized at IMARPE on anchoveta stomach contents, covering the years 1954 to the present, be complemented by a comparison of gill raker counts and gut length analysis of fish taken at the sites previously sampled by the two authors cited above. Such comparison would indeed provide a clear-cut test of the postulated "southernization" of the northern/central stock of Peruvian anchoveta.

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VPA Estimates of the Monthly Population Length Composition, Recruitment, Mortality, Biomass and Related Statistics of Peruvian Anchoveta, 1953 to 1981*

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Abstract

A recently developed version of length-structured Virtual Population Analysis, implemented in the form of a graphic-oriented microcomputer program (ELEFAN III) was used to estimate, on a monthly basis, the population in number and weight by 1 cm length class of the Peruvian anchoveta (*Engraulis ringens*, northern/central stock). The analyses were performed with predation (by three species of guano birds, by bonito and two species of seals) accounted explicitly, and with estimates of (residual) natural mortality obtained by back calibration with independent acoustic estimates of biomass. The estimated biomasses rather faithfully reflect environmental perturbations (El Niño events) and human interventions (fishing and overfishing).

Likely sources of errors involved in the analysis are discussed.

Introduction

Numerous previous estimates of the biomass of Peruvian anchoveta exist and may be found in the form of time series in various pamphlets, reports and/or books on topics ranging from the economics of soya bean exports to oceanographic forecasting. Yet these time series not being structured by size (or age group) nor having a time scale sufficiently small to reflect the rapid changes of biomass experienced by the anchoveta, are largely useless for research, e.g., as element of models for predicting fisheries yields.

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We shall present here biomass estimates that are structured by length (1 cm classes) and which have a monthly time scale. Also, the time span covered shall extend from 1953 to 1981, i.e., covering the Peruvian anchoveta fishery from its beginning to a period shortly preceeding its total demise at the height of the 1982-1983 El Niño.

The estimates we present do not call into question the overall magnitude of previous estimates of biomass as obtained previously, mainly through acoustic surveys. The reason for this is that the model we used - Virtual Population Analysis (VPA) - and the specific fashion we implemented it, i.e., adding fish removed by major predators to fish taken by the fishery, necessitated estimates of residual mortality (i.e., that part of natural mortality *not* caused by major predators (here coded "M_O") which we had no way of estimating independently.

Therefore, we have used available estimates of biomass for calibration, i.e., to obtain estimates of M_O, with the result than our analysis, rather than challenging the existing anchoveta estimates, actually gives them additional coherence by integrating them with other information.

Materials and Methods

Computation of Total Withdrawals and Catch-at-Length Data

The bulk of the material used here is represented by the nominal catch and catch composition data in Tables 1 to 30 of Tsukayama and Palomares (this vol.). To account for unrecorded catches (Castillo and Mendo, this vol.), we have multiplied all monthly nominal catches by 1.2. Much could be said *pro* or *contra* this value; however, it has little impact on VPA estimates of biomass given that the M_O values estimated from the independent biomass estimates are inversely related to such multiplicative factor.

The estimated quantities of anchoveta consumed monthly by cormorants, boobies and pelicans (from Muck and Pauly, this vol.) by bonito (from Pauly, Palomares and Gayanilo, this vol.), and by two species of seals (from Muck and Fuentes, this vol.) were then added to the corrected catches of the fishery to obtain total withdrawals on a monthly basis (Table 1). We shall refer to these total withdrawals as "catches" and use the terms "catch-at-length" when referring to the monthly "number-of-fish-withdrawn-by-length-class", except in cases where *fishery catches* must be explicitly differentiated from *predatory losses*.

The detailed analyses on each of the major anchoveta predators considered here shows that they consumed anchoveta of sizes largely matching those of the fishery (see Jordan 1959; Figs. 1-3 in Muck and Pauly, this vol.; Fig. 7 in Pauly, Vildoso, et al., this vol.; Fig. 1 in Muck and Fuentes, this vol.), thus justifying the approach of pooling the withdrawals by the fishery with those of the birds, the bonito and the seals.

The % catch composition data in Tables 1 to 30 of Tsukayama and Palomares (this vol.) were raised to this catch (i.e., total withdrawals) by means of raising factors (R.F.) computed, for each month (i) separately, from

$$R.F_{(i)} = \text{catch}_i / W_{s(i)} \qquad ...1)$$

where $W_{s(i)}$ is the weight of the % composition data in month (i). The values of $W_{s(i)}$ were obtained from

$$W_{s(i)} = \sum_{j=1}^{n} f_{ij} \cdot \overline{W}_{ij} \qquad ...2)$$

where $\overline{W}_{ij}$ is the mean weight of fish in class j of sample (i.e., month) (i), n the total number of length classes in that sample, and f_{ij} the % frequency of class (j) in sample (i). The values of W_j were estimated, given a length weight relationship of the form

$$W = a_i \cdot L^b, \qquad \text{...3)}$$

from

$$\overline{W} = 1/(L_{j2} - L_{j1}) \cdot a_i/(b + 1) \cdot [L_{j2}^{b+1} - L_{j1}^{b+1}] \qquad \text{...4)}$$

where L_{j1} and L_{j2} are the lower and upper limits of class (j), and which provides an unbiased estimate of the mean weight of fish in a given length class (Beyer 1987). All computations were performed with the value of b in equation (4) set equal to 3 (i.e., isometric growth and the appropriate values of a = c.f./100; see Tsukayama and Palomares, Tables 1 to 30 and text).

This procedure, implemented here through the ELEFAN III program was applied 360 times, i.e., to all % length-frequency samples in Tsukayama and Palomares (this vol.) as well as to the samples interpolated to fill in gaps (see below). The resulting matrix of monthly catch at length data, covering the years 1953 to 1982 was used for all VPAs.

Brief Description of Length-Structured VPA

Beverton and Holt (1957) showed that the catch (C_i) from population during a unit time period (i) is equal to the product of the population size at the beginning of the time period (N_i) times the fraction of the deaths caused by fishing, times the fraction of total deaths, or

$$C_i = \frac{F_i}{Z_i} (1 - e^{-Z_i}) N_i \qquad \text{...5)}$$

where F_i is the fishing mortality in the ith period, M is the natural mortality, generally assumed constants for all period and $Z_i = F_i + M$.

The version of Beverton and Holt's catch equation which has become most widely used for stock assessment purposes, however, is

$$\frac{N_{i+1}}{C_i} = \frac{Z_i \cdot e^{-Z_i}}{F_i (1 - e^{-Z_i})} \qquad \text{...6)}$$

also written

$$\frac{C_i}{N_{i+1}} = \frac{F_i}{Z_i} (e^{Z_i} - 1) \qquad \text{...7)}$$

which is the equation in Gulland's (1965) VPA and which can be derived from (5) by substituting for N_i the relationship

$$N_i = N_{i+1} \cdot e^{Z_i} \qquad \text{8)}$$

Given values of C_i and an estimate of M (here: "M_o") equation (7) can be used to estimate (retroactively) the size of past cohorts (i.e., of groups of fish born at the same time and exposed to the same mortalities throughout their lives), given an estimate of N_{i+1} from which to start the computation. Such estimate of N_{i+1} (expressing the last population size a cohort had before it went extinct) are usually called "terminal populations" (N_t). Values of N_t can be obtained from

$$N_t = C_t / F_t \qquad \text{...9)}$$

where C_t is the terminal catch (i.e., the last catch taken from a cohort before it went extinct) and F_t is the terminal fishing mortality, i.e., the fishing (here inclusive of predation) pressure that generated C_t (Mesnil 1980; Pauly 1984).

The feature of VPA that is most important in the context of this contribution is that, given a high fishing pressure, estimates of population size obtained by repeated application of equations (6) or (7) tend to rapidly converge toward their true value, and hence usually provide, given reasonable estimates of M, very reliable estimates of recruitment (Pope 1972; Pauly 1984). Moreover, the speed of convergence from the guessed values of N_t (i.e., values of N_t based on guessed values of F_t) toward accurate values of N_i is a function of the ratio of F to M. That is, the higher the proportion of the cohort is which ends up being caught by the fishery (here: and eaten by birds, bonito or seals), the more reliable will the population estimates be. This is the reason why we have here, through the contributions of Muck and Pauly; Pauly, Palomares and Gayanilo; Muck and Fuentes (this vol.) accounted explicitly for the anchoveta consumed by birds, bonito and seals, respectively, and thus left M_o low, rather than replace predation by a higher constant estimate of M.

Three forms of VPA, all included in the ELEFAN III program may be distinguished (Pauly and Tsukayama 1983):

i) VPA I, which is the version originally proposed by Gulland (1965) and which Pope (1972) reformulated as "Cohort Analysis",

ii) VPA II, the VPA equivalent of Jones' (1981) "Length Cohort Analysis" (see also Jones and van Zalinge 1981; Pauly 1984), and

iii) VPA III, the model used here as originally proposed by Pope et al. (MS).

VPA III is a version of VPA I performed on "cohorts" obtained by superimposing growth curves, drawn at monthly intervals, onto a set of catch-at-length data, the catch pertaining to each "cohort" and month being simply that part of the monthly catches contained between two adjacent growth curves (see Fig. 1).

For such cohorts to really consist of fish recruited at the same time, the growth curves used for "slicing up" a cohort must be obviously as close to the true growth curve of that cohort as possible. This, among other things, makes it imperative that a seasonally oscillating growth curve be used since, as shown in Pauly and Ingles (1981) and Pauly (1982), virtually all natural fish stocks, including those occurring in tropical waters, display seasonally oscillating growth (see also Palomares et al., this vol.).

In reality, not all fish of a given cohort have the same growth parameters, however, and it can be expected that some fish will "leave their cohort" because they grow either faster or slower than predicted by the mean cohort growth curve. Such differences in growth rate should here have the effect of artificially increasing the autocorrelation between estimates of recruitment (see Mendelsohn and Mendo, this vol.; Pauly, this vol.).

The growth curves used here to "slice cohorts" were based on the seasonally oscillating version of the von Bertalanffy Growth Function (VBGF) presented by Pauly and Gaschütz (1979) i.e.,

$$L_t = L_\infty (1-\exp(-[[K(t-t_o)] + [KC/2\pi \sin 2\pi(t-t_s)]]) \qquad ...10)$$

where Lt is the length at age t, L_∞ the asymptotic length, K a growth constant, to the "age" at which length is zero if the fish always grew according to the equation, C is a dimensionless constant expressing the amplitude of the growth oscillations and t_s is the time (with respect to t = 0) at the beginning of a sinusoïdal growth oscillation of period one year.

For practical purposes the estimation of t_s was replaced by the estimation of a Winter Point (WP), defined as

$$t_s + 0.5 = WP \qquad ...11)$$

which expresses (as a fraction of the year) the time during which growth is slowest. It should be mentioned here that the ELEFAN programs, being based on length-frequency data (rather than length-at-age data) do not allow for the estimation, nor require estimates of t_o, hence of *absolute* ages (see Palomares et al., this vol.); all "ages" used internally by the programs are *relative* ages, expressed in relation to an arbitrary birthdate that is set internally and not output by the program.

The VPA III routines of ELEFAN III were applied to the available catch-at-length data using the growth parameters given in Table 2. The small year-to-year differences in the values of

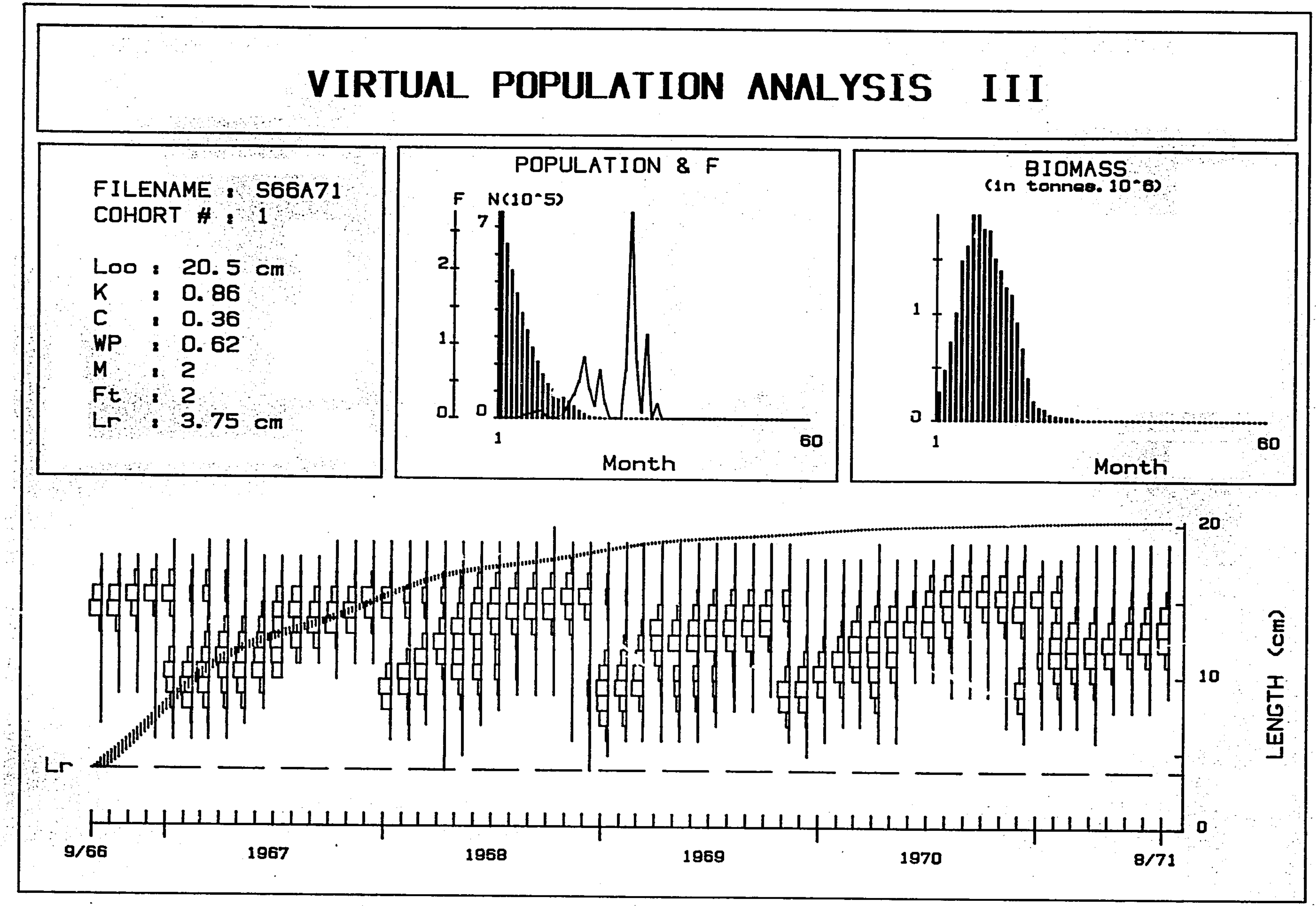


Fig. 1. Facsimile of an ELEFAN III output (via plotter) showing monthly catch-at-length data (not to scale) and one of the many monthly cohorts which can be superimposed on these data. The upper two panels show the population and fishing mortality estimate pertaining to this cohort, along with its biomass (rightmost panel). The population estimate pertaining to month 1 is an expression of recruitment of fish of length L_r (here 3.75 cm, i.e., the lower limit of the class with midlength 4.25 cm).

these parameters caused a slight overlap of some "cohorts" (i.e., some of the catch data were used twice), and small gaps (i.e., some of the catch data were not included in any cohort). This source of error could have been avoided by using the same growth parameters throughout. This, however, would have caused a large bias, given the strong positive trend in anchoveta growth performance documented in Palomares et al. (this vol.).

Interpolation of Missing Sets of Monthly Size-Composition Data

Although the monthly catch data (in weight) used for the present analyses are complete, the monthly size composition data needed to derive monthly catch-at-length data are not (see Tables 1 to 30 in Tsukayama and Pauly, this vol.). Since uninterrupted series of catch-at-length data are needed for VPA III, we have linearly interpolated size-frequency distributions where gaps appeared in the original data (except for January-October 1953, where we have used the corresponding values for 1954). We believe this approach had no major detrimental impact on our results for three reasons:

i) linearly interpolated % length-frequency samples are very similar to "real" samples (see Fig. 2) if only because the overall shape of such samples is determined mainly by continuous, rather "smooth" processes (i.e., growth and mortality);

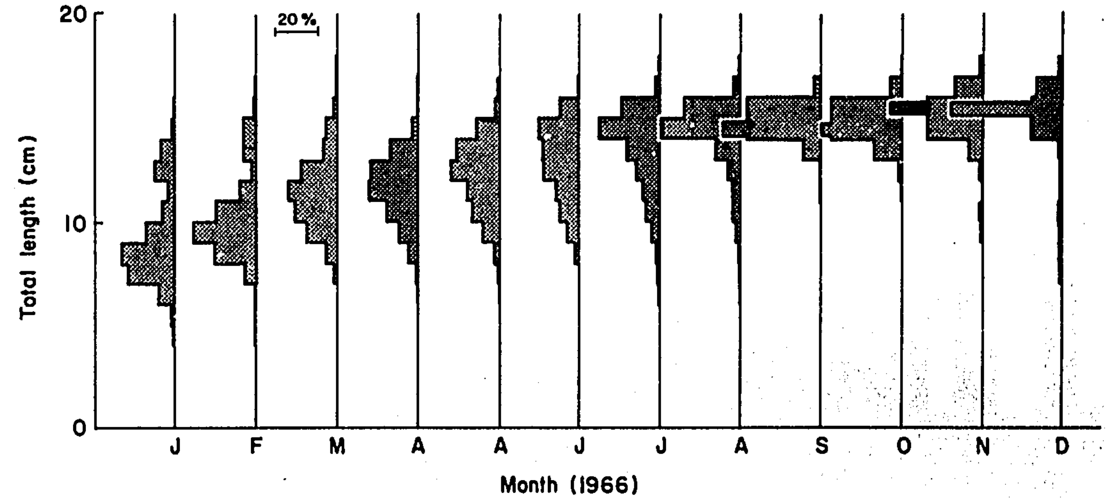


Fig. 2. Length-frequency data of Peruvian anchoveta (northern/central stock), including samples that were linearly interpolated. The reader is invited to guess which samples were interpolated.

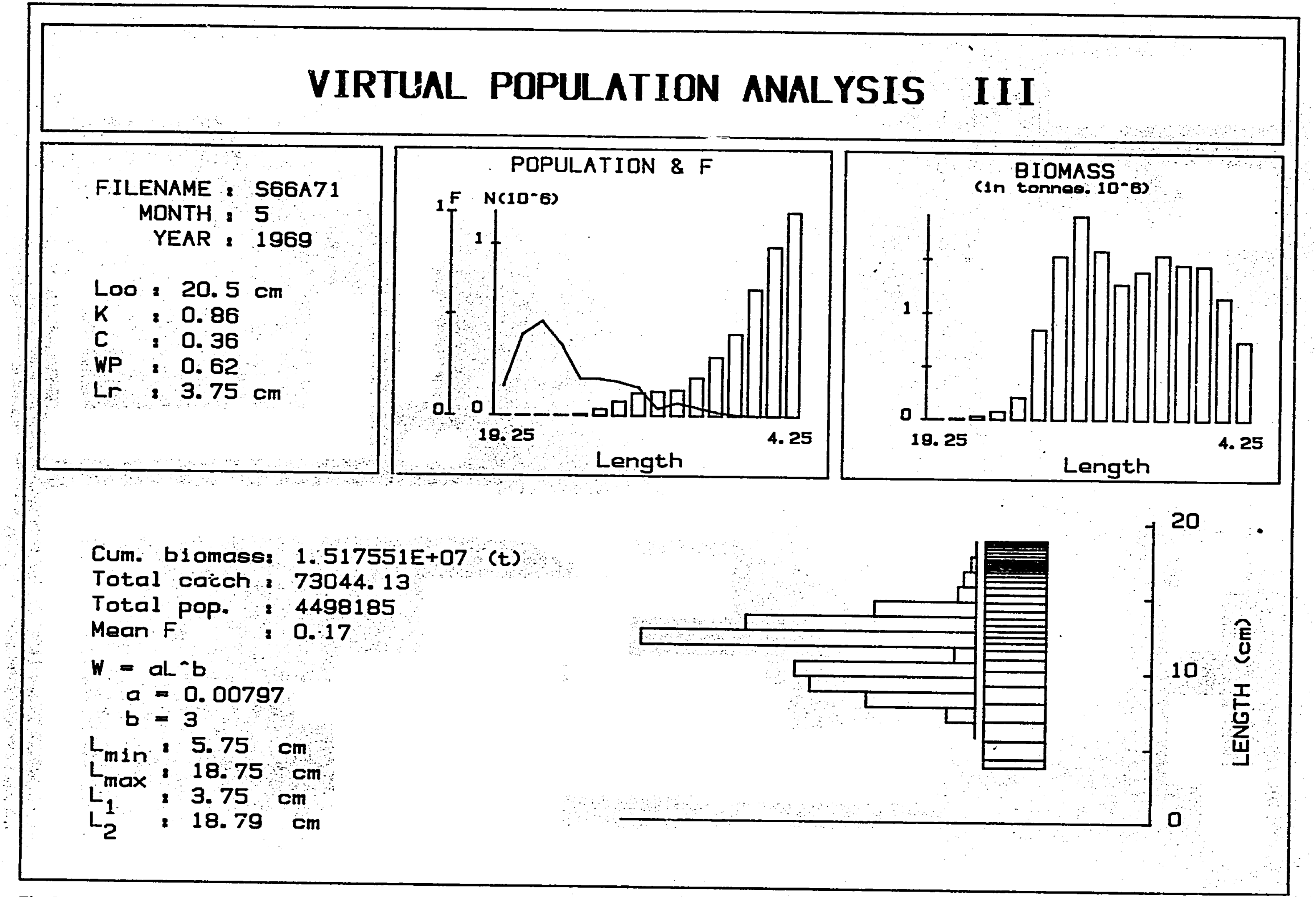
(The interpolated months are June, July, August and November.)

ii) VPA estimates of F and population size in a given time interval are not predominantly determined by the catch composition in that very interval, but by the catch in that interval and the catches and catch composition in *previous* intervals (VPA runs *backwards!*). Hence whatever error is introduced by interpolating will be spread over several intervals, and its absolute impact on mortality and population estimates pertaining to a given interval thus reduced.

iii) catch-at-length data as used in VPA III are estimated from both length composition data *and* catch data in weight. While the former were interpolated in some cases, the latter were always "real" and hence the overall number of fish caught in a given month tended to be reasonably approximated, even though their size composition was interpolated.

Estimation of Monthly Recruitment and Biomass

Monthly population estimates per length class were obtained by regrouping monthly values of N_i obtained on a cohort basis into regular class intervals (the same intervals as those in which the catch data were originally grouped). The population estimates in the smallest class considered here (3.75 to 4.75 cm) are here defined as "recruitment" (of fish with mean length 4.25 cm).



VIRTUAL POPULATION ANALYSIS III

FILENAME : S66A71
MONTH : 5
YEAR : 1969

Loo : 20.5 cm
K : 0.86
C : 0.36
WP : 0.62
Lr : 3.75 cm

Cum. biomass: 1.517551E+07 (t)
Total catch : 73044.13
Total pop. : 4498185
Mean F : 0.17

W = aL^b
a = 0.00797
b = 3
L_{min} : 5.75 cm
L_{max} : 18.75 cm
L_1 : 3.75 cm
L_2 : 18.79 cm

Fig. 3. Facsimile of an ELEFAN III output (via plotter) showing summary of result of a VPA III pertaining to a given month (here May 1969), and showing the catch data (lower panel, right, histograms) the cohorts "passing through" that month (box with narrowing lines), the size structure of the population (upper boxes, center and left, as well as summary statistics (lower panel, left). Details are given in the software documentation.

The population estimates (in numbers), by length class, were then multiplied, for each month and length class separately by the appropriate value mean weight values (see equation 4) to obtain monthly population biomass by length class (Fig. 3).

All analyses were run with $F_t = 2(y^{-1})$. It is recalled that these values (a) pertain to Z-M_0 (i.e., to the sum of true fishing mortality plus all sources of natural mortality represented by distinct predators and (b) that values of F_t have little impact on final results, especially on recruitment estimates.

Estimation of Natural and Fishing Mortalities

The natural mortality (M_p) exerted by any given predator (p) with anchoveta consumption ($C_p(i)$) was estimated, for each month (i) from

$$M_{p(i)} = \text{anchoveta consumption } (C_p(i))/\text{anchoveta biomass } (i) \quad \text{...12)}$$

Similarly, fishing mortality (F) was estimated from

$$F_i = \text{anchoveta fishery catch } (i)/\text{anchoveta biomass } (i) \quad \text{...13)}$$

Thus, all estimates of mortality presented here pertain to weights, not numbers. [Note, however, that computations of number-based mortality values are possible, based on the data presented in this volume.] From these data, total mortality (Z) can be estimated from

$$Z_i = F_i + M_0 + \sum_{m=1}^{3} M_{p(i)} \quad \text{...14)}$$

where m is the number of predator groups considered here (i.e., birds, bonito and seals).

Results and Discussion

Estimate of M_0 and Their Implications

Table 3 gives the values of M_0 obtained iteratively, i.e., by changing values of M_0 until biomass were obtained which closely matched the independent biomass estimates in that same table. The same values of M_0 are also plotted as time series in Fig. 4. As might be seen, the estimates of biomass in Table 3 force us to assume that M_0, which took values of about $2y^{-1}$ in the 1960s, dropped to about $0.5y^{-1}$ in 1975, rapidly increased to about $4y^{-1}$ in 1976 and stayed at this high level until the late 1970s. (We shall present below evidence suggesting that the natural mortality of anchoveta did decrease in the early 1970s, as illustrated on Fig. 4.) The value of $M_0 = 4y^{-1}$ for the late 1970s suggest that an important predator, ignored in our analyses, managed to continue consuming a large amount of anchoveta in spite of their very reduced biomasses in the late 1970s (Pauly, this vol.).

Estimates of Anchoveta Biomass and Recruitment, 1953 to 1981

Tables 4 to 33 present the key results of our analyses, i.e., the monthly recruitment estimates and the monthly biomasses, by length group, respectively, obtained through the VPA III routine of the ELEFAN III program.

Fig. 5, based on Tables 5 to 33, shows the monthly sums of biomass over all length groups, for 1953 to 1982. One part of this time series, covering the years 1963 to 1979 illustrates the match of our biomass estimates to the independent biomass estimates used to calibrate the VPA (i.e., to esimate M_0). That part of the time series presents no surprise, except perhaps for the fact

Table 1. Total monthly withdrawals of anchoveta, 1953-1982 (4-14°S) in tonnes.[a]

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual sum
1953	172,325	199,136	92,571	154,261	152,967	186,928	137,930	118,142	153,313	212,868	263,163	218,188	2,061,792
1954	166,672	202,551	187,266	235,332	269,842	296,327	222,086	177,561	201,589	210,850	281,843	193,539	2,645,458
1955	169,085	210,267	180,784	216,229	238,964	275,663	229,692	208,169	224,131	197,935	242,713	186,845	2,580,477
1956	151,439	180,214	209,841	248,458	227,417	254,725	217,918	163,157	171,757	203,191	223,343	176,286	2,427,746
1957	196,044	103,777	109,546	124,942	105,958	153,424	113,117	86,445	123,365	196,850	235,230	188,419	1,737,117
1958	159,711	136,415	142,203	180,142	192,855	163,362	97,394	122,120	141,740	186,491	221,291	202,956	1,946,680
1959	278,720	224,134	294,788	331,039	298,496	262,756	246,974	186,905	201,499	309,220	488,693	476,245	3,599,469
1960	489,499	456,819	452,101	329,552	270,635	433,151	269,128	219,058	272,677	338,971	530,660	589,976	4,652,227
1961	633,344	566,837	439,200	536,879	633,954	526,594	389,189	331,984	343,770	562,806	813,396	822,460	6,600,413
1962	601,292	577,221	635,309	756,421	889,586	649,631	526,208	423,099	482,055	687,302	1,056,724	1,092,780	8,377,628
1963	1,020,448	358,030	832,859	922,170	877,415	480,807	294,012	278,416	337,413	540,481	824,818	954,703	7,721,572
1964	1,300,665	893,868	1,269,644	1,097,514	862,785	586,399	555,688	323,171	338,564	853,595	1,130,233	1,215,972	10,428,098
1965	1,329,674	838,527	1,317,907	994,144	849,356	650,866	73,284	46,125	118,250	285,351	809,297	1,435,436	8,748,217
1966	1,637,331	1,226,818	1,366,247	1,205,989	1,126,118	43,646	42,323	44,500	717,298	1,077,463	44,028	1,188,973	9,720,734
1967	1,855,000	732,557	1,105,166	1,499,645	1,355,314	197,963	45,434	51,915	333,988	1,370,470	1,519,904	1,675,723	11,743,079
1968	1,795,685	1,108,654	922,816	1,320,189	1,167,869	23,432	23,933	25,926	1,519,219	1,511,769	1,149,290	1,079,544	11,648,326
1969	1,497,099	24,485	2,143,191	1,529,121	975,930	22,316	19,933	20,733	600,449	585,527	469,795	2,186,282	10,074,861
1970	2,419,500	1,205,395	1,218,595	2,301,691	1,017,383	68,653	30,163	18,488	1,431,385	1,539,584	1,211,783	896,093	13,358,713
1971	23,572	24,075	2,866,270	1,771,166	788,862	134,698	24,654	23,932	1,362,641	1,495,016	1,298,701	1,438,913	11,302,500
1972	29,418	20,514	2,000,955	1,647,038	426,029	188,817	14,098	13,493	12,680	12,290	11,994	27,474	4,404,800
1973	10,226	301,114	1,171,497	419,390	10,272	9,755	8,837	11,417	31,154	21,334	49,555	5,482	2,050,033
1974	3,568	3,987	600,264	1,046,470	580,670	3,471	4,072	3,876	43,472	751,095	644,109	3,060	3,688,114
1975	213,905	371,281	393,258	963,940	648,223	19,507	5,191	4,369	5,426	15,944	6,906	19,625	2,667,575
1976	321,080	66,033	422,216	691,773	384,836	621,501	175,766	3,133	2,995	96,150	470,255	426,057	3,681,795
1977	225,300	3,710	4,362	322,235	159,643	3,971	3,890	4,407	4,212	4,939	6,359	6,052	749,080
1978	3,980	63,705	5,248	102,001	105,761	113,735	58,077	3,513	3,617	3,711	27,554	251,471	742,373
1979	2,784	3,597	312,380	726,659	2,838	2,624	2,200	2,085	1,967	81,281	33,898	1,547	1,173,860
1980	2,253	2,360	2,770	3,376	150,690	35,208	3,284	3,079	3,186	3,726	4,377	59,270	273,579
1981	2,176	2,295	2,044	35,049	66,048	63,234	1,576	1,471	1,270	31,445	12,778	143,730	363,116
1982	2,139	60,890	177,414	224,304	251,896	237,787	337,080	1,966	5,118	22,173	67,112	89,142	1,477,021

[a] Total withdrawals = nominal catch x 1.2 plus consumption by guano birds, bonitos and seals (see text).

Table 2. Inputs used for VPA III estimates of monthly anchoveta biomass off Peru, 1953 to 1982.[a]

Year	$L_{(\infty)}$[b]	K'[c]	M_0[d]	Year	L_∞	K	M_0
1953	18.4	0.78	2.00	1968	20.4	0.87	2.00
1954	18.6	0.78	2.00	1969	20.5	0.88	2.00
1955	18.7	0.79	2.00	1970	20.7	0.88	2.00
1956	18.8	0.79	2.00	1971	20.8	0.89	2.00
1957	19.0	0.80	2.00	1972	20.9	0.90	1.95
1958	19.1	0.81	2.00	1973	21.1	0.90	1.75
1959	19.2	0.81	2.00	1974	21.2	0.91	1.15
1960	19.4	0.82	2.00	1975	21.3	0.92	0.80
1961	19.5	0.82	2.00	1976	21.5	0.93	1.70
1962	19.6	0.83	2.00	1977	21.6	0.94	3.90
1963	19.8	0.84	2.00	1978	21.7	0.94	4.00
1964	19.9	0.84	2.00	1979	21.9	0.95	4.00
1965	20.0	0.85	2.00	1980	22.0	0.96	4.00
1966	20.2	0.85	2.00	1981	22.1	0.97	4.00
1967	20.3	0.86	2.00	1982	22.2	0.98	4.00

[a] Other inputs, used throughout, were C = 0.3, WP = 0.7 and F_t = 2 (see text).

[b] Total length, in cm; from Fig. 7 in Palomares et al. (this vol.).

[c] y^{-1}; from Fig. 7 in Palomares et al. (this vol.).

[d] Monthly means, as read off eye fitted line in Fig. 4; values used for VPA III linearly interpolated in steps of 3 months.

Table 3. Independent estimates of anchoveta biomass off Peru (4-14°S) and estimated values of baseline natural mortality (M_0) using VPA III.

Date	Independent biomass estimate (t x 10^6)[a]	Source of biomass estimates	VPA III estimates of M_0
Jan 64	14.20	Fig. 1 and text IMARPE (1974a)	1.90
Jan 65	11.20		2.15
Jan 66	13.30		1.78
Jan 67	13.80		1.68
Jan 68	13.30		1.67
Jan 69	12.50		2.38
Jan 70	18.30		2.23
Jan 71	15.40		2.03
Mar 72	3.00		(<0)
Sep 72	2.00		1.40
Jan 73	3.16	IMARPE IM-168 (1974b)	1.54
Feb 73	3.30[b]		1.35
Sep 73	3.09		1.17
Nov 73	4.48		1.48
Feb 74	3.39		0.73
May 74	2.19		0.25
Aug 74	3.92		1.28
Sep 74	3.09		0.84
Nov 74	3.25	IMARPE (1975)	1.19
Feb 75	4.32		1.55
Aug 75	3.39	Johannesson and Vilchez (1981)	2.60
Sep 75	4.27		3.18
Jan 76	7.41		3.52
Aug 76	4.62		3.99
Feb 77	1.89		5.15
Jul 77	1.39		4.17
Jun 78	3.78		3.79
Nov 78	2.02		2.99
Apr 79	2.15		4.27

[a] All values adjusted to pertain only to the region between 4 and 14°S.

[b] See also Johannesson and Robles (1977).

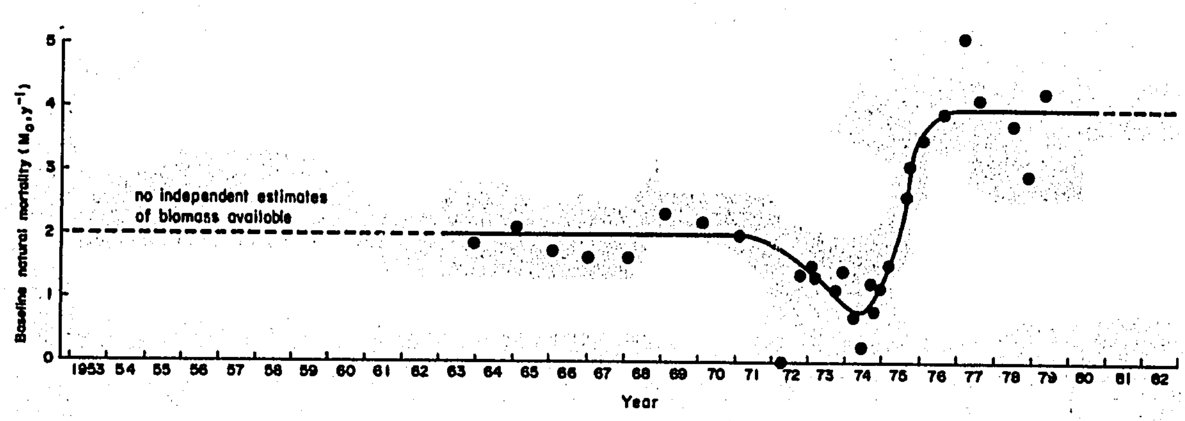


Fig. 4. Estimates of baseline natural mortality (M_0) as required to reproduce independent estimates of anchoveta biomass using the VPA III routine of the ELEFAN III program. Line is eye fitted. Note forward and backward extrapolations of $M_0 = 4\ y^{-1}$ and $M_0 = 2\ y^{-1}$, respectively (see also Table 2 and text).

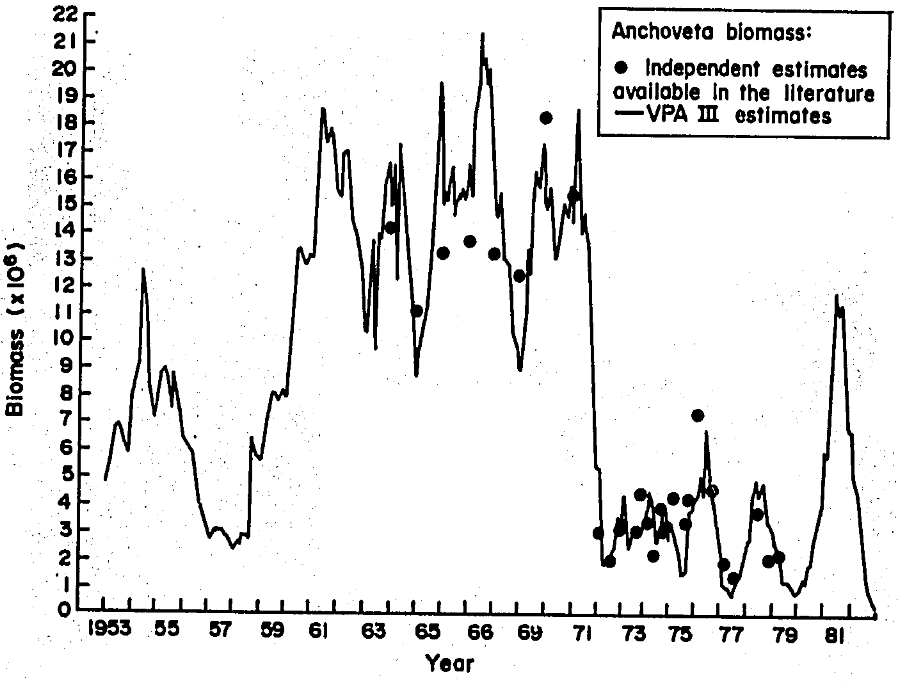


Fig. 5. Biomass estimates of Peruvian anchoveta, 4-14°S, obtained through the VPA III routine of the ELEFAN III program (see text), and showing independent biomass estimates used to calibrate VPA.

that seasonal oscillations and other within-year changes appear to be far more intense and rapid than had previously be assumed.

Little comments are needed for the parts covering 1980 to 1982, except perhaps that the decline of the biomass to a very low level prior to the onset of the 1982-1983 El Niño is, in part, an artifact due to the absence of catches and consumption estimates to "feed into" the VPA in 1983 to estimate the 1982 biomasses. For this reason, we have omitted the year 1982 from the detailed results on biomasses given in Tables 5 to 33.

The anchoveta biomasses estimated for the 10 years preceding the first available independent standing stock estimates, i.e., the years 1953 to 1962, are interesting in that they are lower than expected (see Table 3 in Muck and Pauly, this vol.). Interestingly, these biomass estimates suggests that the anchoveta suffered from the 1957 El Niño almost as much as from that of 1971-1972. This indeed would explain the massive bird mortalities recorded from that period (see Tovar et al., this vol.). It should be noted, however, that this point is, in part at least, a circular argument, since we used, among other things, bird population data to estimate bird

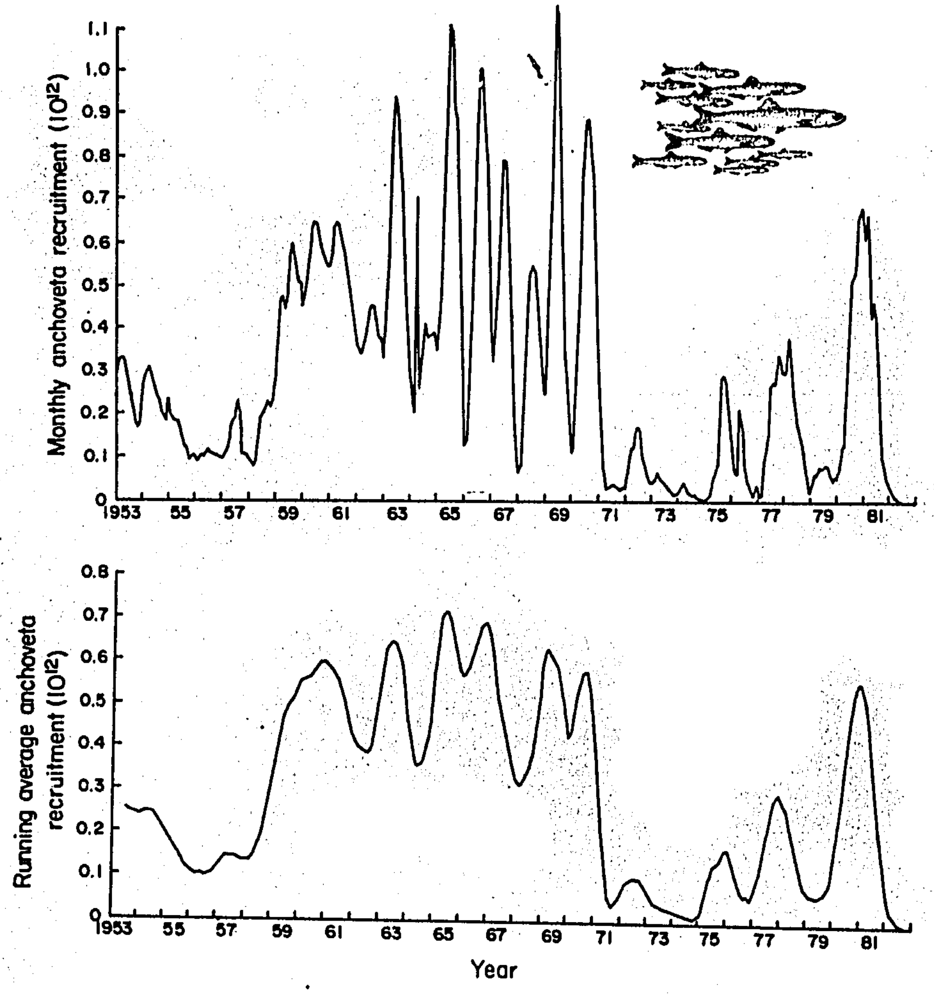


Fig. 6. Time series of recruitment (of fish ranging from 3.75 to 4.75 cm, slightly less than 3 months old) into the anchoveta stock, January 1953 to mid-1982. *Above:* monthly recruitment, showing increasing variability, from the late 1950s to 1970, probably due to increasing fishing pressure and leading to recruitment collapse in early 1971, prior to the onset of the 1971-1972 El Niño. *Below:* smoothed data (using a 12-month running average), showing that the 1960s, which saw the buildup of the fishery, may have been a period of exceptionally and steadily high recruitment.

anchoveta consumption, and since such consumption, at a time when the fishery was just starting, should have had a great impact on the VPA estimates of biomass.

Fig. 6, based on Table 4, shows two time series of anchoveta recruitment: one consists of monthly estimates of the number of young fish (of 3.75-4.75 cm, i.e., about 3 months old) entering the fishery, the other illustrating the same data, but as 12 months' running average to show interyear changes.

As might be seen, these time series closely resemble the time series of biomass, which is not surprising in a fish with a short lifespan. Important aspects of the time series in Fig. 6 are:

i) the increased within year variability of recruitment from the late 1950s to the late 1960s, presumably an effect of fishing, and

ii) the fact that the major recruitment collapse of 1971 appears to have occurred *before the onset of the 1971-1972 El Niño* (see also Mendelsohn and Mendo, this vol.)

These two aspects, already apparent in the earlier analysis of Pauly and Tsukayama (1983) imply that much of what has been written about the 1971-1972 El Niño being the *cause* of the collapse of the fishery in 1972 is probably wrong.

Fig. 7 shows time series of anchoveta fishing mortality, both of a monthly basis and smoothed (12 months' running average) to allow the interyear trend to become fully visible. As might be seen, fishing mortality increased steadily through the 1950s and 1960s, then fluctuated violently through the 1970s, mainly due to successive El Niño events and associated closures of the fishery.

Table 4. Number (x 10^6) of 3-month old fish of 3.75-4.75 cm entering (i.e., recruiting into) the Peruvian anchoveta stock, 4-14°S, January 1953 to April 1982.[a]

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	292,401	310,721	333,392	333,215	323,787	295,573	266,126	233,973	209,821	179,433	165,217	153,384
1954	249,439	284,852	301,348	311,256	291,585	275,693	258,460	240,727	231,057	204,386	196,399	184,062
1955	235,808	200,231	186,493	186,377	183,130	172,522	151,500	128,960	122,539	94,755	98,014	107,883
1956	99,192	92,438	100,919	106,241	105,940	113,487	120,299	114,224	108,228	104,495	103,797	100,531
1957	98,802	104,425	119,649	144,631	179,945	191,625	198,293	235,740	203,330	106,741	109,698	105,208
1958	98,305	91,993	83,066	95,486	146,211	192,280	203,730	215,991	233,897	222,661	220,453	259,231
1959	290,360	391,308	470,026	478,302	446,391	478,298	557,056	604,380	571,127	542,146	512,860	508,012
1960	452,402	480,002	527,558	569,098	635,323	650,442	649,351	628,579	592,214	576,450	562,711	547,614
1961	545,625	579,497	640,034	651,976	638,188	612,918	594,073	560,883	506,098	475,374	438,089	406,372
1962	362,585	353,028	341,388	346,496	379,772	414,732	442,193	456,562	453,308	411,526	380,585	379,867
1963	333,775	399,409	561,871	751,350	892,165	945,165	925,158	859,530	736,234	584,076	463,815	364,578
1964	291,377	231,958	207,921	707,987	266,083	314,189	377,694	415,750	383,285	386,175	390,310	394,284
1965	354,200	430,984	591,307	768,595	965,290	1,114,012	1,093,886	924,414	889,437	670,164	503,727	344,684
1966	131,628	146,412	258,973	436,005	670,170	885,004	1,005,247	1,010,747	957,588	864,360	714,970	539,031
1967	389,989	326,571	411,111	561,766	695,692	796,117	793,659	675,627	498,822	330,448	207,687	116,550
1968	67,936	77,018	160,739	307,547	449,171	525,030	550,165	539,435	502,771	433,467	353,524	258,926
1969	248,893	407,409	632,203	924,522	1,157,515	1,137,915	949,410	668,179	440,827	332,922	235,251	170,479
1970	117,493	123,425	272,582	490,554	673,910	788,302	886,948	893,627	833,132	755,162	563,238	415,561
1971	288,236	185,926	86,146	35,334	30,558	35,050	39,901	40,875	36,314	32,498	28,143	35,137
1972	32,736	57,495	89,919	127,568	125,830	172,909	176,716	165,981	103,255	86,838	68,987	52,680
1973	43,722	47,107	54,743	71,554	56,077	53,162	44,122	39,910	28,571	21,957	18,207	17,560
1974	19,278	29,963	41,083	45,748	30,754	21,631	17,785	15,983	19,569	10,409	8,608	6,310
1975	5,402	5,026	7,932	15,467	37,852	60,945	76,139	87,443	288,019	296,152	274,886	228,886
1976	172,989	110,704	70,135	65,028	219,249	171,504	104,307	66,939	41,295	22,019	12,883	24,396
1977	40,044	13,789	17,526	90,982	118,117	160,906	270,437	277,585	276,708	339,961	342,728	306,785
1978	302,504	302,123	385,998	343,541	268,315	224,379	180,306	162,623	134,142	99,121	64,460	38,620
1979	22,224	53,964	63,291	63,344	80,103	79,173	82,955	86,365	83,558	64,060	49,260	58,880
1980	56,999	78,146	123,280	138,152	258,423	416,862	513,687	530,905	561,133	662,001	681,893	685,038
1981	609,353	674,405	565,089	429,434	473,128	414,134	303,297	198,820	120,694	81,765	57,983	42,310
1982	33,952	23,751	13,666	7,624								

[a]Month beyond April 1982 not included due to their decreasing reliability; the values for early 1982 given here to allow computation of $\log_e$ (Rec./Eggs) with egg production pertaining to 3-4 months prior to recruitment (see Mendelsohn and Mendo, this vol. and Pauly, this vol.).

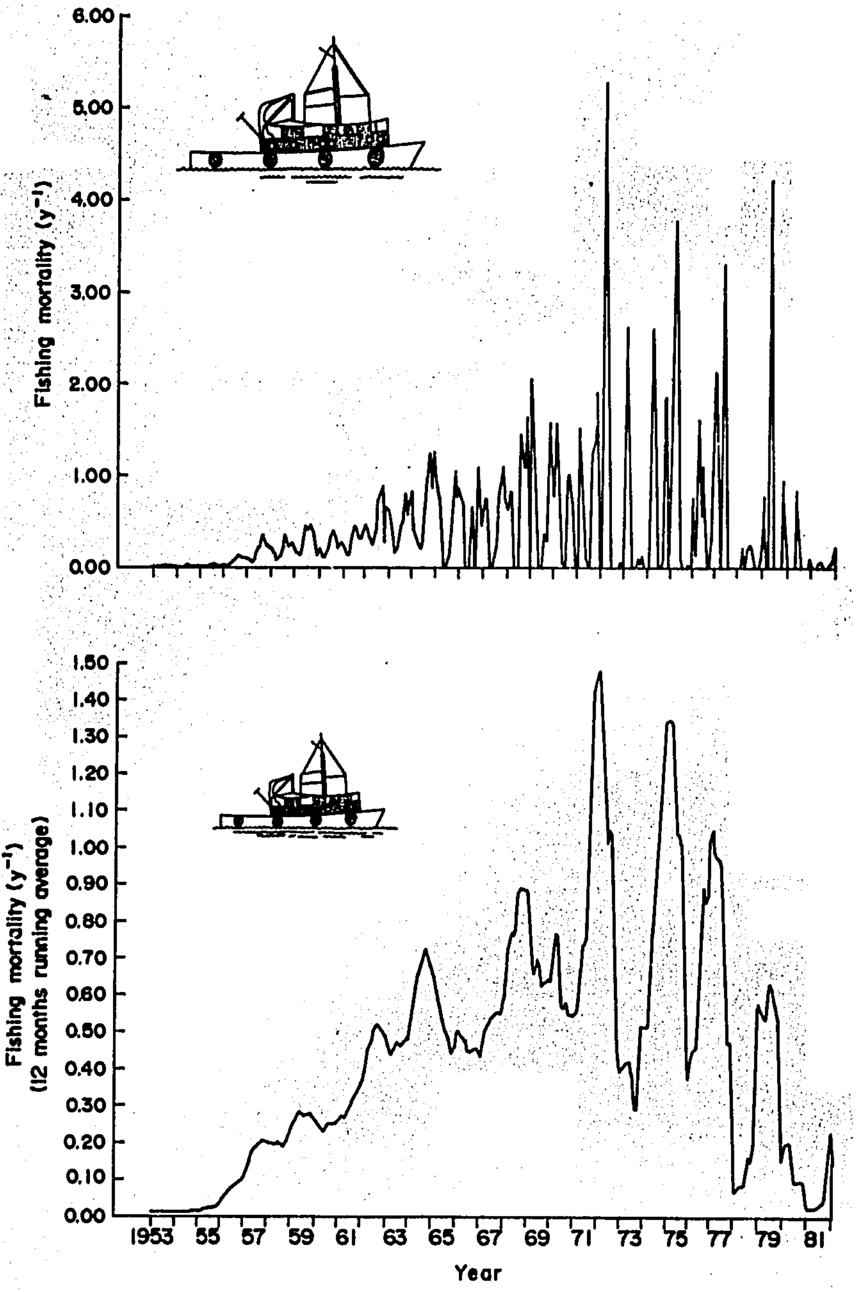


Fig. 7. Fishing mortality (i.e., catch in weight/biomass) exerted on Peruvian anchoveta (northern/central stock, 4-14°S) from January 1953 to December 1981. *Above*: actual values, by month. Note sharp spikes, partly due (from 1972 on) to closures of the fishery. *Below*: running average (over 12 months) of monthly values, to show major, increasing trend from the 1950s to the early 1970s.

Estimation of Anchoveta Mortality Caused by Various Predators

Figs. 8A, 8B and 8C show that part of natural mortality is attributable to the birds, the bonito and the seals, respectively. As might be seen, birds and bonito had a roughly similar impact on the anchoveta stock with peaks of 0.3-0.4y^{-1} in the late 1950s and negligible impact thereafter. The impact of the seals on the anchoveta stock, on the other hand, was negligible throughout the whole period considered here.

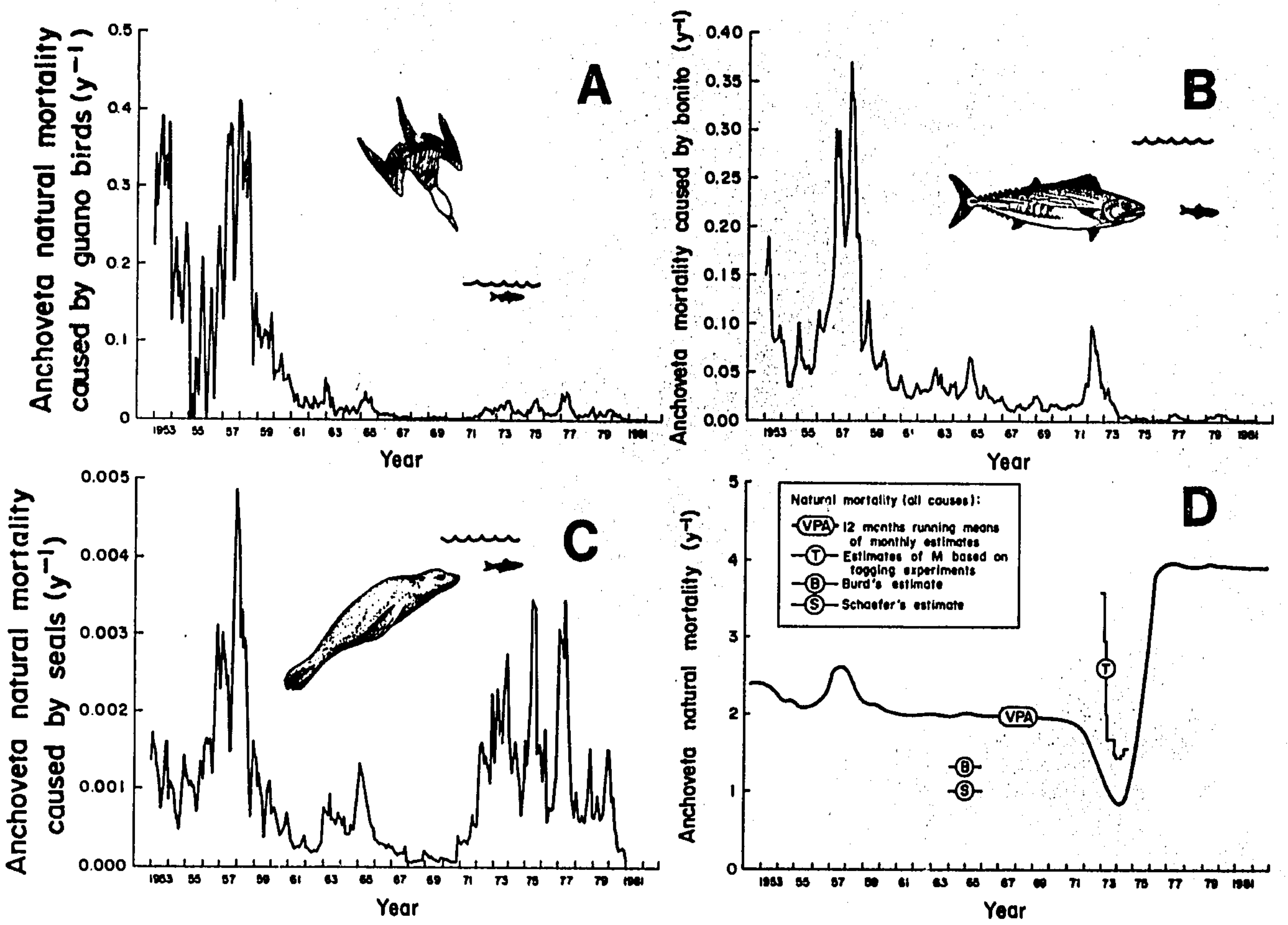


Fig. 8. Monthly time series of natural mortality in juvenile and adult anchoveta, 1953 to 1981. A. Mortality caused by cormorants (mainly), boobies and pelicans. B. Mortality caused by bonito (*Sarda chiliensis*) (note similarity of estimates to those pertaining to the birds). C. Mortality caused by sea lion (mainly) and fur seals. Note that the scale, ranging from zero to 0.005 implies a negligible pinniped impact on anchoveta natural mortality due to all causes. Note that shape of curve resembles that of Fig. 4, except for small "bumps" in the 1950s, corresponding to periods of bird and bonito abundances. Important here is that decline of M from 1971 to 1974 is confirmed by analysis of tagging/recapture data performed by Malaga and Armstrong (MS). Note also that little support is available for low M estimates (B & S) in Schaefer (1967).

Fig. 8D, finally, shows a time series of natural mortality as a whole, i.e., combining the predators considered here and the estimates of M_0 from Fig. 4. As might be seen from the overall shape of the curve, it is the estimates of M_0 which, throughout determine the overall level of natural mortality, clearly illustrating that the predators explicitly considered here do not explain but a small fraction of overall natural mortality. Interestingly, the drop of M observed in 1973-1974 is closely matched, albeit at higher level by a drop of M-estimates based on tagging data and reported in Table 11 of Malaga and Armstrong (MS).

Fig. 8D also shows that the values of M reported in Schaefer (1967) and based on his simulations ("S") and on a personal communication of T. Burd ("B") appear low compared with our estimates. We note, finally that values of M computed from the empirical equation of Pauly (1980) ranged between 1.3 and 1.6, and thus were intermediate for the 1960s at least, between the estimates reported in Schaefer (1967) and the M_0 values estimated by backcalibration of VPA estimates.

Overall Assessment of Results

Overall, our results both confirm and expend on previous results, and provide biomass and recruitment estimates for use in deriving further quantities (see, e.g., Pauly and Soriano, this vol.; Mendelsohn and Mendo, this vol.).

Both the data and the software we used have serious liabilities associated with them: the former had gaps which were "filled" using interpolation procedures which might not have all the required properties, while the latter is structured around assumptions about the growth of fish (i.e., that all fish in a given cohort have the same growth parameters) which are known not to be true.

Improved estimates of biomass and recruitment may thus result from more sophisticated interpolation methods and by using a length-structured VPA model not based on the assumption that all fish of a cohort have the same growth parameters.

However, such improvement might be minor compared with what we considered to be the main problem with our analysis, i.e., the fact that we did not account through the explicit inclusion of predators of as large a fraction of overall natural mortality as we would have liked.

This is due to the fact that, following earlier authors, we believed the birds to be the key anchoveta predators in the Peru current system (see Pauly and Tsukayama, this vol.; Pauly this vol.). We have here been proven wrong.

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Table 5. VPA III estimates of biomass per length class and month for Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1953, in tonnes.

Midlength (TL, cm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	150,651	155,979	163,468	166,234	166,318	155,506	140,428	124,918	111,697	96,079	88,209	97,053
5.25	246,736	256,082	268,853	290,405	299,155	287,546	261,596	235,166	224,497	194,201	163,424	147,046
6.25	355,358	373,906	389,585	423,039	460,206	459,071	430,666	392,482	367,151	335,218	296,942	249,128
7.25	493,665	493,098	522,148	562,948	620,094	640,901	622,552	584,173	567,793	506,434	459,511	418,277
8.25	543,892	630,895	644,279	702,307	769,568	802,954	783,631	769,836	765,476	723,605	666,542	601,273
9.25	564,511	637,988	763,431	818,461	861,480	908,902	914,698	911,803	845,925	862,593	857,248	824,606
10.25	581,969	625,532	688,214	856,940	979,635	989,725	970,551	960,050	936,729	905,941	892,837	942,307
11.25	695,506	605,725	616,872	724,747	849,031	952,835	987,529	976,229	924,686	923,087	911,526	899,584
12.25	525,188	655,811	643,606	619,633	649,835	694,131	694,189	745,741	800,932	846,011	809,037	778,887
13.25	330,535	328,285	403,450	563,377	615,018	551,879	487,787	469,110	466,902	473,638	479,233	523,439
14.25	181,542	206,674	206,999	222,173	236,562	355,913	396,378	379,897	278,534	230,963	237,194	219,597
15.25	114,352	108,246	103,508	117,790	134,147	143,821	142,743	120,566	90,242	64,772	74,189	90,009
16.25	23,977	40,955	56,829	70,397	48,938	57,474	59,152	57,105	14,883	17,584	21,207	23,250
17.25												
18.25												
19.25												
20.25												
Sum	4,807,883	5,119,178	5,471,243	6,138,452	6,689,988	7,000,659	6,891,899	6,727,077	6,395,448	6,180,125	5,957,099	5,814,454

Table 6. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1954, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	130,264	147,649	157,606	165,938	157,266	150,626	140,205	133,021	126,958	112,114	106,692	96,552
5.25	209,584	227,237	266,486	279,161	268,821	268,158	247,917	232,066	232,260	212,948	185,394	174,249
6.25	321,394	323,982	358,655	421,605	394,315	401,120	394,503	368,030	369,382	340,993	315,452	271,929
7.25	518,177	457,317	468,474	518,606	622,884	548,812	522,065	519,988	548,561	498,006	457,786	422,008
8.25	804,133	702,089	626,071	634,007	965,754	890,098	706,570	655,518	710,603	677,118	639,274	580,378
9.25	1,108,199	1,028,213	929,070	824,732	1,164,896	1,154,265	1,126,184	1,001,703	864,531	832,680	794,254	755,946
10.25	1,401,394	1,340,485	1,276,100	1,193,344	1,562,388	1,395,453	1,277,616	1,226,920	913,196	913,726	908,875	881,580
11.25	1,589,295	1,578,199	1,563,586	1,523,905	2,106,932	1,857,371	1,599,042	1,437,777	925,012	885,513	893,528	919,160
12.25	1,084,147	1,543,890	1,707,410	1,720,633	2,523,592	2,294,526	1,992,258	1,792,748	953,383	895,657	853,719	840,323
13.25	527,202	639,369	1,036,336	1,490,034	2,076,967	2,468,922	2,287,613	2,122,634	1,133,526	966,375	842,797	742,438
14.25	223,346	287,689	374,254	479,457	581,818	734,819	1,090,182	1,320,943	1,461,192	1,367,751	1,185,879	904,182
15.25	102,485	121,499	138,280	163,134	201,713	251,588	282,217	279,724	254,203	258,415	349,001	507,336
16.25	15,470	22,267	37,490	60,770	67,539	79,071	80,885	77,895	32,919	36,929	30,144	9,408
17.25								166				
18.25												
19.25												
20.25												
Sum	8,035,088	8,419,884	8,939,819	9,475,324	12,694,884	12,494,827	11,747,256	11,169,134	8,525,723	7,998,227	7,562,796	7,105,490

Table 7. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1955, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	118,924	102,852	98,408	97,476	97,773	92,378	81,358	69,956	66,091	51,622	53,016	57,766
5.25	216,441	210,107	177,698	170,666	170,687	164,804	155,261	139,312	155,904	124,672	89,379	87,766
6.25	345,343	341,844	335,728	270,635	284,937	257,130	242,912	229,640	277,806	239,317	195,882	138,927
7.25	512,818	504,125	503,592	475,789	472,104	411,190	351,121	327,853	436,635	396,133	340,601	281,821
8.25	718,159	705,494	692,757	672,041	648,296	608,851	563,495	480,090	614,855	565,613	515,939	453,956
9.25	980,260	936,892	923,930	872,324	860,103	797,737	730,893	666,905	801,988	750,919	694,906	641,233
10.25	1,225,587	1,230,451	1,189,930	1,127,962	1,074,190	1,005,913	931,490	813,245	970,301	916,607	863,869	817,659
11.25	1,063,154	1,398,007	1,482,036	1,398,879	1,332,274	1,229,135	1,106,365	999,113	1,200,208	1,109,692	1,000,940	957,545
12.25	802,281	957,978	1,338,992	1,589,815	1,525,482	1,428,696	1,247,891	1,123,187	1,987,667	1,636,764	1,286,874	1,067,995
13.25	645,115	677,768	823,813	954,678	1,022,068	1,146,779	1,172,829	1,174,342	1,117,901	1,232,124	1,414,494	1,541,598
14.25	839,524	631,541	580,761	578,313	630,215	708,852	732,221	729,888	617,506	664,249	693,479	681,319
15.25	341,290	641,827	691,801	696,869	533,568	396,609	381,116	377,758	344,313	330,479	335,943	297,707
16.25	5,465	6,196	36,326	73,494	283,832	421,453	420,323	405,511	227,040	236,309	236,381	231,467
17.25				514			158	379				
18.25												
19.25												
20.25												
Sum	7,814,363	8,345,081	8,875,772	8,979,455	8,935,528	8,669,526	8,117,433	7,537,180	8,818,215	8,254,501	7,721,704	7,256,757

Table 8. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14oS) for 1956, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	51,878	47,338	51,367	55,234	55,572	59,884	63,666	60,984	58,120	56,440	55,902	54,299
5.25	94,168	86,853	82,267	93,176	101,545	94,242	94,426	102,396	97,477	94,170	91,368	95,061
6.25	134,201	144,539	133,191	130,299	164,040	155,547	140,082	129,739	136,792	143,453	138,217	136,571
7.25	220,891	188,606	206,843	195,249	218,939	222,807	218,251	191,821	175,310	167,962	184,386	190,663
8.25	384,923	297,680	253,677	280,978	304,374	287,763	272,389	259,300	250,667	225,254	208,659	227,484
9.25	590,669	495,864	397,673	331,268	376,932	381,427	349,452	305,813	285,481	287,055	281,669	261,160
10.25	753,217	717,965	633,999	535,970	452,673	422,274	419,236	390,335	357,267	323,448	301,716	320,229
11.25	916,666	882,052	841,084	809,195	681,269	565,443	460,909	411,036	391,948	381,237	356,851	327,004
12.25	961,097	964,000	965,156	958,547	848,490	750,119	619,059	530,475	442,065	375,014	335,804	346,278
13.25	1,211,989	1,008,610	928,684	957,427	954,974	876,988	724,238	591,957	512,257	416,995	354,849	295,259
14.25	666,105	915,502	1,051,658	1,017,547	789,109	729,057	690,876	629,381	575,350	486,867	383,033	272,966
15.25	336,170	397,486	451,646	521,963	741,614	742,623	706,236	671,818	575,525	468,742	388,474	344,376
16.25	120,424	149,849	158,005	174,161	234,397	276,098	285,431	287,068	233,802	330,672	383,592	367,224
17.25			10,699	36,356		5,942	23,021	32,927				5,057
18.25												
19.25												
20.25												
Sum	6,456,791	6,310,710	6,182,133	6,112,664	5,937,209	5,583,914	5,078,527	4,605,280	4,101,877	3,768,965	3,477,099	3,258,294

Table 9. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14oS) for 1957, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	52,135	51,445	59,132	71,815	88,790	96,045	100,776	122,743	107,450	56,241	57,800	53,223
5.25	90,811	85,900	91,929	106,643	124,554	149,510	162,046	157,814	173,836	197,573	102,445	94,336
6.25	134,307	131,439	135,577	144,330	162,026	184,811	208,418	234,459	226,501	232,655	290,433	168,573
7.25	176,591	181,382	189,677	194,997	201,138	219,453	236,646	254,860	283,278	306,927	297,306	366,544
8.25	226,145	221,965	245,622	257,892	255,359	259,658	263,421	272,263	287,462	295,687	352,865	359,526
9.25	244,459	262,357	285,298	307,547	328,830	316,228	307,543	297,594	295,426	287,581	318,924	382,651
10.25	308,888	279,135	310,373	348,394	344,914	375,648	371,254	347,953	321,774	299,983	288,521	307,655
11.25	302,568	319,972	330,636	332,503	360,466	376,696	376,726	383,986	368,499	325,954	273,247	250,859
12.25	293,397	265,055	303,217	331,551	308,540	309,136	329,090	339,648	330,108	298,164	275,073	218,277
13.25	227,585	208,863	216,456	222,650	235,127	248,321	201,547	185,768	204,314	212,582	200,382	139,623
14.25	271,110	163,666	131,592	145,380	149,241	137,352	106,892	90,814	97,627	105,194	99,688	77,730
15.25	290,329	239,157	206,790	157,378	128,131	107,248	86,077	80,318	73,972	65,205	56,413	48,963
16.25	356,057	331,538	328,069	266,154	222,767	194,099	172,755	142,829	97,085	94,959	80,603	62,937
17.25		19,419	48,799	106,415	60,458	95,355	106,001	114,495			13,989	28,263
18.25												
19.25												
20.25												
Sum	2,990,330	2,777,737	2,902,278	3,035,479	2,994,961	3,089,527	3,049,796	3,050,043	2,876,937	2,791,409	2,720,782	2,573,984

Table 10. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14oS) for 1958, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	48,813	45,392	41,117	48,676	76,014	100,862	107,186	115,318	124,878	118,706	116,842	138,404
5.25	87,235	84,608	78,896	72,690	83,000	125,934	162,883	174,326	198,834	198,694	195,995	199,691
6.25	133,441	135,582	132,670	125,895	110,117	123,130	159,265	218,424	278,347	285,717	287,631	295,275
7.25	216,872	191,106	196,524	196,088	156,885	153,042	157,640	168,450	298,222	349,454	379,606	387,386
8.25	391,100	304,142	260,391	271,646	252,486	216,488	192,894	186,451	307,910	312,492	381,655	466,022
9.25	430,660	467,509	436,064	330,813	329,500	314,109	281,349	242,751	719,162	420,629	336,883	428,615
10.25	317,291	491,300	528,292	576,324	355,090	373,150	348,326	338,071	604,019	782,109	714,289	403,238
11.25	250,869	271,656	480,030	584,951	695,879	559,741	342,284	369,837	598,279	531,872	515,080	787,355
12.25	171,967	208,772	229,546	231,641	472,701	503,902	611,353	493,385	621,151	576,348	498,393	384,005
13.25	81,216	88,390	104,535	0	185,821	218,670	299,216	323,349	569,959	519,178	[illegible]9,634	455,083
14.25	61,616	64,581	41,394	0	80,620	77,463	73,672	21,438	604,779	549,680	502,499	470,696
15.25	41,225	35,700	16,606	5,715	2,328	3,291	8,226	0	728,079	647,420	577,599	530,216
16.25	50,409	43,638	41,603	39,141	33,438	23,528	16,107	10,761	759,727	753,409	698,842	638,088
17.25	4,700	15,818	21,766	15,171	11,350	15,711	17,965	19,110	321	22,375	100,159	203,603
18.25												
19.25												
20.25												
Sum	2,287,413	2,448,192	2,609,434	2,498,751	2,845,229	2,809,021	2,778,367	2,681,671	6,413,668	6,068,086	5,785,107	5,787,677

Table 11. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14oS) for 1959, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	150,504	196,129	237,778	245,687	232,422	252,386	297,846	324,561	305,814	288,608	271,422	264,902
5.25	227,025	262,409	376,148	431,765	427,597	397,556	406,160	463,328	491,733	488,590	477,819	454,623
6.25	293,705	352,587	422,852	608,493	678,350	626,023	603,670	547,581	597,939	672,082	712,969	710,978
7.25	397,204	408,859	520,486	614,727	858,243	829,776	843,758	822,467	752,261	734,582	859,362	979,928
8.25	488,146	489,764	556,874	653,438	796,306	918,033	987,639	1,012,967	1,003,715	968,949	878,109	1,001,538
9.25	536,017	516,180	598,910	626,526	756,133	883,114	930,761	994,562	1,100,983	1,118,968	1,140,599	1,082,766
10.25	479,395	516,510	561,437	623,307	672,607	767,295	799,917	814,823	904,919	1,026,985	1,180,009	1,200,803
11.25	910,908	657,181	463,134	544,766	551,168	661,808	678,541	634,593	679,888	774,005	813,983	840,253
12.25	342,941	607,350	900,832	535,677	474,977	536,207	548,368	547,330	532,634	509,950	487,477	519,341
13.25	341,984	321,134	308,831	772,109	829,816	601,669	413,908	431,645	359,295	301,731	291,727	317,318
14.25	382,587	347,169	330,997	318,559	294,361	525,294	746,125	664,298	558,725	330,870	178,544	191,897
15.25	468,826	417,927	389,709	364,606	340,185	313,885	286,354	260,489	224,392	355,808	465,272	399,111
16.25	543,580	505,585	471,452	440,853	408,370	374,398	339,826	303,728	268,809	238,118	212,607	190,069
17.25	10,240	106,493	206,721	282,102	169,256	215,736	239,836	247,011	27,707	57,791	83,926	106,805
18.25												
19.25												
20.25												
Sum	5,621,667	5,775,070	6,423,434	7,133,181	7,547,085	7,964,133	8,184,362	8,128,765	7,864,754	7,925,474	8,119,588	8,335,227

Table 12. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14oS) for 1960, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	234,496	246,934	272,631	299,413	338,211	346,766	348,711	336,577	317,566	309,562	302,184	289,814
5.25	408,252	410,729	448,494	498,434	564,777	573,783	575,667	565,329	532,405	515,341	514,060	507,388
6.25	636,390	637,216	648,642	714,616	835,001	849,979	845,682	825,667	784,646	768,936	758,373	765,793
7.25	915,652	911,012	931,696	958,864	1,038,462	1,135,562	1,148,446	1,110,580	1,052,090	1,046,281	1,048,687	1,046,488
8.25	1,087,594	1,230,327	1,243,366	1,284,702	1,283,446	1,329,555	1,382,118	1,397,976	1,295,867	1,287,515	1,301,497	1,326,802
9.25	942,163	1,338,489	1,576,380	1,607,434	1,626,769	1,568,370	1,528,256	1,480,916	1,491,203	1,498,220	1,496,626	1,555,648
10.25	1,158,115	1,068,304	1,535,039	1,845,724	1,959,716	1,859,133	1,746,742	1,612,225	1,580,659	1,546,983	1,634,375	1,717,459
11.25	960,075	1,061,548	1,138,755	1,527,922	1,985,163	2,037,981	1,947,663	1,826,340	1,706,567	1,622,502	1,624,768	1,684,182
12.25	524,347	715,548	851,297	979,153	1,237,526	1,668,044	1,849,349	1,870,630	1,812,700	1,722,405	1,659,723	1,551,754
13.25	227,550	341,517	454,289	606,084	689,453	863,827	971,663	1,143,524	1,316,067	1,468,154	1,570,733	1,461,177
14.25	158,017	164,882	198,282	286,431	346,390	445,186	510,628	520,202	520,345	570,183	691,633	874,931
15.25	408,404	358,078	186,327	164,016	169,190	193,497	221,452	234,272	251,686	216,298	170,208	197,647
16.25	171,094	164,530	333,232	336,433	306,442	275,240	208,387	126,002	121,600	107,502	79,035	77,823
17.25	74,145	103,295	126,923	144,862	86,480	101,723	157,049	223,290	130,925	123,093	115,946	110,534
18.25												
19.25												
20.25												
Sum	7,980,528	8,835,601	10,035,488	11,345,051	12,557,060	13,327,448	13,509,919	13,333,638	12,973,742	12,869,625	13,042,398	13,250,594

Table 13. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14oS) for 1961, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4,25	282,817	293,158	339,722	353,165	341,723	318,174	297,757	293,344	282,810	267,862	238,669	212,535
5.25	482,130	493,639	553,267	625,568	607,726	562,264	511,679	505,061	512,590	470,433	433,848	390,066
6.25	748,970	734,811	818,210	881,140	959,017	892,032	807,776	784,628	771,316	750,808	681,687	632,341
7.25	1,017,978	1,064,097	1,123,721	1,213,668	1,238,174	1,271,996	1,180,474	1,143,004	1,120,477	1,056,291	989,698	923,508
8.25	1,281,975	1,349,015	1,524,657	1,562,445	1,588,371	1,555,359	1,518,713	1,568,984	1,541,656	1,443,912	1,314,868	1,234,181
9.25	1,590,841	1,614,818	1,822,848	1,992,946	1,944,910	1,876,318	1,793,339	1,785,247	1,906,117	1,897,335	1,711,919	1,578,254
10.25	1,746,525	1,889,215	2,099,263	2,252,671	2,344,848	2,266,295	2,061,108	2,039,918	2,130,651	2,056,177	2,050,932	1,986,571
11.25	1,804,715	1,954,542	2,292,622	2,514,161	2,501,221	2,426,368	2,331,082	2,322,205	2,314,130	2,242,123	2,186,522	2,155,969
12.25	1,561,342	1,840,135	2,239,165	2,445,055	2,596,824	2,492,108	2,306,642	2,326,872	2,445,067	2,404,963	2,252,020	2,164,741
13,25	1,337,263	1,374,389	1,708,746	2,154,749	2,324,475	2,239,041	2,126,363	2,148,048	2,222,138	2,179,442	2,096,726	2,103,808
14.25	924,170	872,013	979,861	1,250,361	1,510,564	1,625,588	1,624,007	1,670,501	1,670,730	1,677,500	1,607,136	1,496,940
15.25	187,258	238,259	391,339	468,718	514,256	576,607	639,145	702,199	839,847	879,548	815,084	674,194
16.25	70,019	76,933	59,413	73,876	80,602	106,721	119,316	136,272	148,688	164,388	129,500	89,198
17.25	30,063	38,113	3,808	5,597	5,420	5,760	6,562	7,604	4,687	6,535	6,696	4,818
18.25												
19.25												
20.25												
Sum	13,157,818	13,931,733	16,070,130	17,898,810	18,646,938	18,285,164	17,382,564	17,484,460	17,963,564	17,553,450	16,573,039	15,709,465

Table 14. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1962, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	194,713	182,437	184,924	184,455	195,963	205,287	220,945	239,140	250,136	231,244	218,005	212,863
5.25	359,441	326,395	338,693	317,303	316,250	319,854	339,259	371,139	402,750	413,669	399,530	365,125
6.25	585,714	539,376	533,856	517,294	478,338	458,185	468,101	502,077	538,542	574,430	617,138	596,027
7.25	869,114	815,784	818,272	761,434	714,077	643,711	625,177	633,760	679,509	715,430	785,773	841,923
8.25	1,221,443	1,137,835	1,166,597	1,093,130	991,665	905,646	845,447	815,617	822,606	835,878	905,414	985,431
9.25	1,526,809	1,522,962	1,548,684	1,477,765	1,356,368	1,194,717	1,113,319	1,084,781	1,042,070	993,607	986,686	1,046,592
10.25	1,921,621	1,813,884	1,963,416	1,888,167	1,743,920	1,558,261	1,406,386	1,318,644	1,306,008	1,247,932	1,113,375	1,144,009
11.25	2,228,015	2,211,722	2,286,742	2,249,352	2,135,145	1,867,485	1,704,019	1,619,425	1,557,215	1,451,802	1,427,572	1,362,142
12.25	2,182,356	2,322,334	2,599,352	2,553,387	2,392,951	2,161,376	1,988,211	1,857,180	1,772,128	1,663,238	1,583,763	1,499,755
13.25	2,089,439	2,185,871	2,497,450	2,667,879	2,619,693	2,335,910	2,150,553	2,046,548	1,960,981	1,813,353	1,653,655	1,496,690
14.25	1,442,881	1,649,937	1,979,780	2,136,219	2,175,110	2,102,246	2,064,318	1,998,656	1,921,279	1,760,937	1,644,787	1,318,706
15.25	604,311	608,672	832,240	1,045,765	1,154,550	1,131,984	1,196,071	1,244,321	1,270,182	1,271,101	1,197,362	970,782
16.25	106,416	120,724	160,532	179,491	179,614	215,396	270,841	370,771	441,089	450,177	421,367	354,518
17.25	4,826	4,136	5,850	8,912	20,778	25,542	27,779	31,577	24,884	30,304	31,406	30,494
18.25				207			70	175				
19.25												
20.25												
Sum	15,398,889	15,503,244	16,976,522	17,137,542	16,529,090	15,174,950	14,466,353	14,179,311	14,036,962	13,499,910	13,113,644	12,287,342

Table 15. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1963, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	176,904	205,163	287,302	411,672	491,604	353,826	489,622	436,828	375,886	331,840	264,236	207,417
5.25	304,722	306,768	384,955	594,473	753,610	572,065	830,509	775,061	726,544	716,134	565,816	445,636
6.25	480,391	446,643	484,135	641,221	923,245	767,696	1,170,432	1,156,514	1,122,222	1,189,770	1,100,269	863,392
7.25	746,206	672,371	684,626	791,976	955,348	864,767	1,397,178	1,439,424	1,498,081	1,669,929	1,649,126	1,561,022
8.25	978,871	982,604	923,384	1,003,503	1,068,455	829,259	1,429,760	1,527,609	1,682,620	2,004,139	2,144,613	2,181,602
9.25	1,037,596	1,224,381	1,276,867	1,267,157	1,275,905	855,241	1,331,165	1,414,556	1,600,174	2,024,377	2,315,458	2,569,045
10.25	1,039,416	1,196,396	1,506,605	1,670,892	1,510,115	1,000,607	1,374,537	1,312,862	1,378,044	1,747,023	2,029,589	2,520,529
11.25	1,144,065	1,161,359	1,354,177	1,781,776	1,885,235	1,186,171	1,501,842	1,367,485	1,350,147	1,475,971	1,624,680	2,074,936
12.25	1,355,164	1,255,522	1,288,085	1,523,837	1,718,307	1,276,457	1,735,630	1,526,142	1,380,906	1,465,255	1,456,367	1,583,238
13.25	1,351,294	1,332,034	1,401,417	1,366,438	1,393,686	1,006,874	1,464,328	1,459,325	1,451,981	1,528,325	1,336,951	1,268,915
14.25	1,037,597	929,387	1,126,911	1,210,510	1,078,712	634,168	902,195	923,322	952,003	1,088,471	1,076,558	941,280
15.25	625,222	440,153	499,572	563,106	556,526	290,404	346,198	320,777	349,553	380,904	436,514	372,482
16.25	189,003	140,928	127,018	123,052	104,112	55,706	69,344	68,471	59,107	63,593	67,637	42,491
17.25	22,374	23,569	22,277	26,230	25,044	17,214	7,544	6,903	4,758	4,665	4,498	4,927
18.25		46	275	202	276	1,179	61	59			2	23
19.25												
20.25												
Sum	10,548,011	10,412,240	11,473,243	13,114,423	13,740,181	9,711,634	14,050,346	13,735,337	13,997,264	15,757,467	16,134,135	16,694,301

Table 16. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1964, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	145,815	115,538	108,096	387,913	150,967	174,593	210,470	236,530	211,497	213,392	226,917	221,249
5.25	304,065	242,189	199,923	548,370	236,525	253,545	284,765	335,146	327,951	341,958	375,901	376,694
6.25	597,125	458,043	390,195	594,109	317,084	349,461	369,186	399,217	405,268	450,793	522,992	555,723
7.25	1,080,651	832,224	674,007	747,700	485,203	438,451	461,854	485,270	483,885	521,631	631,333	702,557
8.25	1,815,547	1,445,269	1,140,199	958,666	806,252	632,597	574,816	559,239	559,584	584,933	678,262	786,228
9.25	2,356,868	2,303,717	1,908,581	1,202,573	1,283,596	1,047,566	841,756	720,998	635,937	633,818	720,419	770,085
10.25	2,534,438	2,808,807	2,884,281	1,644,037	2,030,414	1,625,350	1,333,308	1,103,711	887,630	759,959	733,907	775,649
11.25	2,271,774	2,834,187	3,301,842	1,710,820	3,001,160	2,399,324	2,002,266	1,701,104	1,363,362	1,142,187	988,992	838,920
12.25	1,646,901	2,141,440	2,996,046	1,474,201	3,588,194	3,227,603	2,833,723	2,395,530	2,001,609	1,700,239	1,497,850	1,198,166
13.25	1,218,238	1,245,877	1,844,859	1,329,465	3,257,862	3,276,246	3,114,158	2,970,552	2,611,749	2,348,407	2,085,353	1,727,439
14.25	697,363	602,227	813,299	1,200,358	1,645,609	2,095,813	2,379,551	2,532,548	2,400,381	2,324,515	2,255,421	1,890,447
15.25	219,835	173,800	232,124	546,896	431,707	619,723	856,390	998,277	1,180,037	1,310,849	1,312,537	1,137,474
16.25	23,606	21,519	26,595	31,613	58,858	89,054	124,142	176,029	199,163	250,742	275,828	234,255
17.25	935	627	968		4,823	6,991	11,599	16,116	15,048	17,281	16,755	14,500
18.25			37			19	7	103			425	309
19.25												
20.25												
Sum	14,959,008	15,262,800	16,559,079	12,508,669	17,341,928	16,281,603	15,446,168	14,676,388	13,326,207	12,649,246	12,383,800	11,296,899

Table 17. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1965, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	190,210	207,294	295,450	384,632	477,054	547,953	581,473	483,473	451,335	367,189	278,349	191,002
5.25	353,879	294,446	410,049	563,318	696,293	822,037	977,180	960,998	1,005,593	849,589	629,003	465,065
6.25	524,201	502,904	495,336	652,032	860,699	1,048,006	1,275,885	1,361,608	1,729,775	1,680,539	1,348,489	962,320
7.25	703,351	695,917	752,455	775,826	929,393	1,211,343	1,476,783	1,570,944	1,875,249	2,358,207	2,395,599	1,938,182
8.25	825,414	854,918	1,016,009	1,023,084	1,018,754	1,158,662	1,560,673	1,685,724	1,807,262	2,303,876	2,893,316	3,227,584
9.25	855,864	910,860	1,151,473	1,313,878	1,300,426	1,200,653	1,439,411	1,606,976	1,802,867	2,157,416	2,561,347	3,427,573
10.25	797,616	822,994	1,126,414	1,398,566	1,507,560	1,528,[illegible]3	1,494,917	1,460,132	1,567,449	1,952,751	2,320,037	2,702,253
11.25	763,887	717,776	896,557	1,175,078	1,458,980	1,568,561	1,723,036	1,648,896	1,517,604	1,643,154	1,800,239	2,339,569
12.25	893,313	695,727	745,618	832,728	1,016,051	1,215,291	1,442,660	1,555,723	1,549,795	1,661,847	1,619,458	1,741,169
13.25	1,359,094	943,181	750,709	628,518	642,179	657,638	762,288	959,190	1,119,354	1,367,856	1,454,148	1,383,080
14.25	1,547,551	1,200,109	1,032,265	667,933	453,923	342,091	326,267	396,113	466,775	636,703	817,978	857,457
15.25	924,797	788,667	843,107	551,116	326,219	164,806	95,851	119,096	146,808	215,468	250,633	253,519
16.25	219,155	146,811	180,695	127,349	79,838	45,278	20,212	22,471	28,576	37,838	46,388	47,140
17.25	18,285	10,398	12,260	7,500	4,530	3,094	3,171	3,315	3,460	3,896	4,508	4,592
18.25	756	42	461	796	537	706	870	904	1,147	1,207	1,263	96
19.25											22	
20.25												
Sum	10,040,059	8,870,319	9,818,282	10,223,384	10,917,194	11,653,795	13,294,794	13,919,170	15,149,436	17,313,482	18,491,620	19,591,456

Table 18. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1966, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	67,203	78,169	133,832	245,678	395,358	473,882	541,396	545,932	506,786	475,610	384,505	268,072
5.25	163,067	109,858	143,921	291,745	497,561	630,395	780,015	878,013	889,156	877,006	785,501	597,044
6.25	406,906	247,204	174,317	260,748	479,399	682,951	891,615	1,072,848	1,207,385	1,317,290	1,282,425	1,111,032
7.25	920,315	550,817	320,101	298,732	442,800	615,343	862,597	1,059,221	1,274,453	1,576,876	1,749,284	1,674,488
8.25	1,856,134	1,215,128	656,714	451,194	430,947	487,012	730,851	925,869	1,114,879	1,480,955	1,871,910	2,125,885
9.25	2,935,653	2,263,026	1,338,028	880,017	607,975	444,106	537,054	710,869	862,086	1,183,754	1,565,103	2,080,083
10.25	2,877,660	3,449,748	2,482,983	1,696,907	1,155,483	695,503	535,367	534,974	577,294	831,235	1,131,185	1,470,808
11.25	2,355,288	3,077,374	3,620,018	3,172,731	2,121,809	1,233,955	947,199	723,712	555,493	568,995	668,402	948,382
12.25	1,706,121	2,564,697	3,163,370	3,979,282	3,801,800	2,480,210	1,829,226	1,375,955	1,015,383	801,038	582,108	577,741
13.25	984,345	1,277,243	2,184,[illegible]62	2,982,394	3,597,607	3,455,214	3,299,691	2,686,724	1,983,547	1,517,502	1,035,941	726,354
14.25	614,034	555,045	732,872	1,542,300	2,399,196	2,404,104	2,713,682	2,985,494	3,019,638	2,663,662	1,898,540	1,341,297
15.25	153,720	153,816	189,584	262,662	576,023	900,341	1,367,895	1,682,538	1,868,305	1,799,426	1,652,397	1,839,364
16.25	24,672	25,204	23,736	33,759	81,223	122,455	171,006	271,560	371,000	556,468	606,933	740,838
17.25	2,145	1,647	2,009	2,791	6,930	9,924	18,010	25,002	32,242	44,478	41,201	59,044
18.25	97		87	25	171	509	573	702	553	1,006	1,976	3,426
19.25												
20.25												
Sum	15,087,634	15,598,824	15,218,628	16,190,278	16,594,282	14,685,901	15,226,176	15,479,413	15,378,590	15,799,823	15,350,529	15,638,768

Table 19. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1967, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	209,733	156,057	211,814	286,811	360,060	462,843	429,295	369,131	263,992	185,171	114,117	65,038
5.25	460,176	304,674	289,103	397,659	545,431	705,442	715,102	724,398	613,337	488,375	309,636	188,239
6.25	973,015	611,787	509,528	469,110	624,660	934,815	956,104	1,027,477	1,039,606	998,311	753,159	473,180
7.25	1,674,207	1,181,659	906,810	718,433	723,425	992,810	1,133,443	1,235,155	1,279,089	1,439,213	1,374,032	1,089,261
8.25	2,340,058	2,018,496	1,660,545	1,185,016	973,043	1,023,569	1,163,280	1,317,112	1,417,135	1,625,395	1,776,708	1,867,773
9.25	2,591,810	2,684,426	2,714,995	2,076,498	1,521,695	1,318,509	1,116,981	1,260,364	1,337,806	1,640,810	1,861,111	2,231,966
10.25	2,322,490	2,745,336	3,464,880	3,253,947	2,595,721	1,990,741	1,512,916	1,347,231	1,187,056	1,456,907	1,713,489	2,174,066
11.25	1,492,384	2,071,858	3,283,090	3,895,029	3,744,890	3,409,911	2,432,950	1,909,127	1,556,583	1,451,767	1,419,977	1,740,343
12.25	843,186	1,268,184	2,211,921	3,197,460	3,863,864	4,319,634	3,737,798	3,279,075	2,505,800	2,076,692	1,654,264	1,524,289
13.25	599,963	643,610	1,204,269	1,941,258	2,624,205	3,567,353	3,788,266	3,923,037	3,618,878	3,324,396	2,448,497	1,874,080
14.25	1,001,429	565,677	562,097	816,060	1,258,196	1,906,862	2,258,397	2,716,803	2,969,205	3,359,512	2,991,540	2,413,586
15.25	1,407,012	715,991	658,311	404,254	377,146	641,417	845,240	1,078,625	1,336,914	1,675,345	1,715,336	1,824,100
16.25	628,379	348,484	439,951	340,790	153,768	131,028	164,256	237,323	309,948	425,560	466,338	496,076
17.25	78,178	42,325	57,413	38,907	33,267	28,620	35,913	44,124	48,607	54,419	46,999	59,444
18.25	2,732	3,200	4,973	6,112	5,099	5,381	5,249	5,327	1,834	3,050	2,587	3,061
19.25												
20.25												
Sum	16,692,067	15,416,511	18,260,088	19,128,740	19,515,116	21,559,890	20,383,538	20,539,244	19,529,614	20,240,102	18,672,496	18,040,522

Table 20. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1968, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	36,007	39,861	84,317	174,252	241,910	286,443	298,872	292,203	255,126	220,633	195,900	142,876
5.25	95,547	52,665	77,211	183,507	342,329	433,634	475,974	489,340	461,550	433,453	406,076	323,308
6.25	276,851	132,414	91,910	154,751	279,437	533,399	625,522	679,402	667,755	671,808	715,321	620,630
7.25	660,417	339,597	171,257	161,642	259,542	400,449	668,905	780,687	824,906	872,481	1,000,019	1,007,129
8.25	1,413,033	803,184	417,068	235,041	224,566	319,608	509,299	707,161	825,484	976,500	1,203,140	1,319,954
9.25	2,258,477	1,654,900	969,669	547,740	293,508	247,869	313,110	489,103	595,251	862,935	1,216,400	1,489,787
10.25	2,432,025	2,573,681	1,964,109	1,236,555	661,350	331,273	250,534	304,466	360,935	538,127	911,985	1,378,675
11.25	2,127,619	2,622,865	2,970,523	2,484,403	1,482,741	868,798	523,029	336,184	254,376	294,920	496,098	830,359
12.25	1,512,518	2,156,835	2,809,811	3,410,017	2,774,085	1,928,283	1,305,174	891,307	528,561	318,679	280,528	358,375
13.25	1,469,507	1,544,949	2,185,736	3,148,666	3,121,498	3,004,897	2,653,618	2,067,126	1,411,916	858,474	521,878	288,089
14.25	1,763,809	1,377,750	1,432,093	1,870,934	2,359,323	2,633,196	2,776,677	2,780,545	2,471,119	1,728,912	1,134,178	658,211
15.25	1,455,551	1,124,835	1,004,186	1,191,082	1,257,620	1,432,386	1,789,612	2,032,134	2,004,569	1,649,296	1,262,407	980,997
16.25	290,400	271,088	430,494	609,553	523,282	545,875	702,487	808,565	924,717	752,243	640,730	443,823
17.25	34,635	35,706	44,816	62,947	80,314	126,061	180,350	217,873	230,296	207,404	164,797	67,573
18.25	2,137	2,448	4,691	8,943	9,761	10,767	11,372	11,410	7,142	7,232	9,870	8,363
19.25				123				56				
20.25												
Sum	15,839,298	14,748,596	14,692,500	15,546,230	13,988,822	13,178,665	13,150,748	12,946,503	11,872,997	10,444,159	10,207,162	9,959,733

Table 21. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1969, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	127,654	211,175	311,456	493,603	717,995	585,393	503,935	355,182	232,270	165,569	123,587	86,508
5.25	195,411	242,008	391,492	643,325	1,136,077	1,049,603	1,020,668	863,802	631,404	372,812	295,874	197,250
6.25	418,882	318,622	425,428	735,447	1,179,753	1,404,470	1,594,265	1,542,114	1,325,164	968,989	604,679	428,341
7.25	791,795	555,999	485,189	792,840	1,352,149	1,407,612	1,926,232	2,066,746	2,133,240	1,777,893	1,515,690	831,078
8.25	1,175,855	950,613	691,298	731,165	1,296,814	1,439,003	1,877,477	2,214,553	2,433,932	2,499,183	2,502,190	1,969,012
9.25	1,475,645	1,342,022	1,162,920	816,505	1,078,803	1,223,034	1,613,786	2,021,007	2,277,245	2,576,060	3,122,519	3,066,724
10.25	1,572,086	1,569,271	1,611,261	1,121,647	1,154,944	945,863	1,201,899	1,602,225	1,926,571	2,164,956	2,894,340	3,481,719
11.25	1,274,695	1,593,684	1,800,811	1,516,692	1,475,049	1,073,566	974,391	1,098,293	1,328,138	1,586,285	2,258,495	2,920,936
12.25	586,757	1,085,244	1,637,057	1,638,374	1,728,646	1,305,507	1,287,545	1,145,728	1,003,991	983,908	1,406,062	1,930,963
13.25	274,192	530,678	1,009,915	1,319,693	1,389,377	1,149,665	1,298,370	1,321,081	1,266,991	960,109	808,773	1,025,248
14.25	278,892	215,938	367,174	586,223	686,681	686,977	893,756	1,021,187	1,080,732	931,565	806,968	735,750
15.25	465,961	204,721	193,880	198,849	206,437	208,271	336,184	468,934	586,842	536,362	529,257	496,163
16.25	266,603	119,447	163,848	136,156	71,658	44,908	69,567	97,718	123,476	141,515	163,335	178,010
17.25	60,483	31,234	45,306	50,655	25,295	14,222	18,520	21,452	24,007	12,693	18,862	25,963
18.25	5,727	5,179	6,558	7,287	4,973	2,685	2,912	2,885	2,089	1,320	1,307	730
19.25				594			11	31				
20.25												
Sum	9,019,245	9,062,797	10,426,553	10,970,390	13,701,294	12,683,407	14,718,343	15,897,048	16,420,824	15,713,012	17,082,750	17,399,852

Table 22. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1970, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	57,334	64,456	152,108	257,708	363,473	415,967	474,923	477,804	459,075	430,217	323,508	244,184
5.25	132,792	97,734	126,860	287,019	526,410	634,703	708,932	768,418	807,145	784,352	731,452	554,297
6.25	272,084	211,684	175,794	245,754	475,744	788,506	944,855	1,016,435	1,117,112	1,251,609	1,194,466	1,122,845
7.25	546,997	396,273	298,308	258,660	439,609	682,697	1,071,233	1,202,294	1,363,676	1,510,318	1,735,952	1,750,882
8.25	1,041,486	733,598	553,489	362,965	350,584	543,947	855,644	1,182,907	1,460,270	1,715,117	1,931,299	2,345,981
9.25	2,053,587	1,354,701	976,490	665,799	409,386	412,838	515,488	875,092	1,214,553	1,598,329	2,051,771	2,454,114
10.25	3,016,926	2,150,729	1,720,157	1,146,546	670,770	482,604	447,698	504,051	721,161	1,078,318	1,663,443	2,384,930
11.25	3,129,866	2,982,270	2,608,461	1,848,856	1,168,008	745,083	616,067	512,114	505,355	643,949	871,907	1,694,273
12.25	2,280,450	2,877,382	3,312,491	2,722,208	1,849,076	1,283,911	999,262	777,758	629,664	519,366	549,750	849,828
13.25	1,337,181	2,119,019	2,961,409	3,050,047	2,639,692	1,998,969	1,651,114	1,334,953	1,086,209	825,222	631,210	544,739
14.25	737,360	1,057,024	1,889,796	2,375,754	2,552,431	2,429,983	2,351,361	2,040,175	1,776,133	1,328,015	914,088	634,153
15.25	425,057	578,989	731,333	1,062,846	1,531,155	1,809,625	2,061,026	2,134,796	2,171,461	1,672,136	1,044,687	630,078
16.25	141,980	167,710	248,412	394,127	488,165	656,336	872,825	1,132,677	1,386,507	1,088,316	724,375	474,960
17.25	20,101	25,360	39,278	44,779	83,003	156,264	231,212	283,636	331,203	267,381	195,213	114,490
18.25	1,080	1,791	5,371	8,114	9,985	15,721	21,001	23,445	24,600	24,964	33,645	38,881
19.25				4				206				440
20.25												
Sum	15,213,037	14,884,085	15,863,660	14,829,540	13,675,834	13,170,683	13,937,112	14,362,456	15,292,421	14,928,420	14,746,377	15,951,843

Table 23. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1971, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	151,197	96,227	43,312	15,747	14,888	16,776	20,993	21,505	18,908	18,034	16,668	19,854
5.25	354,160	234,475	129,478	56,629	28,820	25,092	31,101	34,016	33,034	34,105	32,889	27,641
6.25	726,444	494,797	303,917	144,483	71,671	43,372	41,982	44,982	44,715	53,065	55,929	48,129
7.25	1,341,331	973,954	641,517	376,748	182,070	99,013	67,490	58,878	52,611	62,964	80,065	77,116
8.25	2,027,123	1,749,111	1,235,750	792,480	513,332	258,702	169,362	89,858	69,744	68,246	86,017	102,582
9.25	2,438,593	2,623,398	2,184,002	1,459,797	1,010,961	669,746	448,528	267,483	142,153	99,080	87,497	103,057
10.25	2,398,864	3,081,177	3,229,709	2,506,855	1,816,838	1,316,495	1,027,891	702,940	404,290	251,128	136,022	107,786
11.25	2,105,935	2,847,193	3,629,741	3,441,563	2,901,113	2,182,950	1,860,417	1,440,038	999,807	672,330	423,273	208,961
12.25	1,246,475	2,291,503	3,194,211	3,211,119	3,437,372	3,186,877	3,072,550	2,474,592	1,833,276	1,379,924	1,085,704	626,347
13.25	583,404	1,133,421	2,288,836	2,474,131	2,712,363	3,098,977	3,611,368	3,515,603	2,981,600	2,285,216	1,840,338	1,363,553
14.25	368,299	485,128	737,503	980,803	1,591,360	2,104,781	2,673,241	3,054,438	3,185,176	2,992,943	2,561,639	2,081,496
15.25	340,927	344,461	417,680	369,654	502,271	749,924	1,352,258	1,716,979	1,928,527	2,092,682	2,085,408	1,870,863
16.25	269,471	304,984	328,365	177,435	227,773	234,213	310,469	436,352	567,988	848,165	985,755	820,343
17.25	92,028	158,842	212,298	94,990	73,594	59,091	94,108	128,840	146,003	156,740	140,517	155,953
18.25	27,948	29,413	41,790	20,991	16,986	15,841	19,499	20,454	17,856	18,752	14,639	20,430
19.25			1,076	964	104	8	280	650			155	646
20.25												
Sum	14,524,045	16,873,188	18,629,492	16,132,739	15,109,547	14,071,250	14,812,420	14,018,011	12,434,075	11,041,080	9,641,873	7,662,549

Table 24. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1972, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	17,070	29,086	46,328	57,783	61,305	87,068	88,710	84,742	53,601	45,011	35,597	31,857
5.25	28,017	38,506	68,138	86,726	104,259	110,616	149,186	152,240	105,363	94,655	78,872	72,667
6.25	40,329	46,372	81,266	114,200	152,806	171,739	170,791	218,850	171,171	166,673	149,980	145,257
7.25	61,611	61,079	73,343	113,801	178,455	231,444	242,370	247,229	229,712	246,081	244,961	260,399
8.25	93,718	81,287	90,263	98,068	166,552	248,537	292,196	320,123	276,969	295,568	337,718	403,751
9.25	122,042	121,960	109,877	108,817	151,247	220,359	289,165	334,807	320,902	334,318	370,985	526,023
10.25	111,100	151,771	158,761	121,211	164,324	163,299	235,381	304,493	283,761	349,366	418,900	545,808
11.25	123,204	132,247	191,609	149,429	186,762	174,827	158,248	217,315	215,139	288,561	371,140	575,524
12.25	294,918	150,561	155,270	143,906	159,786	151,400	141,995	151,392	132,292	190,649	261,995	446,800
13.25	850,938	416,476	192,468	130,179	136,575	92,424	74,417	99,661	83,677	101,407	146,066	286,522
14.25	1,505,623	1,173,644	717,796	240,907	100,245	48,793	35,039	43,580	53,591	64,627	81,035	136,282
15.25	1,533,526	1,681,047	1,554,842	657,759	125,997	35,312	20,041	23,676	30,775	33,366	43,646	72,025
16.25	538,706	949,211	1,549,156	830,629	117,175	43,544	21,773	17,599	21,931	21,396	21,787	29,318
17.25	104,282	242,057	424,279	230,247	31,260	19,039	17,613	19,423	28,618	23,944	18,038	15,848
18.25	13,356	17,490	21,689	12,378	9,613	9,509	8,961	8,978	17,946	17,493	14,453	16,592
19.25		469	1,398	1,456	1,184	2,085	2,567	2,904		377	2,401	5,261
20.25												
Sum	5,451,439	5,313,729	5,466,524	3,127,368	1,885,170	1,853,263	1,989,596	2,283,613	2,047,050	2,300,883	2,611,186	3,584,466

Table 25. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1973, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	21,233	22,951	31,997	37,312	29,765	28,549	23,900	21,774	15,543	11,860	9,706	9,457
5.25	42,449	40,549	55,062	59,847	48,696	55,269	47,458	43,735	32,884	28,554	21,165	18,474
6.25	83,397	67,386	83,833	86,305	72,516	83,426	83,999	77,925	60,004	54,193	46,610	33,810
7.25	164,630	118,567	119,635	114,860	90,573	113,076	121,260	126,551	98,960	91,892	82,379	71,778
8.25	279,968	221,721	191,521	155,495	113,937	131,941	154,687	167,515	146,024	142,869	132,525	121,200
9.25	373,890	374,618	331,578	226,405	147,225	157,163	174,906	189,247	184,273	192,564	197,222	187,629
10.25	397,915	499,629	537,593	365,939	210,002	195,698	203,672	211,932	186,899	217,680	247,167	270,691
11.25	446,338	508,889	712,735	560,054	340,587	287,351	257,561	248,008	208,212	223,052	251,704	317,377
12.25	495,323	579,222	608,103	624,529	504,729	462,337	393,687	342,954	258,668	247,945	259,928	294,385
13.25	322,214	550,952	768,833	435,284	426,514	588,100	610,034	551,400	406,170	338,797	300,701	310,207
14.25	149,281	301,924	574,961	406,496	237,431	351,603	516,983	655,681	596,928	558,000	476,173	403,841
15.25	61,489	108,490	224,419	220,017	152,351	197,878	248,810	315,602	385,074	514,438	630,986	662,947
16.25	21,129	42,252	68,451	38,610	42,661	89,684	133,155	166,954	180,579	217,241	278,696	431,630
17.25	7,992	10,896	16,554	10,957	5,738	10,293	19,911	35,705	51,844	80,261	117,422	159,029
18.25	7,320	7,915	7,974	6,429	3,823	4,342	4,698	4,992	4,192	4,843	9,586	22,607
19.25	478	1,275	2,549	4,015	1,651	2,114	2,438	2,691	248	668	1,154	1,826
20.25												
Sum	2,905,451	3,469,293	4,444,552	3,372,050	2,441,329	2,770,415	3,007,292	3,171,552	2,821,991	2,929,347	3,067,438	3,321,788

Table 26. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1974, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	10,293	15,718	22,957	23,748	16,037	11,195	9,412	8,558	10,585	5,995	5,011	3,403
5.25	15,971	23,642	37,742	42,437	35,471	29,860	21,411	18,144	22,097	12,443	10,808	8,258
6.25	26,770	30,259	52,439	67,534	62,294	57,641	51,038	38,016	44,847	23,559	20,344	15,945
7.25	48,425	40,292	54,703	78,892	90,652	97,546	93,113	80,531	91,976	59,706	35,888	28,432
8.25	106,940	67,499	64,185	85,481	105,156	133,257	144,344	144,223	172,410	138,443	89,961	47,286
9.25	168,670	138,010	99,897	89,680	107,867	114,116	184,879	198,042	285,921	254,893	203,941	115,175
10.25	249,783	227,824	191,839	123,334	99,865	131,801	184,596	226,336	348,852	373,879	354,784	259,497
11.25	354,727	328,363	325,966	231,827	110,971	106,601	144,512	203,165	346,003	422,398	466,825	437,516
12.25	356,140	445,423	463,313	369,220	252,590	134,347	126,352	153,016	252,721	364,415	473,045	523,205
13.25	334,187	424,036	586,356	495,965	388,720	294,555	236,775	176,210	208,586	255,295	331,210	438,366
14.25	367,816	398,398	528,235	546,692	439,876	371,285	386,162	377,556	388,312	308,629	227,873	278,964
15.25	581,307	478,504	490,360	449,010	368,824	363,209	423,197	457,243	528,891	552,837	393,992	193,442
16.25	621,756	753,909	743,917	512,920	457,365	286,628	326,660	368,149	486,651	563,168	431,187	188,250
17.25	208,900	358,090	694,953	698,607	327,020	275,784	295,298	310,664	364,340	401,795	250,944	155,294
18.25	43,420	93,602	161,647	177,907	66,222	121,118	176,974	220,410	287,732	341,807	163,316	78,452
19.25	1,138	2,035	6,748	15,589	12,189	17,262	22,541	26,994	10,969	19,510	22,558	23,408
20.25												
Sum	3,502,906	3,834,864	4,536,528	4,017,808	2,946,709	2,580,489	2,831,122	3,010,567	3,854,431	4,101,132	3,483,558	2,796,205

Table 27. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1975, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	3,119	2,894	4,297	8,486	20,533	32,586	40,828	47,299	156,015	169,410	149,757	123,271
5.25	6,622	5,624	6,751	12,083	28,598	37,040	56,748	69,052	210,908	255,462	257,598	243,230
6.25	13,894	10,165	8,560	13,625	37,045	48,502	58,925	85,988	256,495	304,783	350,795	371,094
7.25	25,404	19,115	14,222	13,545	32,408	55,162	68,060	80,125	270,736	331,041	379,830	483,540
8.25	41,638	36,044	24,021	20,605	34,663	44,005	69,666	82,573	241,610	310,936	377,287	483,139
9.25	72,077	56,049	45,473	32,809	45,336	44,329	56,872	76,176	203,877	262,852	318,779	448,470
10.25	167,978	93,751	69,553	59,547	69,765	57,226	50,429	62,242	165,510	217,090	254,213	346,422
11.25	369,169	211,369	110,551	91,801	120,588	88,107	73,314	63,708	146,983	164,861	195,365	257,820
12.25	587,017	466,108	237,599	141,405	169,167	145,934	119,137	93,567	191,087	159,269	148,413	182,383
13.25	610,835	690,811	496,520	320,506	227,168	187,256	175,109	157,983	294,892	233,108	170,930	140,006
14.25	457,410	643,984	651,832	564,228	374,655	243,989	213,073	198,161	365,909	339,473	262,956	194,527
15.25	247,240	397,752	514,943	591,295	418,713	248,614	266,700	252,998	424,428	370,844	311,764	282,112
16.25	214,087	220,844	271,687	354,078	278,280	126,365	158,196	196,214	393,245	408,294	356,446	306,849
17.25	189,631	171,031	179,281	170,838	125,582	70,036	77,232	85,154	138,870	178,970	209,733	247,432
18.25	102,551	99,461	113,250	106,198	[illegible]	15,784	20,468	27,748	59,676	67,500	65,556	71,884
19.25	24,667	29,957	35,538	35,644	15,163	2,846	2,839	3,075	2,604	3,591	7,038	10,128
20.25												
Sum	3,134,674	3,156,949	2,787,702	2,542,396	2,071,632	1,466,883	1,530,732	1,610,736	3,609,140	3,860,241	3,874,515	4,242,010

Table 28. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1976, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	88,320	53,591	35,098	27,734	98,287	72,345	44,487	34,645	21,854	10,934	6,898	12,854
5.25	183,085	118,194	75,562	50,686	150,994	135,352	105,810	79,039	53,415	28,661	16,622	10,045
6.25	322,867	236,601	153,136	82,379	216,910	199,847	177,581	165,271	112,570	63,417	39,369	20,965
7.25	475,089	414,410	319,594	172,403	274,736	251,820	239,126	256,761	207,658	127,232	82,426	45,639
8.25	567,562	599,693	532,516	315,757	413,759	297,682	280,878	303,307	304,483	212,258	159,395	93,770
9.25	519,467	714,034	781,364	534,973	636,937	424,372	313,969	338,922	307,949	276,996	248,912	175,808
10.25	429,618	631,801	904,792	763,628	946,580	626,465	377,320	365,469	333,237	279,679	290,285	265,634
11.25	327,943	461,669	798,473	807,437	1,176,700	866,610	532,760	417,702	351,134	280,484	279,972	285,311
12.25	225,179	296,996	528,130	636,140	1,178,621	983,123	726,634	611,070	448,985	299,129	269,025	255,032
13.25	154,316	153,447	303,942	381,569	795,010	876,254	785,740	788,951	642,328	432,931	311,880	213,549
14.25	138,949	100,805	131,201	156,382	390,417	441,472	501,020	661,795	652,550	536,013	443,464	233,585
15.25	211,719	145,897	111,326	93,156	183,836	190,848	187,143	244,631	321,439	352,914	405,962	233,275
16.25	250,821	198,343	173,593	108,318	113,629	88,726	74,074	87,957	105,598	112,853	145,889	106,420
17.25	255,292	179,373	165,548	127,645	125,385	77,034	39,033	35,978	37,590	34,109	39,435	27,767
18.25	66,719	58,719	86,247	74,637	64,018	34,908	14,771	14,382	14,474	13,298	13,233	7,232
19.25	11,908	10,682	11,976	9,111	6,014	5,536	3,656	4,160	3,645	2,972	2,631	2,308
20.25			36	385			33	0				
Sum	4,259,693	4,392,372	5,129,297	4,358,797	6,817,118	5,599,326	4,420,911	4,422,099	3,926,128	3,067,779	2,761,484	1,993,476

Table 29. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14oS) for 1977, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	16,549	6,986	8,866	46,026	61,408	84,405	143,124	148,203	148,596	182,564	182,450	161,882
5.25	14,582	20,632	14,469	57,173	77,620	99,186	122,248	199,289	206,944	211,316	278,243	270,257
6.25	9,777	46,334	17,466	22,117	85,039	120,498	134,407	157,518	231,698	259,124	276,072	402,069
7.25	16,847	15,784	57,920	23,621	27,739	104,892	141,662	147,299	176,166	247,787	307,734	344,997
8.25	37,473	20,490	43,303	52,096	31,796	42,487	115,550	136,637	156,326	178,925	263,411	357,379
9.25	81,844	39,586	22,976	69,397	52,671	34,885	34,663	96,239	112,514	153,125	178,409	289,929
10.25	150,019	81,212	39,911	25,498	78,890	60,138	32,900	34,088	62,980	100,687	137,784	180,214
11.25	208,730	162,661	80,212	40,321	22,989	63,698	75,284	35,167	28,682	27,609	77,881	125,957
12.25	199,876	228,369	166,093	83,769	27,199	15,112	29,577	63,489	51,848	24,600	23,818	59,295
13.25	149,719	205,461	225,686	169,451	50,458	12,293	10,596	12,174	24,153	45,868	34,487	20,191
14.25	95,013	116,099	172,501	203,185	89,761	18,284	11,999	8,162	6,962	7,896	18,838	34,036
15.25	74,363	42,153	78,802	128,783	67,455	19,777	16,083	11,798	7,600	5,044	4,084	5,614
16.25	34,465	8,215	22,089	41,504	20,835	12,517	12,088	10,214	7,807	5,193	2,668	2,380
17.25	8,411	1,985	4,125	6,818	4,917	2,954	3,956	3,945	3,260	2,346	805	845
18.25	2,044	575	706	962	756	749	723	582	467	225	90	138
19.25	262	243	247	231	71	6	5	20	20	27	9	2
20.25			4	18		0	0	0				
Sum	1,104,856	1,003,387	988,753	1,035,236	756,876	787,754	990,416	1,171,427	1,356,536	1,582,271	1,901,792	2,375,803

Table 30. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14oS) for 1978, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	159,153	122,506	197,373	157,214	119,865	87,839	79,847	88,217	66,085	48,601	32,258	19,718
5.25	255,022	209,343	323,680	282,223	225,231	154,317	142,644	138,953	111,847	93,780	70,934	45,170
6.25	356,892	300,416	386,804	440,648	379,434	256,896	225,986	223,177	159,562	140,131	123,423	92,118
7.25	481,104	369,113	496,577	474,531	525,256	401,036	346,545	324,361	237,231	186,717	171,488	152,027
8.25	449,908	442,799	602,899	566,314	608,852	531,591	510,546	474,518	325,785	260,210	214,394	205,106
9.25	386,665	465,420	676,004	642,182	629,503	582,191	638,899	647,983	459,898	347,164	283,946	239,418
10.25	299,918	355,693	710,927	673,335	674,051	568,112	617,452	775,220	581,772	473,226	369,685	304,405
11.25	177,392	253,433	490,574	685,083	668,874	574,773	605,609	644,859	590,093	557,499	475,764	386,882
12.25	105,567	137,532	299,733	434,758	599,688	535,218	554,236	606,919	509,928	463,375	502,838	473,640
13.25	37,403	72,067	131,541	238,851	333,465	372,605	452,435	507,742	431,368	396,710	393,761	439,624
14.25	15,740	18,776	51,285	92,054	139,797	178,440	194,391	299,310	309,147	314,825	317,611	334,797
15.25	13,394	12,071	12,442	24,363	45,049	49,371	73,893	118,744	126,360	148,398	197,335	231,106
16.25	2,697	4,022	11,020	10,170	9,895	10,642	20,473	29,035	28,309	44,515	64,639	84,483
17.25	1,118	1,136	912	3,234	5,642	4,012	3,493	4,816	5,418	8,698	12,278	16,009
18.25	9	85	61	88	137	102	937	2,046	1,774	1,642	1,543	1,892
19.25				1	11	1					26	374
20.25												
Sum	2,859,430	2,881,044	4,524,491	4,817,250	5,037,767	4,357,821	4,518,977	4,937,056	3,978,978	3,508,661	3,246,901	3,041,674

Table 31. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14oS) for 1979, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	11,606	28,182	30,540	28,742	41,956	42,086	44,032	45,841	44,612	28,967	22,811	30,840
5.25	25,952	39,471	52,165	50,179	63,014	65,132	60,371	62,298	64,260	54,091	41,722	40,049
6.25	54,438	29,090	65,269	71,712	82,106	93,263	85,759	77,155	77,019	68,453	72,985	60,221
7.25	108,424	59,597	49,321	85,361	103,394	100,584	110,681	98,847	91,407	74,593	84,875	103,465
8.25	177,724	114,641	57,050	84,180	127,053	123,660	113,198	114,065	105,687	83,226	85,113	115,043
9.25	228,880	197,712	106,354	54,409	121,868	141,734	129,657	117,207	107,602	95,869	89,652	106,930
10.25	244,737	257,319	188,907	99,807	56,601	122,360	136,724	130,145	112,695	81,540	95,306	106,155
11.25	308,300	261,019	252,445	176,781	75,261	58,294	94,840	118,646	115,951	88,578	[illegible]	104,953
12.25	400,029	315,091	252,818	233,306	117,788	78,036	56,489	50,839	82,994	82,491	78,120	87,684
13.25	467,437	407,357	290,228	219,503	143,527	122,179	83,849	56,029	41,185	37,790	50,468	76,399
14.25	339,786	424,516	381,651	222,372	116,185	124,516	110,884	86,213	60,666	34,134	15,988	35,898
15.25	149,646	251,127	312,844	239,516	46,231	65,225	85,765	81,851	73,156	50,891	19,131	9,760
16.25	49,747	92,875	150,302	126,060	33,203	40,806	32,210	35,374	40,861	39,789	19,080	3,373
17.25	5,532	14,309	37,812	35,567	7,970	9,774	13,503	19,227	18,274	12,801	6,959	1,066
18.25	1,901	2,504	2,804	2,291	367	1,246	2,038	3,022	3,412	2,950	4,143	82
19.25	6	6	408	120	2	0	2	2	9	113	159	
20.25									0			
Sum	2,594,252	2,519,700	2,253,472	1,756,572	1,166,245	1,219,586	1,192,828	1,128,458	1,063,974	852,059	786,337	911,478

Table 32. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1980, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	29,722	40,628	63,517	49,782	122,687	182,009	272,259	284,277	301,336	355,504	364,594	408,395
5.25	42,927	65,399	105,187	85,422	165,046	203,778	317,619	390,674	400,034	434,935	547,256	629,686
6.25	52,529	74,167	101,030	111,047	162,471	240,923	347,999	410,350	478,005	506,507	581,691	889,522
7.25	74,952	71,041	110,768	115,609	189,599	180,515	350,066	386,489	486,142	542,539	613,603	883,808
8.25	110,471	86,913	109,400	113,110	214,375	210,206	247,141	350,136	366,291	512,817	603,061	821,486
9.25	143,398	126,313	103,613	98,170	178,402	219,456	265,761	262,571	303,699	368,519	519,830	755,948
10.25	94,723	156,965	134,667	80,935	142,530	168,066	247,227	256,786	245,012	242,116	365,713	602,836
11.25	103,610	117,241	164,587	97,547	110,536	125,622	182,224	195,812	226,670	220,191	212,388	389,235
12.25	92,769	105,948	128,939	118,397	130,204	90,070	126,975	144,168	148,654	173,779	195,731	225,188
13.25	78,510	89,994	103,309	85,532	152,061	91,513	89,518	83,768	96,798	112,469	120,696	185,562
14.25	45,302	72,574	83,107	66,645	86,469	75,144	86,296	73,995	63,677	59,089	71,665	106,320
15.25	12,182	27,759	60,794	49,161	70,369	39,067	41,750	52,120	54,325	49,115	43,466	53,693
16.25	4,481	7,097	9,924	23,153	46,120	19,646	17,695	20,701	20,007	25,278	29,598	36,071
17.25	1,315	1,495	2,158	3,073	6,035	4,140	4,128	4,296	5,601	7,001	8,678	12,341
18.25	123	6	289	394	819	531	470	487	934	1,108	1,179	2,201
19.25					31	46	31	55	65	68	74	112
20.25												2
Sum	916,992	1,091,711	1,335,348	1,165,950	1,914,287	2,003,593	2,797,802	3,132,562	3,447,449	3,866,282	4,533,611	6,313,676

Table 33. Biomass per length class and month of Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) for 1981, in tonnes.

Midlength	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4.25	323,437	350,618	295,105	216,909	241,557	197,578	162,403	106,459	65,190	43,654	31,003	25,125
5.25	531,256	602,525	548,205	411,339	394,645	339,400	319,006	231,640	153,632	90,857	63,106	49,164
6.25	722,548	793,727	884,696	714,245	543,601	526,745	498,823	408,200	299,601	195,329	113,355	89,798
7.25	852,922	978,394	1,128,610	1,079,008	876,121	614,182	709,979	585,494	486,693	352,899	231,135	142,494
8.25	858,240	1,118,642	1,327,163	1,466,949	1,281,106	928,801	777,993	755,831	645,708	537,288	400,034	283,796
9.25	746,892	1,139,050	1,420,554	1,550,162	1,732,426	1,311,144	1,129,725	833,251	751,697	673,084	575,979	485,022
10.25	609,529	845,338	1,413,653	1,572,937	1,696,166	1,681,831	1,520,839	1,180,237	877,583	706,382	704,411	675,359
11.25	509,553	704,364	999,817	1,478,001	1,669,424	1,585,654	1,773,961	1,503,279	1,187,108	884,587	670,446	785,311
12.25	250,866	529,980	764,417	1,049,484	1,496,086	1,466,688	1,627,679	1,533,100	1,043,411	1,130,763	888,216	741,693
13.25	158,055	236,504	520,722	720,795	939,653	1,183,846	1,396,238	1,325,905	1,220,818	1,162,477	1,081,903	970,318
14.25	104,044	140,493	215,613	417,951	579,706	662,633	893,232	987,858	995,609	942,733	899,332	1,046,115
15.25	53,441	85,911	120,865	170,540	293,441	370,383	459,173	494,506	568,066	629,102	590,574	816,477
16.25	12,725	26,391	55,084	77,823	95,296	110,258	177,910	222,293	249,968	270,931	315,591	476,903
17.25	5,254	7,921	11,958	25,464	37,961	31,497	30,442	42,667	51,974	85,626	107,676	165,153
18.25	123	272	2,743	4,357	4,505	2,196	1,919	4,167	6,199	9,892	11,282	19,921
19.25	4	9	14	38	166	247	286	369	324	299	368	1,267
20.25					1							25
Sum	6,006,778	7,783,819	9,880,657	11,134,656	12,036,891	11,119,268	11,555,976	10,260,610	8,994,927	7,738,607	6,801,230	6,789,097

Monthly Spawning Stock and Egg Production of Peruvian Anchoveta *(Engraulis ringens)*, 1953 to 1982*

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Abstract

Available data on the reproductive biology of the Peruvian anchoveta (*Engraulis ringens*, northern/central stock, 4-14°S) are reviewed and used to estimate monthly spawning size and egg production from January 1953 to December 1982. Basic information used are: (a) monthly biomass by length class (4 to 20 cm), (b) a model relating the shape and position of the maturation ogive to sea surface temperature, (c) seasonal patterns of maturity, (d) batch fecundity estimates of females anchoveta and (e) various ancillary information woven into a coherent whole. Potential uses of the time series derived are discussed along with sources of errors and ways of reducing these.

Introduction

The reproductive output of the Peruvian anchoveta (*Engraulis ringens*) has been earlier reported either in the form of relative egg densities, as estimated from egg surveys, or computed through the "egg-production method", applied once to data from the 1981 peak reproductive season (Santander et al. 1984).

In this contribution, the literature on anchoveta reproduction is reviewed. Available information is used to estimate parameters used subsequently to compute monthly egg output by the stock of anchoveta from 4 to 14°S off Peru, from January 1953 to December 1982, based on monthly biomass data derived by Pauly, Palomares and Gayanilo (this vol.) and ancillary data presented in detail further below.

Materials and Methods

Basic Model Structure

Reproductive output (RO) in a given month (i = 1-360) can be viewed as the ultimate product of different factors summed up over all length classes, i.e.,

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* ICLARM Contribution No. 382.

$$RO_i = \sum_{j=1}^{n} B_{ij} \cdot P_{ij} \cdot A_j \cdot S_k \cdot PF_j \cdot RF \qquad ...1)$$

where B_{ij} is the biomass of male and female anchoveta in length class j, P_{ij} is the fraction of mature fishes in length class j, A_j is a size-specific empirical factor relating anchoveta fecundity per unit weight to length j, S_k is the average number of times a female anchoveta spawns per month, with k = 1 (January) to k = 12 (December), PF_j is the fraction of females of length j in the population and RF is the relative batch fecundity (eggs/body weight in g) of a female anchoveta whose value of A_j is equal to unity.

The following sections document each of the variables and constant used in implementing equation (1).

Biomass by Length Class

The estimates of monthly biomass by length class used here were taken from Pauly, Palomares and Gayanilo (this vol.). The median lengths considered ranged from 4.25 to 20.25 cm. As will be seen below, only fish above 12 cm contributed significantly to egg production. However, all computations were performed with all length classes included.

The Fraction of Mature Fish as Function of Length

Fig. 1 presents maturation ogives for anchoveta, based on data gathered by various authors in the 1950s and 1960s. As might be seen, these data suggest that under average condition anchoveta have a mean total length at first maturity of L_{50} = 14 cm. The mean maturation range (i.e., the length where 75% of the anchoveta have reached first maturity minus the length where 25% have) is 1.8 cm. As will be noted from Fig. 1 and Table 1, the latter estimate is not very reliable, being based on three authors whose work suggest a mean range of about 2.9 cm, and another group of three authors whose work suggest a mean range of about 1.1 cm.

Tsukayama and Alvarez (1981) showed that in "warmer years" (i.e., in years during El Niño events), mature fish were usually smaller than during cold years. Their figure has been redrawn here as Fig. 2, and temperatures added, together with estimates of L_{50} based on the median of the class immediately preceding the model class - in analogy with length-converted catch curves, where the length class immediately to the left of the sample mode usually provides reasonable estimate of mean size at first capture (see Ingles and Pauly 1984).

The mean of these rough estimates of L_{50} is, in colder years indeed higher than the mean of warmer years (Table 1). Moreover, the mean of the 10 values of L_{50} in Fig. 1, corresponding to an intermediate mean temperature, fits neatly between the points for the "cold" and "warm" years (Fig. 3), confirming that the estimates of L_{50} in Fig. 2 are indeed reasonable.

These 3 sets of averages, representing a total of 25 pairs of L_{50} and temperature values, along with the mean maturation range of 1.8 cm provide the key elements of our model for estimation of the factor P_{ij} in equation (1). This model is structured around the logistic equation, which generates curves resembling the graphs in the lower panels of Fig. 1, and has the form

$$P = 1/(1+\exp(-r_m(L_p-L_{50}))) \qquad ...2)$$

Given a knowledge of L_{50} and L_{25} (or L_{75}) as obtained from the relationships in Fig. 3, the parameters r_m of equation (2) can be estimated from

$$r_m = \log_e(0.75/0.25))/L_{50}-L_{25} \qquad ...3)$$

or through the equivalent equation pertaining to L_{75}.

The model was implemented using the mean monthly temperatures for 1953 to 1982 in Pauly and Tsukayama (this vol.)

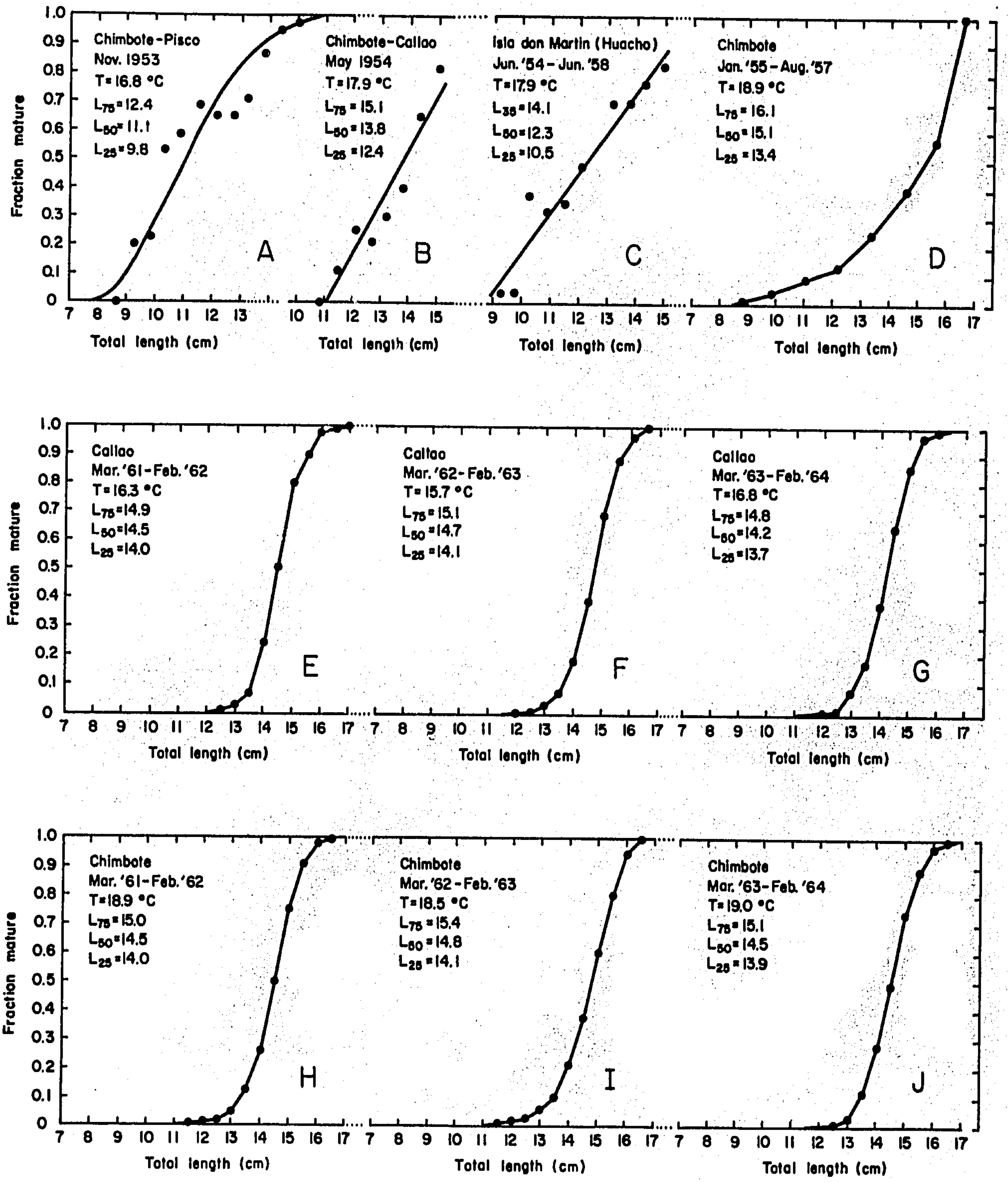

Fig. 1. Relationship between the fraction of mature anchoveta *(E. ringens)* and their total length off Peru (1953-1964).
A: based on Clark (1954, Fig. 5, both sexes combined)
B: based on Clark (1954, Fig. 5, males only)
C: based on Jordan (1959, Fig. 9, erroneous values <130 mm SL omitted)
D: based on Miñano (1958, Table VIII, females, n = 6,142)
E-J: based on Einarsson et al. (1966, Fig. 8, both sexes combined) n = 726, 686, 565, 508, 929 and 614 for D-J, respectively.

Table 1. Summary of data on anchoveta maturation as a function of length and temperature (see also Figs. 1 and 2).

Code in Fig. 1 or 2	Temp (°C)	TL_{50} (cm)	Maturation range (cm) L_{75}-L_{25}	Remarks
A	16.8	11.1	2.6	*early years:* mean temp = 17.67°C mean L_{50} = 13.95 cm n = 10 (see Fig. 1)
B	17.9	13.8	2.7	
C	17.9	12.3	3.6	
D	18.9	15.1	2.7	
E	16.3	14.5	0.9	
F	15.7	14.7	1.0	
G	16.8	14.2	1.1	
H	18.9	14.5	1.0	
I	18.5	14.8	1.3	
J	19.0	15.5	1.2	
K	16.4	14.25	-	*cold years:* mean temp = 16.84°C mean L_{50} = 14.38 cm n = 8 (see Fig. 2)
L	17.2	14.25	-	
M	16.5	14.25	-	
N	17.6	14.25	-	
O	16.1	14.25	-	
P	16.2	13.25	-	
Q	17.4	14.25	-	
R	17.3	16.25	-	
S	19.5	14.25	-	*warm years:* mean temp = 18.64°C mean L_{50} = 12.68 cm n = 7 (see Fig. 2)
T	17.9	14.25	-	
U	17.2	12.25	-	
V	20.7	12.25	-	
W	19.9	11.25	-	
X	17.7	12.25	-	
Y	17.6	12.25	-	
mean	17.7	13.77	1.81	
n	25	25	10	
s.e.	0.25	0.26	0.31	

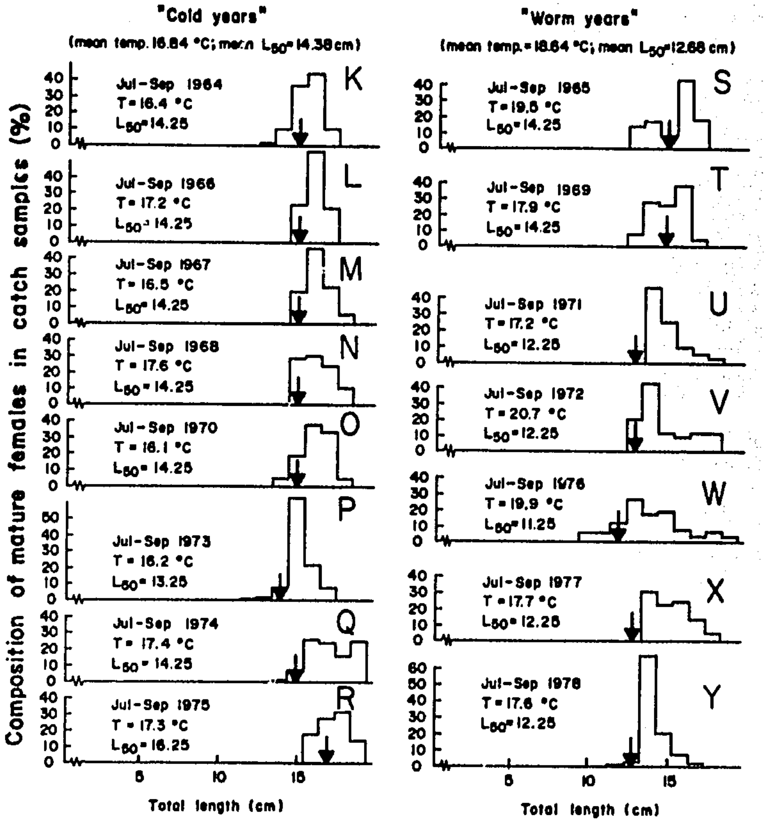

Fig. 2. Relationship between two groups of estimates of mean length at first maturity (L_{50} as approximated by position of arrows, see text) and environmental temperature. Note that L_{50} values during "warm years" are lower than during cold years. The letters K to Y refer to the rows of Table 1 (adapted from Tsukayama and Alvarez 1981 and I. Tsukayama, IMARPE, pers. comm.).

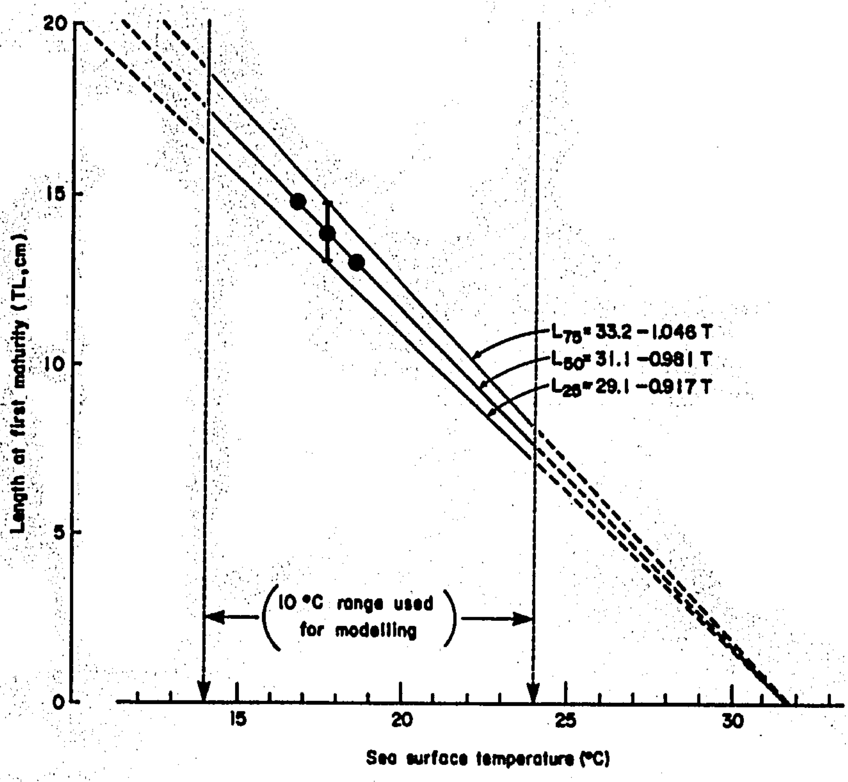

Fig. 3. Model used to estimate values of L_{25}, L_{50} and L_{75} in anchoveta for temperature between 14 and 24°C. The points refer to the means L_{50} values in Figs. 1 and 2 (see also Table 1 and text).

Relative Fecundity and Spawning Frequency as a Function of Anchoveta Size

Not all anchoveta are equal. Major differences occur in the relative fecundity of mature anchoveta as well as frequency of spawning (Parrish et al. 1986). As no data on these size-specific differences are available for Peruvian anchoveta, data presented by the abovementioned authors have been assembled and analyzed (see Table 2). These data yielded values of the factor A_j in equation (1) ranging from near zero for very small fish (which are likely to be immature in any case), 1 in fish of 26 g (the mean weight of Peruvian anchoveta used by Santander et al. 1984 for estimating batch fecundity and spawning frequency) and about 6 in anchoveta of 50 g (Table 3).

As presented and used here, these values of the factor A_j account for the fact that larger anchoveta spawn more frequently, have a longer spawning season and produce more eggs per spawning than smaller ones, a feature also reported for numerous fishes other than engraulids (see Parrish et al. 1986 and references therein).

Table 2. Data on the size dependence of fecundity in northern anchovy *(E. mordax)*.[a]

Spawning season	1st	2nd	3rd	4th plus
Range of weights (g)	11.0-15.4	15.5-18.3	18.3-22.7	20.9-26.6
Mean weight (g)	12.38	16.71	19.76	23.23
Spawnings per season	5.3	11.9	19.2	23.5
Eggs/g female per season[b]	2,803	6,550	11,434	13,386

[a] Adapted from Table 3 in Parrish et al. (1986).

[b] Estimated relationship between relative fecundity (R.F. and body weight is R.F. = 0.582 $W^{2.64}$ (r^2 = 0.981, 2 d.f.).

Table 3. Multiplication factor ("A") accounting for the size-related variability of reproductive output in *Engraulis mordax* females.[a]

ML[b] (cm)	Mean[c] weight (g)	A[d]	Fraction of female anchoveta in catch samples[e]
4.25	0.517	0.00003	0.500
5.25	0.975	0.00018	0.500
6.25	1.65	0.00070	0.500
7.25	2.57	0.00226	0.500
8.25	3.78	0.00626	0.500
9.25	5.33	0.01550	0.500
10.25	7.26	0.03505	0.500
11.25	9.60	0.07329	0.500
12.25	12.4	0.14404	0.515
13.25	15.7	0.26854	0.540
14.25	19.5	0.47592	0.600
15.25	23.9	0.81435	0.710
16.25	28.9	1.34447	0.835
17.25	34.6	2.16273	0.945
18.25	41.0	3.38525	0.990
19.25	48.1	5.16065	1.000
20.25	56.0	7.71006	1.000

[a] Based on R.F. – W relationship in Table 2, footnote [b].

[b] Median of length classes in the anchoveta catch (see Tsukayama and Palomares, this vol.).

[c] Estimated through the mean relationship $W = 0.00674L^3$.

[d] The mean weight of females in Santander et al. (1984) was 25.84 g; the relationship $A = 0.000187W^{2.64}$ generates a factor A = 1 when W = 25.84 g.

[e] From Fig. 4.

The Seasonality of Anchoveta Spawning

Numerous authors give accounts of the seasonal pattern of maturation of anchoveta and its link to spawning (see e.g., Simpson and Gil 1967; Vildoso and Alegre 1969; Santander and Castillo 1969). Here, graphs showing seasonal patterns in the percentage of mature females of anchoveta caught off Chimbote and Callao and presented by Jordan (1980) were used to relate the monthly change in the fraction of mature fish in the stock as a whole to the fraction mature in September, i.e., of the only month for which an estimate of spawning frequency is available (see Table 4). This procedure allows scaling of every month of the year in terms of the September spawning frequency, leading to an estimate of annual number of spawnings (for females of about 26 g) of 24 per year. This value is sufficiently close to the estimate of 20 times per year in northern anchovy (Hunter and Leong 1981) to be acceptable. The estimated mean number of spawnings per month in Table 4 shall thus be used here as estimates of S_k in equation (1).

The Fraction of Female Anchoveta in the Population

Data are available from three different authors showing that the proportion of females in anchoveta catch samples increases rapidly from about 0.5 at 12 cm (TL) to about unity near 17-18 cm (Fig. 4). Moreover the data from two of these authors (Clark 1954; Miñano 1958) contradict Jordan's contention that "the sex ratio is moderately in favor of females in the small fish" (Jordan 1980, based on Jordan 1959 and see Fig. 4). Santander et al. (1984) show that the proportion of females in anchoveta of mean weight 26 g may range from 0.1 to 0.9. Thus, small samples such as will occur when fish of very small sizes are considered separately, may suggest trends that are difficult to explain. A gradual increase of the proportion of females such as suggested by the line superimposed on the data points of Fig. 4 would be, on the other hand, very

Table 4. Selected information on the seasonality of spawning in Peruvian anchoveta *(Engraulis ringens)*.

Month[a]	% mature females in catch samples Callao[b]	 Chimbote[b]	Mean	% mature as fraction of September value	Absolute no. of spawning per month[c]
Jan	11	10	10.5	0.157	0.755
Feb	15	19	17	0.254	1.222
Mar	7	18	12.5	0.187	0.900
Apr	2	4	3	0.045	0.217
May	1	1	1	0.015	0.072
Jun	9	7	8	0.119	0.573
Jul	20	25	22.5	0.336	1.617
Aug	53	50	51.5	0.769	3.700
Sep	73	61	67	1.000	4.812[d]
Oct	74	78	76	1.134	5.457
Nov	43	70	56.5	0.843	4.057
Dec	12	11	11.5	0.172	0.828
					= 24.210[e]

[a] Mean for the years 1966 to 1970.

[b] As read off Fig. 3 in Jordan (1980).

[c] As computed with reference to September value.

[d] Based on Santander et al. (1984) who report that 16.04% of the females sampled in September 1981 had been spawning during the previous 24 hours. (The values in this column correspond to the values of S_k in equation 1, see text).

[e] Note that 24.2 spawnings per year per female (of 26 g, see text) is close to the value of 20 estimated by Hunter and Leong (1981) for northern anchovy *(E. mordax)*.

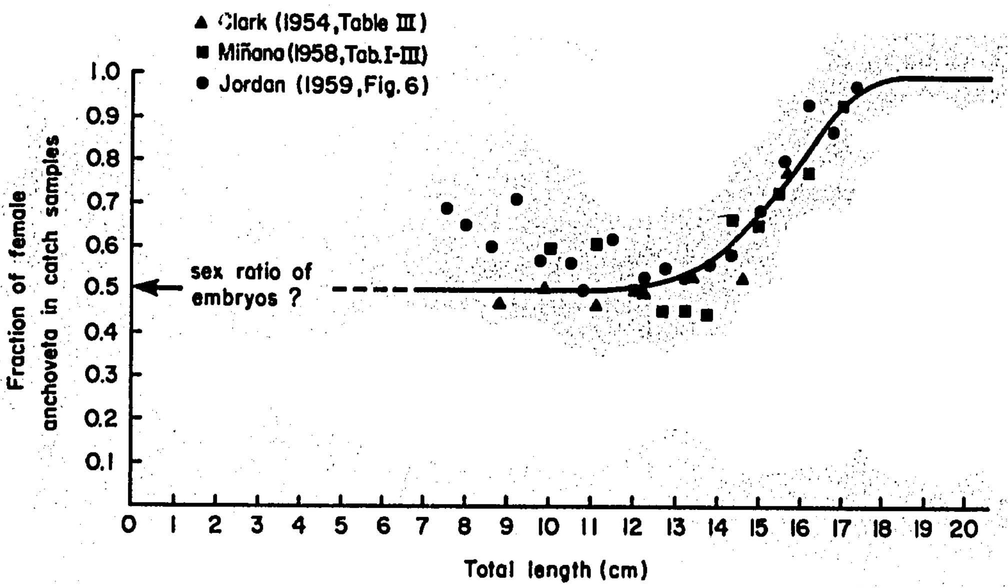

Fig. 4. Relationship between length of anchoveta catch samples and the fraction of females. With the exception of four less credible data points (dots) between 7 and 10 cm, all available data suggest an increase of females toward larger sizes.

easy to explain, as the result of a slightly lower mortality among the females, ultimately linked to slight differences in growth parameters. The eye-fitted curve in Fig. 4 assumes that the sex ratio of anchoveta embryos is 1:1, as should be assumed when no information is available suggesting otherwise (Conover and Heins 1987). The curve was used here to provide estimates of the mean proportion of females in the anchoveta population by length class, i.e., of the parameter PF_j in equation (1), (see also Table 3).

The Batch Fecundity of Female Anchoveta

As mentioned above, only one estimate of batch fecundity in the Peruvian anchoveta is presently available (Santander et al. 1984). It pertains to fish with a mean weight of 25.84 g and is of 15,401 eggs per female. Expressed as relative fecundity, this amounts to 596 eggs/g female, similar to values for the northern anchovy, where relative batch fecundity values ranging between 556 and 720 have been reported (Hunter and Goldberg 1980; Lyczkowsky-Laroche and Richardson 1980)

The reader will notice that the form of equation (1) makes monthly egg output of anchoveta directly proportional to the relative fecundity (RF) value used here. Hence, use of another value of RF would imply a rather straightforward rescaling of final results but no change in the appearance of any of the graphs presenting these results.

Computation of Reproductive Output

A BASIC program available on request from the authors was used to compute, for each length class (from ML = 4.25 to ML = 20.25 cm) and every month (from January 1953 to December 1982) multiplicators which were subsequently applied to the biomasses by length classes in Pauly, Palomares and Gayanilo (this vol.) to give estimates of egg production.

Results and Discussion

Fig. 5 shows the total biomass (from Pauly, Palomares and Gayanilo, this vol.), spawning biomass (females and males) and mature female biomass, for every month from January 1953 to December 1982 (see also Tables 5 and 6). All of these display strong seasonal and interannual oscillations, reflective of spawning/recruitment seasonality and of major events such as the 1971/1972 collapse of the fishery.

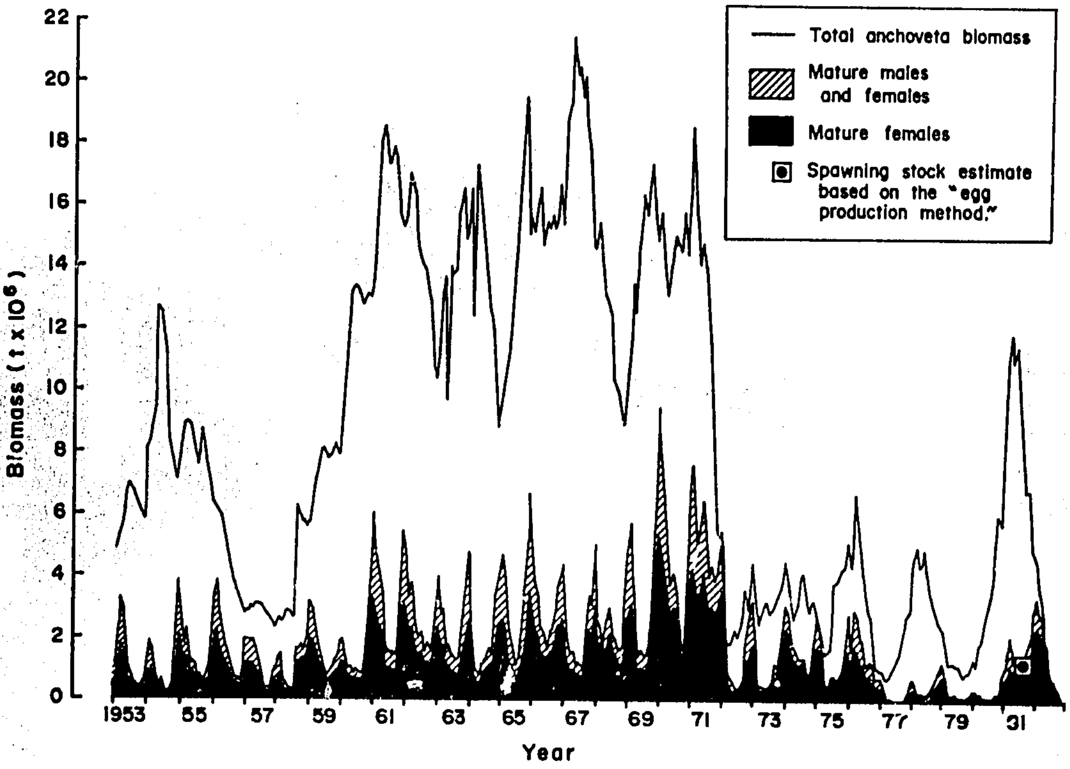

Fig. 5. Total biomass, parent (mature) stock and biomass of mature anchoveta females off Peru, 4-14°S, 1953 to 1982. Note strong, regular seasonal oscillations and also very good match with independent spawning stock estimate in August-September 1981 by Santander et al. (1984).

Table 5. Estimated biomass of mature female and male anchoveta *(Engraulis ringens)* off Peru (4-14°S), 1953 to 1981 (in tonnes).

Date	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	1,101,937	2,231,080	3,317,855	2,955,181	1,715,232	887,920	802,925	481,772	432,953	299,084	355,906	547,272
1954	1,114,237	1,862,158	1,669,903	900,324	663,342	393,733	633,657	245,535	270,727	278,579	465,742	1,830,984
1955	3,818,367	2,990,407	1,640,273	2,312,623	1,269,131	1,214,193	1,084,533	718,045	741,423	514,055	677,972	1,008,368
1956	2,022,882	3,436,052	3,871,157	2,769,103	2,261,131	1,904,923	1,665,332	1,227,079	851,891	674,239	703,180	576,115
1957	934,906	1,953,957	1,958,200	1,923,840	1,935,852	1,626,589	1,226,208	708,169	357,478	382,458	359,280	823,295
1958	1,033,769	1,397,276	1,526,377	646,861	523,424	366,572	360,117	145,397	1,659,263	1,632,507	1,769,059	1,535,579
1959	1,937,039	3,167,238	3,002,390	2,641,178	1,964,495	1,563,931	1,176,471	979,052	741,835	863,518	996,828	1,335,447
1960	1,398,188	1,893,285	1,941,318	1,393,424	1,006,903	1,082,592	897,994	1,025,889	914,385	854,318	847,712	1,649,447
1961	3,185,292	6,097,497	4,624,528	4,260,150	3,700,503	2,324,159	1,610,900	1,582,807	1,485,906	1,517,057	1,415,162	1,648,559
1962	4,986,926	5,524,700	4,304,486	3,326,390	3,785,605	2,644,778	2,128,486	1,959,337	2,227,742	1,522,194	1,810,225	1,596,590
1963	1,855,765	3,009,503	4,083,481	2,797,470	2,985,038	1,479,294	1,796,051	1,470,797	1,397,778	1,275,029	1,281,386	2,085,961
1964	2,995,569	4,135,050	4,803,659	2,160,991	1,159,568	880,377	810,130	1,186,305	1,301,322	1,545,419	1,731,584	1,470,287
1965	2,579,329	3,678,943	4,245,975	4,775,363	3,838,356	2,391,526	1,960,683	1,594,674	1,080,843	1,276,406	1,856,835	2,795,117
1966	4,277,278	6,773,214	5,067,000	3,856,401	3,577,115	2,406,994	2,196,815	2,159,686	1,529,259	2,243,032	2,300,820	2,664,493
1967	3,624,301	3,916,894	4,397,793	2,429,393	1,770,207	1,473,478	1,573,797	1,128,436	1,252,839	1,098,865	1,127,815	2,514,322
1968	3,438,439	3,015,294	5,082,356	2,601,436	2,404,957	1,489,790	2,086,114	2,510,095	3,021,141	2,045,573	1,979,449	1,654,563
1969	1,614,892	1,749,620	4,587,486	4,943,181	5,772,725	3,090,998	1,401,738	1,527,544	1,576,925	1,477,807	1,457,568	2,003,091
1970	4,269,720	7,065,151	9,532,422	7,719,537	6,643,855	5,061,117	3,669,402	3,966,850	4,102,173	3,638,361	2,242,982	1,665,952
1971	1,754 127	3,895,876	7,126,115	7,635,624	5,552,118	4,607,634	5,871,848	6,468,841	5,120,592	3,971,640	4,331,058	3,814,441
1972	4,086,428	4,733,777	4,950,483	2,467,541	904,159	695,461	591,351	468,269	305,053	377,667	546,871	1,924,012
1973	2,390,139	2,987,910	3,289,321	1,069,764	491,190	443,296	408,980	371,737	444,619	693,043	1,173,970	1,068,288
1974	1,494,718	2,287,048	3,080,939	2,881,127	1,932,834	1,721,473	1,506,453	1,365,201	1,356,463	1,379,573	1,151,494	642,609
1975	947,723	1,804,664	2,611,611	2,238,619	1,414,223	520,599	518,336	439,006	770,871	760,153	623,191	804,357
1976	861,315	1,831,948	2,796,799	1,613,161	2,955,161	2,780,036	2,030,119	1,990,957	1,120,721	1,142,474	1,231,079	1,211,618
1977	685,150	689,810	711,919	659,494	237,035	63,979	47,870	33,868	24,036	21,408	29,775	57,493
1978	79,513	379,191	710,600	669,427	356,495	180,114	235,518	198,581	238,450	334,968	509,041	629,390
1979	917,762	1,074,841	1,276,980	900,820	290,680	208,938	212,094	196,876	155,692	127,843	79,159	114,943
1980	149,524	223,371	362,472	280,497	312,954	181,906	158,261	114,713	104,373	108,903	138,160	273,256
1981	212,684	732,513	1,035,224	1,390,938	2,104,529	1,513,989	1,213,016	1,302,727[a]	967,981	1,548,488	1,527,565	1,938,022

[a] The mean of the values for August and September 1981 is 1,302,727 + 967,981/2 = 1,135,354 t or roughly 1.14 t x 10^6, very close to the independent estimate of 1.2 t x 10^6 of Santander et al. (1984).

Table 6. Estimated biomass of mature female anchoveta *(Engraulis ringens)* off Peru (4-14°S), 1953 to 1981 (in tonnes).

Date	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	615,827	1,195,172	1,746,176	1,579,691	952,866	528,122	483,260	298,056	255,258	176,814	210,933	319,216
1954	619,042	1,019,209	936,109	532,104	398,314	243,347	390,367	153,989	168,490	174,619	293,512	1,106,943
1955	2,102,940	1,725,540	1,015,925	1,395,691	839,801	823,599	743,283	506,431	492,227	349,387	453,805	652,163
1956	1,204,884	1,987,935	2,239,360	1,688,618	1,437,081	1,247,581	1,114,805	850,716	590,174	486,461	514,749	429,610
1957	659,363	1,175,588	1,180,478	1,166,533	1,125,296	971,329	758,680	483,371	233,449	246,108	233,716	471,723
1958	556,477	740,904	802,036	347,326	293,339	210,726	207,139	88,171	1,202,768	1,189,938	1,288,487	1,139,298
1959	1,298,637	1,944,351	1,890,045	1,732,905	1,312,675	1,102,878	869,291	738,760	518,156	608,704	702,702	885,948
1960	897,964	1,156,378	1,216,551	936,361	688,785	730,515	627,003	707,929	610,475	566,382	550,639	1,010,306
1961	1,803,530	3,306,876	2,582,563	2,432,481	2,154,049	1,408,025	1,004,056	995,503	946,035	971,338	900,793	1,022,946
1962	2,865,660	3,168,473	2,574,768	2,058,058	2,341,634	1,686,657	1,392,822	1,310,750	1,492,937	1,048,169	1,231,766	1,080,919
1963	1,180,530	1,779,473	2,364,620	1,689,052	1,777,134	885,558	1,070,337	885,941	845,779	779,355	790,169	1,226,490
1964	1,662,957	2,231,810	2,617,670	1,298,227	699,003	548,477	518,564	767,702	853,077	1,024,071	1,150,214	978,396
1965	1,650,085	2,214,192	2,507,260	2,653,662	2,100,665	1,313,716	1,070,955	891,108	624,621	747,579	1,080,974	1,584,004
1966	2,295,652	3,565,841	2,744,425	2,177,035	2,111,526	1,491,288	1,411,529	1,427,034	1,044,861	1,549,580	1,609,084	1,896,141
1967	2,436,599	2,334,488	2,614,873	1,498,499	1,078,631	917,369	998,251	741,759	837,119	752,685	781,682	1,715,421
1968	2,222,367	1,923,715	3,093,793	1,743,305	1,617,222	1,048,551	1,486,107	1,803,690	2,177,900	1,507,961	1,452,011	1,185,830
1969	1,055,306	1,016,052	2,509,428	2,716,689	3,115,582	1,729,460	857,072	953,507	1,001,667	940,335	930,858	1,233,504
1970	2,409,218	3,933,168	5,357,801	4,570,454	4,132,194	3,356,075	2,596,775	2,865,352	3,021,776	2,648,402	1,647,051	1,189,665
1971	1,131,605	2,302,287	4,058,420	4,227,804	3,224,927	2,776,311	3,616,858	4,057,276	3,359,786	2,741,999	3,004,173	2,663,019
1972	2,735,506	3,289,209	3,602,592	1,790,756	554,684	394,682	329,180	269,242	195,745	232,479	320,698	1,036,342
1973	1,257,987	1,601,170	1,825,469	647,634	309,359	295,932	285,064	268,286	324,868	508,249	853,686	820,983
1974	1,155,108	1,731,812	2,340,212	2,175,286	1,425,581	1,266,740	1,188,521	1,124,136	1,150,822	1,192,959	947,942	515,298
1975	732,287	1,254,699	1,746,167	1,575,713	1,015,652	385,496	394,168	348,143	614,395	619,606	521,352	667,123
1976	700,702	1,147,345	1,634,760	995,073	1,724,294	1,600,457	1,186,017	1,191,105	727,369	746,797	815,008	741,795
1977	392,412	380,355	410,443	402,287	152,140	43,395	33,726	24,341	17,233	14,480	18,082	33,772
1978	45,800	200,144	375,241	363,658	206,234	108,776	144,651	127,302	152,809	217,194	330,686	410,997
1979	550,627	673,443	818,801	587,381	182,048	141,044	145,140	139,119	114,046	93,754	55,598	65,879
1980	85,702	129,989	210,861	169,394	199,110	114,365	100,586	76,519	70,606	74,298	92,702	173,842
1981	129,919	418,334	600,842	821,279	1,240,078	933,408	783,706	856,102	663,872	1,046,769	1,058,028	1,374,739

On the other hand, our estimate of spawning stock size for August/September 1981 of 1.14 t x 10^6, is extremely close to the *independent* estimate of 1.2 t x 10^6 (with 95% conf. interval = 56.8%) obtained by Santander et al. (1984) for the area between 4 and 14°S (see Table 5, footnote [a] and Fig. 5). This extremely good match between two estimates that were obtained based on completely independent data sets, assumptions and models is extremely encouraging, as it suggests that our approach for estimating past spawning stock size may be realistic.

Tsukayama and Alvarez (1981) reported a range of 0.067 to 0.244 and an overall mean of 0.133 for the ratio of spawning stock to total anchoveta biomass, for the period 1964 to 1978. Our results (Fig. 6), expressed on a finer temporal scale than those of Tsukayama and Alvarez (1981) not only have a greater range, but a higher overall mean of 0.254, due to our different definition of mature biomass (Tsukayama and Alvarez 1981 defined this as "the biomass of all fish >14 cm"; our definition is "$B_{ij}.P_{ij}$", see equation 1).

Fig. 7 presents our estimates of monthly anchoveta egg production, from January 1953 to December 1981 (1982 was excluded because the VPA III estimates of anchoveta biomasses for the last year of the series are questionable, see Pauly, Palomares and Gayanilo, this vol.). As might be seen, monthly egg production had, during the period covered, several peaks, notably in 1968, 1970, 1971 and 1974. However, these peaks of egg production did not lead to peak

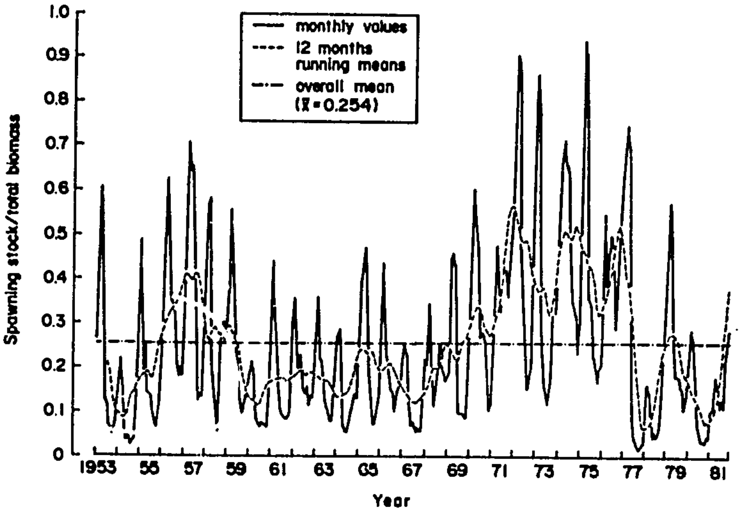

Fig. 6. Relationship between spawning stock and total biomass of Peruvian anchoveta, 1953 to 1981. Note strong oscillations, with two peaks per year, corresponding to the main (September-November) and the lesser (February-April) spawning seasons.

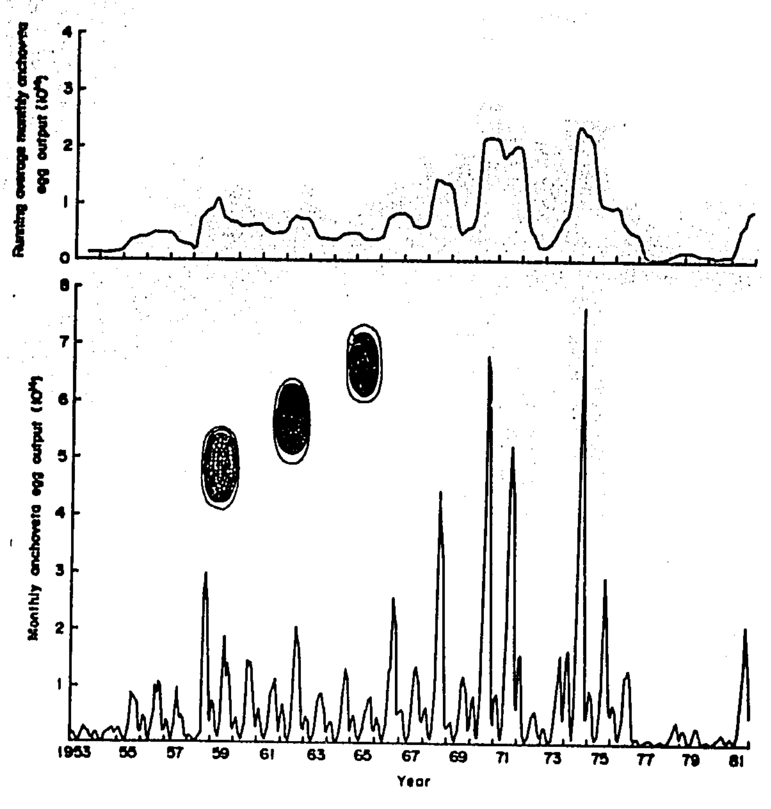

Fig. 7. Total monthly egg output by Peruvian anchoveta (4-14°S), 1953 to 1981. *Above:* 12 months running average to emphasize interyear variability. *Below:* monthly values, to illustrate existence of two spawning seasons, September-November and February-April, of which the former leads to higher production. The drawing of eggs added to this graph are from Santander and Castillo (1973) and illustrate an initial, an intermediate and an advanced stage, respectively.

recruitment. In fact, the annual season of peak egg production (September-November) is usually not followed, a few months later, by a recruitment peak. Rather, it is the minor egg production peak occurring in February to April which usually leads to massive recruitment (see Mendelsohn and Mendo, this vol.; Pauly, this vol.).

Assessing the overall reliability of the egg production estimates in Fig. 7 and Table 7 is difficult. Assuming that the biomass estimates used here were reasonable, we think that the weakest point in our analysis are:

i) lack of data on size-specific egg production in *E. ringens*, and

ii) lack of readily quantifiable evidence on temporal changes in the fecundity of anchoveta.

Table 7. Estimated monthly egg output by the anchoveta stock off Peru (4-14°N), 1953 to 1982 in billions (10^9).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	65,667	162,924	143,223	39,231	10,315	62,991	171,452	274,100	221,913	190,765	169,988	47,987
1954	65,631	167,086	135,885	23,885	6,198	33,796	148,440	149,104	182,401	217,744	228,999	140,146
1955	192,594	240,819	115,618	43,099	17,397	180,024	479,671	826,324	778,989	708,793	640,918	170,418
1956	185,667	451,958	375,879	84,843	22,344	174,638	497,583	1,004,837	829,386	1,061,622	935,160	172,800
1957	204,871	382,666	309,286	84,519	21,132	179,256	479,960	978,112	393,580	460,725	367,908	94,940
1958	54,879	106,952	86,201	13,090	4,979	34,385	93,898	139,860	2,482,968	2,960,861	2,553,971	554,406
1959	352,267	727,599	624,069	166,804	41,560	336,522	880,939	1,852,922	1,123,983	1,378,462	1,084,233	257,249
1960	194,393	384,033	417,947	100,548	24,580	198,923	556,467	1,445,520	1,328,413	1,402,997	977,491	270,551
1961	265,672	571,954	350,565	89,147	28,205	161,973	341,365	790,464	943,793	1,127,001	743,430	160,577
1962	369,270	673,979	447,320	88,255	33,125	210,403	541,371	1,332,815	2,003,316	1,798,188	1,480,403	266,011
1963	215,052	450,209	395,373	76,407	24,766	104,455	340,737	677,512	807,531	861,704	633,174	178,527
1964	185,516	345,418	323,110	46,753	10,022	68,209	193,212	681,985	951,820	1,328,338	1,124,598	193,820
1965	281,072	496,123	374,679	71,605	18,473	105,038	248,511	535,486	556,161	767,545	821,745	222,761
1966	211,101	444,150	336,152	83,771	30,041	172,146	461,883	1,186,560	1,340,525	2,535,393	2,032,671	505,610
1967	527,859	592,172	542,334	95,179	20,401	130,624	412,685	825,421	1,214,606	1,367,367	1,060,139	400,393
1968	355,580	519,640	639,489	127,538	39,366	253,279	1,019,790	2,832,135	4,391,395	3,773,991	2,609,660	354,249
1969	250,636	272,443	371,636	101,184	30,764	168,017	315,948	814,015	1,117,203	1,185,641	915,506	234,347
1970	299,953	738,752	827,515	212,524	71,546	574,098	1,624,671	4,518,802	6,767,713	6,487,205	3,309,029	478,173
1971	327,886	815,886	879,106	166,371	52,456	381,554	1,383,763	3,781,583	4,593,975	5,193,788	4,231,701	781,174
1972	591,728	1,476,866	1,576,613	201,265	12,863	60,192	136,170	315,314	490,235	551,012	423,717	140,856
1973	98,994	248,777	270,108	32,774	5,897	60.655	203,664	510,825	769,852	1,304,407	1,528,727	403,074
1974	562,590	1,464,495	1,618,032	372,631	69,119	517,784	1,671,192	4,155,449	6,004,290	7,610,760	3,774,949	426,594
1975	496,852	926,545	811,228	193,338	41,250	124,851	396,629	973,872	2,301.755	2,916,507	2,041,944	520,579
1976	485,582	678,107	556,813	105,273	39,677	242,818	482,420	1,170,903	1,169,337	1,293,856	1,056,285	162,516
1977	58,380	70,885	70,325	19,859	2,877	9,482	25,432	48,306	47,870	39,427	21,388	6,630
1978	5.754	25,332	38,220	11,586	2,988	14,639	57,307	136,089	200,678	340,920	373,673	98,565
1979	92,511	208,889	216,478	40,457	4,053	30,931	86,501	226,553	281,842	272,974	130,618	10,982
1980	13,075	30,723	31,614	8,492	4,315	18,812	47,003	91,668	120,327	163,237	154,013	50,295
1981	22,550	90,717	113,924	42,434	19,706	129,853	369,512	1,029,983	1,222,403	2,074,030	1,707,866	516,859

Alheit et al. (1983, Table 1, Figs. 1-4) presented data on the size-dependence of batch fecundity of *E. ringens*, based on fish samples from January 1970 to September 1981. Although the analysis presented by these authors is somewhat confused, the key result does emerge that larger anchoveta have higher batch fecundities than small ones. However, we could not use any of the regression lines expressing this relationship, because large engraulid females not only have higher batch fecundities, but also spawn more often than smaller ones. This is the reason why we have used a relationship between size and egg production based on data for *E. mordax* (see Table 2); Fig. 4 in Alheit et al. (1983) shows that *E. ringens* and *E. mordax* are similar enough, at least as far as their batch fecundity is concerned, to justify our approach.

Temporal changes in anchoveta fecundity may be expected, given the density-dependent changes in growth and related parameters discussed in Palomares et al., this vol.). However, concrete evidence for such changes is scanty.

Ware and Tsukayama (1981) write that "in the winter of 1962, the anchovy population was of the order of 24 t x 10^6. According to Miñano (1968, Fig. 5), the gonad weight of a 21-g anchovy at that time averaged 1.1 g. By 1974, the stock declined to 4.5 t x 10^6 and the corresponding gonad weight of a 21-g anchovy was 1.7 g. This finding clearly contradicts the long standing assumption of classical theory that fecundity of marine fish is not affected by fluctuations in population size (Harris 1975)."

Alheit et al. (1983), commenting on their fecundity estimates suggested similarly that "the only remarkable feature is the difference between the relatively low values for the seventies and the high values from 1981". They also noted that "obviously, the fecundity values from the southern Peruvian anchovy stock are higher than in the central and northern stock batch fecundity increases with increasing latitude".

Combining the temporal and the latitudinal trends mentioned above leads to the conclusion that the Peruvian anchoveta may be undergoing, with respect to its fecundity, the same process of "southernization" that is apparent with regard to its growth (see Palomares et al., this vol.).

We have not accounted for "southernization" when deriving our estimates of egg production for the period January 1953 to December 1981. Explicit consideration of this process would obviously have improved our estimates and this should be taken into account in future analyses.

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Relationship between Anchoveta Egg Standing Stock and Parent Biomass off Peru, 4-14°S

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SANTANDER, H. 1987. Relationship between anchoveta egg standing stock and parent biomass off Peru, 4-14°S, p. 179-207. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

A planimetric analysis of ninety maps of anchoveta egg distribution, covering the Peruvian coast from 4 to 14°S, based on egg surveys conducted from 1964 to 1985, was performed and the standing stock of eggs corresponding to each map estimated. The estimates for 1964 to 1981, divided by temperature-related egg development times were plotted against independent estimates of anchoveta parent stock. A dome-shaped curve emerged, suggestive of a strong effect of parental cannibalism on anchoveta egg standing stocks.

Introduction

Numerous anchoveta egg surveys have been conducted since 1964 off Peru, and this paper presents ninety maps summarizing the results of all these surveys. A brief, preliminary investigation of the egg standing stock estimates based on these maps is presented in which egg standing stock, adjusted for the different sea surface temperatures during the different surveys, is related to anchoveta parent stock estimates (i.e., biomass of mature female and male anchoveta, as defined and computed by Pauly and Soriano, this vol.).

Materials and Methods

This contribution is based on ninety surveys carried out between 1964 and 1985. Between 1964 and 1971, four surveys were performed every year, with usually about 120 samples taken on each cruise, covering much of the Peruvian coast, up to 120 nautical miles (nm) offshore.

From July 1972 to 1985, two to four EUREKA surveys were performed per year, with about 350 samples taken during the 2-4 days of these surveys which are performed by commercial vessels operating all along the Peruvian coast (6-18°S), up to 80-100 nm offshore.

A Hensen net (175 cm long, 70 cm aperture diameter and 300 μm was used for all samplings, which consisted of raising the net from a depth of 50 m to the surface. Samples were fixed with 10% formaldehyde immediately after collection; separation and counting of anchoveta eggs were done at IMARPE.

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[a] The author passed away on 25 March 1987. This contribution is based on an analysis of egg distribution maps she compiled and on her extensive notes (The Editors).

Estimation of Egg Standing Stock and Adjusted Egg Standing Stock

The maps presented here were standardized and analyzed in a series of steps implemented such as to ensure greatest possible comparability between maps, as follows:

i) the areas with positive egg records (i.e., 0-500 to >2,000 or >4,000) were estimated by planimetry, ignoring at first the fact that not all surveys covered the whole Peruvian coast;

ii) the surface areas estimated in (i) were multiplied with the midrange of the egg density classes to obtain egg standing stocks, e.g., with 250 eggs/m^2 in the case of the class with limits 1 to 500 eggs/m^2. Ideally, the mean density of samples with counts >4,000 (or >2,000) should have been used to obtain proper factors for these two open-ended classes. Unfortunately, original data allowing computation of such means could be retrieved only for seven maps, all referring to the ">4,000" density class (Table 1). The mean density estimated for this class from the data in Table 1 was 5,013 eggs/m^2 and this value was used with all maps for which a density value for the ">4,000" class was missing. For maps with "2,000" as highest class, a value of 3,000 eggs/m^2 was used (i.e., lower class limit + 1,000, similar to what was used for the ">2,000" class);

iii) standardization of maps for variable coverage of the Peruvian coast was performed in two steps:

a) within each 2° stretch of the coast (i.e., 2-4, 4-6, ..., 12-14°S), simple extrapolations were used. Thus, if a survey had covered only half of the stretch from 10 to 12°S, the estimated number of eggs within that stretch was multiplied with 2;

b) then, using 49 maps representing surveys that had covered all that part of the Peruvian coast of interest here (4-14°S), the mean percentage of total eggs in each 2° stretch of coast was estimated (see Table 2). These percentages were then used to convert estimates of egg standing stock for a given set of 2° stretches (ranging from 1 to 4) to an estimate pertaining to the whole coast. The assumption here is that any given map, with say few eggs between 4 and 10°S, would also have had few eggs between 10 and 14°S had the area also been surveyed. (Readers who disagree with this approach will be able to identify the maps for which this approach was used and delete those in their reanalysis.)

The estimates of total egg numbers for the whole Peruvian coast obtained in this fashion are given in Table 3 where each row corresponds to a given month and in Table 4 where egg standing stock estimates for a few surveys and maps with the same reference month are given separately.

Table 1. Actual egg densities in the density class "> 4,000" in 7 maps for which such information is available.

Map	Date	Latitude south	Eggs/m^2
1	25-02-64 to 18-03-64	10-12°	4,244
5	11-11-64 to 22-12-64	6-8°	4,581
		8-10°	4,594
6	03-03-65 to 22-03-65	6-8°	5,382
		10-12°	6,060
9	22-10-65 to 10-12-65	10-12°	4,151
13	17-11-66 to 13-12-66	6-8°	4,046
		8-10°	5,267
16	08-11-67 to 21-12-67	6-8°	5,864
		8-10°	5,864
		10-12°	5,504
28	16-08-71 to 02-09-71	8-10°	4,604
	Mean		5,013

Table 2. Mean % of total eggs off Peru (4-14°S) in each 2° stretch of coastline.[a]

°Lat. south	Mean %
4-6	3.3
6-8	22.2
8-10	31.9
10-12	21.9
12-14	20.7

[a] Based on 49 surveys which covered the area comprised between 4 and 14°S, i.e., maps with boxed numbers in Table 3.

iv) "adjusting" egg standing stock estimates refers here to dividing the standing stock estimate obtained in step (iii) by the estimated egg development time (itself a function of sea surface temperature (SST); see Table 3 and Pauly, this vol.). This procedure allows comparison of standing stock estimates from periods with different SST and hence different duration of the egg stage itself. Standing stock estimates adjusted in this fashion and expressed on a daily basis are given in Table 3.

Results and Discussion

Tables 3 and 4 summarize the key data derived from the maps. It might be noted that estimates of egg standing stock were generally higher in the 1960s than in the 1970s (means 78 x 10^{12} and 39 x 10^{12}, respectively), as might be expected. Yet adjusted egg standing stocks and estimates of parent stock size in the corresponding month (see Table 3) did not directly correlate with each other. Rather it is log (adjusted standing stock/parent stock) which appears to be linearly related to parent stock (Fig. 1). This suggests a rather strong, density-dependent effect of parent stock on egg survival (see also Fig. 2). Some implications of this finding are discussed in Pauly (this vol.).

Table 3. Key statistics on 90 egg surveys considered in this contribution (see also Table 4).

Map no.[a]	Time of survey[b]		Map eggs standing stock[c] (billions)	Development time[d] (days)	Adjusted egg standing stock[e] (billions/day)	Parent stock (t)[e]
1	25/2-18/3	1964	27,382	1.53	17,946	2,085,961
2	24/3-5/5		16,995	1.74	9,794	2,995,569
$\boxed{3}$	21/5-10/6		12,935	2.02	6,402	4,135,050
$\boxed{4}$	17/8-17/10		136,884	2.10	65,158	880,377
$\boxed{5}$	11/11-22/12		60,267	2.02	29,827	1,301,322
6	3/3-22/3	1965	51,356	1.37	37,467	1,470,287
$\boxed{7}$	29/3-8/4		8,035	1.27	6,341	2,579,329
8	8/7-26/7		55,315	1.55	35,603	4,775,363
$\boxed{9}$	22/10-10/12		44,032	1.72	25,613	1,594,674
$\boxed{10}$	3/2-2/3	1966	16,246	1.37	11,852	1,856,835
$\boxed{11}$	30/4-25/5		4,944	1.78	2,770	6,773,214
$\boxed{12}$	29/8-1/10		418,741	2.14	195,453	2,406,994
13	17/11-13/12		97,376	1.96	49,609	2,159,686
$\boxed{14}$	17/5-26/5	1967	6,357	1.89	3,365	3,916,894
$\boxed{15}$	24/8-8/9		291,933	2.19	133,604	1,473,478
$\boxed{16}$	8/11-21/12		115,701	2.25	51,399	1,128,436
17	6/2-8/3	1968	50,158	1.77	28,369	1,127,815
18	2/9-12/10		168,762	1.98	85,154	1,489,790
$\boxed{19}$	19/11-17/12		15,495	1.85	8,360	3,021,141
20	13/1-27/1	1969	22,023	1.60	13,792	2,045,573
21	13/7-25/7		9,425	1.80	5,231	4,943,181
22	28/8-8/9		82,321	1.84	44,838	3,090,998
23	14/5-31/5	1970	22,089	1.61	13,707	7,065,151
$\boxed{24}$	1/9-21/9		81,971	1.89	43,392	5,061,117
25	15/10-5/11		22,604	1.82	12,429	3,669,402
$\boxed{26}$	20/11-9/12		9,050	1.87	4,837	3,966,850
27	20/5-9/6	1971	107,049	1.60	67,041	3,895,876
$\boxed{28}$	16/8-2/9		12,679	1.70	7,444	5,552,118
$\boxed{29}$	12/11-27/11		29,325	1.85	15,822	6,468,841
30	15/2-13/3	1972	2,075	1.21	1,709	3,814,441
31, 32	8/7-20/7		13,151	1.29	10,200	2,467,541
33	3/8-5/8		23,774	1.42	16,741	904,159
34, 35	4/8-20/9		7,191	1.57	4,587	695,461
$\boxed{36}$	20/10-22/10		5,474	1.55	3,523	591,351
37	15/12-20/12		62,354	1.26	49,636	305,053

Continued

Table 3. Continued

Map no.[a]	Time of survey[b]		Map eggs standing stock[c] (billions)	Development time[d] (days)	Theoretical egg production[e] (billions/day)	Parent stock (t)[e]
$\boxed{38}$	20/1-23/1	1973	35,163	1.08	32,601	377,667
$\boxed{39}$	23/2-16/3		41,320	1.27	32,610	1,924,012
$\boxed{40,}$41	30/5-12/6		19,806	1.94	10,188	3,289,321
42	3/7-7/7		18,941	2.06	9,194	1,069,764
43	1/8-3/8		108,860	2.16	50,314	491,190
$\boxed{44}$	23/9-26/9		60,861	2.12	28,688	443,296
$\boxed{45}$	12/11-13/11		70,731	1.85	38,162	371,737
$\boxed{46}$	26/2-28/2	1974	86,409	1.67	51,682	1,173,970
$\boxed{47}$	28/5-30/5		3,443	1.61	2,137	2,287,048
$\boxed{48}$	7/8-8/8		85,188	1.91	44,667	1,932,834
$\boxed{49}$	3/9-4/9		64,741	2.04	31,732	1,721,473
$\boxed{50}$	14/11-15/11		29,643	1.96	15,102	1,365,201
$\boxed{51}$	14/2-15/2	1975	40,738	1.69	24,141	1,151,494
$\boxed{52}$	6/8-7/8		56,016	2.04	27,456	1,414,223
53	16/9-18/9		55,630	2.06	27,003	520,599
54	26/11-5/12		67,395	1.98	34,006	770,871
$\boxed{55}$	27/1-29/1	1976	17,040	1.84	9,281	760,153
$\boxed{56}$	12/7-25/7		53,835	1.50	35,927	1,613,161
57	11/8-13/8		53,588	1.54	34,806	2,955,161
$\boxed{58}$	16/11-4/12		19,208	1.64	11,703	1,990,957
59	8/3-10/3	1977	45,885	1.35	34,070	1,211,618
$\boxed{60}$	18/4-3/5		6,313	1.35	4,687	685,150
$\boxed{61}$	12/7-14/7		27,966	1.77	15,817	659,494
$\boxed{62,}$63	7/8-27/8		25,419	1.87	13,585	237,035
64,65	18/10-2/11		17,083	1.94	8,787	47,870
66	5/4-18/4	1978	2,672	1.54	1,736	79,513
$\boxed{67}$	19/7-21/7		64,664	1.94	33,262	669,427
$\boxed{68}$	19/10-3/11		6,445	1.94	3,315	235,518
$\boxed{69}$	29/11-18/12		25,479	1.82	14,010	238,450
$\boxed{70}$	6/2-8/2	1979	21,599	1.63	13,281	509,041
71	19/7-7/8		30,123	1.80	16,720	900,820
$\boxed{72}$	4/9-7/9		66,247	1.87	35,404	208,938
$\boxed{73}$	4/11-15/12		69,834	1.66	42,156	155,692
74	12/2-14/2	1980	21,808	1.58	13,783	79,159
$\boxed{75}$	23/9-26/9		68,210	1.94	35,086	181,906
$\boxed{76}$	3/2-4/3	1981	27,259	1.58	17,228	138,160
77	8/4-11/4		40,318	1.66	6,228	212,684
78	22/8-11/9		18,109	2.02	8,962	1,513,989
$\boxed{79}$	4/10-7/10		74,4[illegible]8	1.87	39,814	1,213,016
$\boxed{80}$	27/2-2/3	1982	86,444			
$\boxed{81}$	10/9-14/9		31,585			
82,83	22/11-23/12		9,793			
$\boxed{84}$	17/8-25/9	1984	49,622			
85	30/11-22/12		85,560			
$\boxed{86}$	31/1-4/3	1985	96,169			
87	20/3-7/4		7,764			
88	20/7-12/8		47,457			
$\boxed{89}$	28/8-5/10		138,333			
90	20/1-15/5	1986	10,830			

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[a] Two maps on the same line indicate either surveys conducted in the same months, or which covered a period whose midrange fell in the same month (see Table 4 for separate statistics on these tables); maps with numbers in boxes are those used in Table 2.

[b] In cases where two maps refer to the same month(s), the dates given here refer to the start of the first survey and the end of the second.

[c] Refers to Peruvian coast between 4 and 14°S; see text for inter- and extrapolation methods. Where two map numbers are given, egg standing stock is the mean of these two maps (see also Table 4).

[d] Computed using empirical equation in Pauly (this vol.) and sea surface temperatures in Pauly and Tsukayama (this vol.).

[e] From Pauly and Soriano (this vol.).

Table 4. Egg standing stocks for maps that are combined with another map in Table 3.

Map #	Time of survey (day/month-day/month)	Egg standing stock ($\times 10^{15}$)
31	08/07-20/07, 1972	14.82
32	18/07-20/07, 1972	11.48
34	05/09-08/09, 1972	12.76
35	04/08-20/09, 1972	1.62
40	30/05-12/06, 1973	29.65
41	01/06-04/06, 1973	9.96
62	07/08-26/08, 1977	23.06
63	14/08-27/08, 1977	27.78
64	18/10-21/10, 1977	27.52
65	27/10-02/11, 1977	6.64
82	22/11-23/02, 1982	6.25
83	15/12-23/12, 1982	13.33

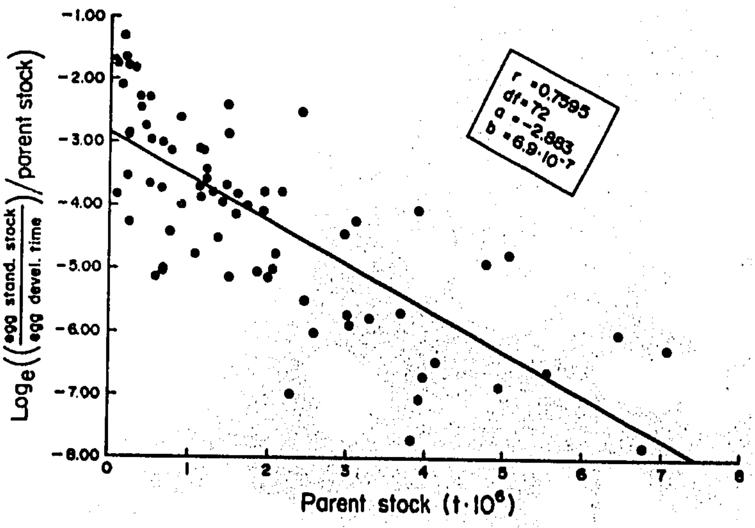

Fig. 1. Relationship between adjusted anchoveta egg standing stock/anchoveta parent biomass and parent biomass, showing strong correlation.

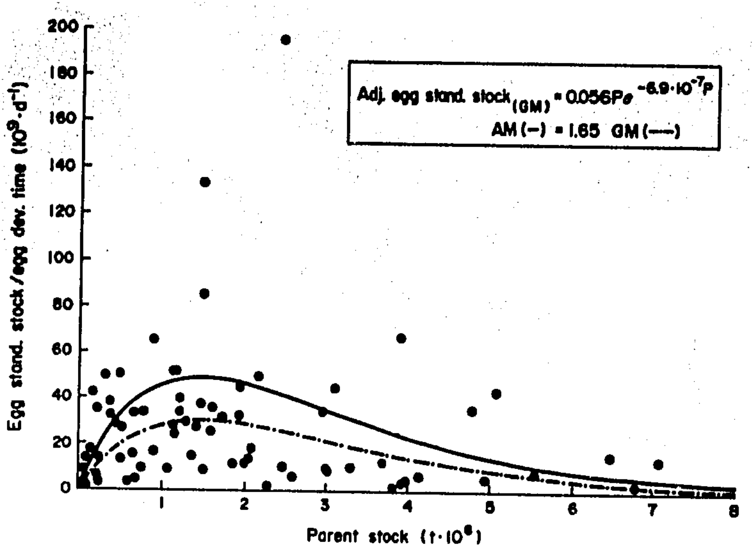

Fig. 2. Relationship between egg standing stock/egg development time (i.e., adjusted egg standing stock) and anchoveta parent stock, suggesting a strong effect of parental cannibalism.

Other findings based on anchoveta egg surveys conducted off Peru are presented in Santander (1981), Santander and Castillo (1981), Santander and Flores (1983), Santander and Tsukayama (1983), Santander and Zuzunaga (1984) and IMARPE (1986).

However, the present contribution is the first in which a comparative analysis of the many egg surveys conducted off Peru has been performed. That these surveys, related to an independent data set (i.e., parent stock estimates), should lead to insights about cannibalism in anchoveta is rather gratifying. It is hoped that future analyses will lead to even more information being extracted from the maps and related data presented here, thus justifying *post hoc* the immense effort and resources that went in obtaining them.

Acknowledgements

Thanks are due to Ms. M.L. Palomares (ICLARM) for her assistance in deriving the egg standing stock estimates and the relationships presented here as Figs. 1 and 2, and to Mr. Christopher Bunao for standardizing and redrafting the maps presented here in Figs. 3 to 25.

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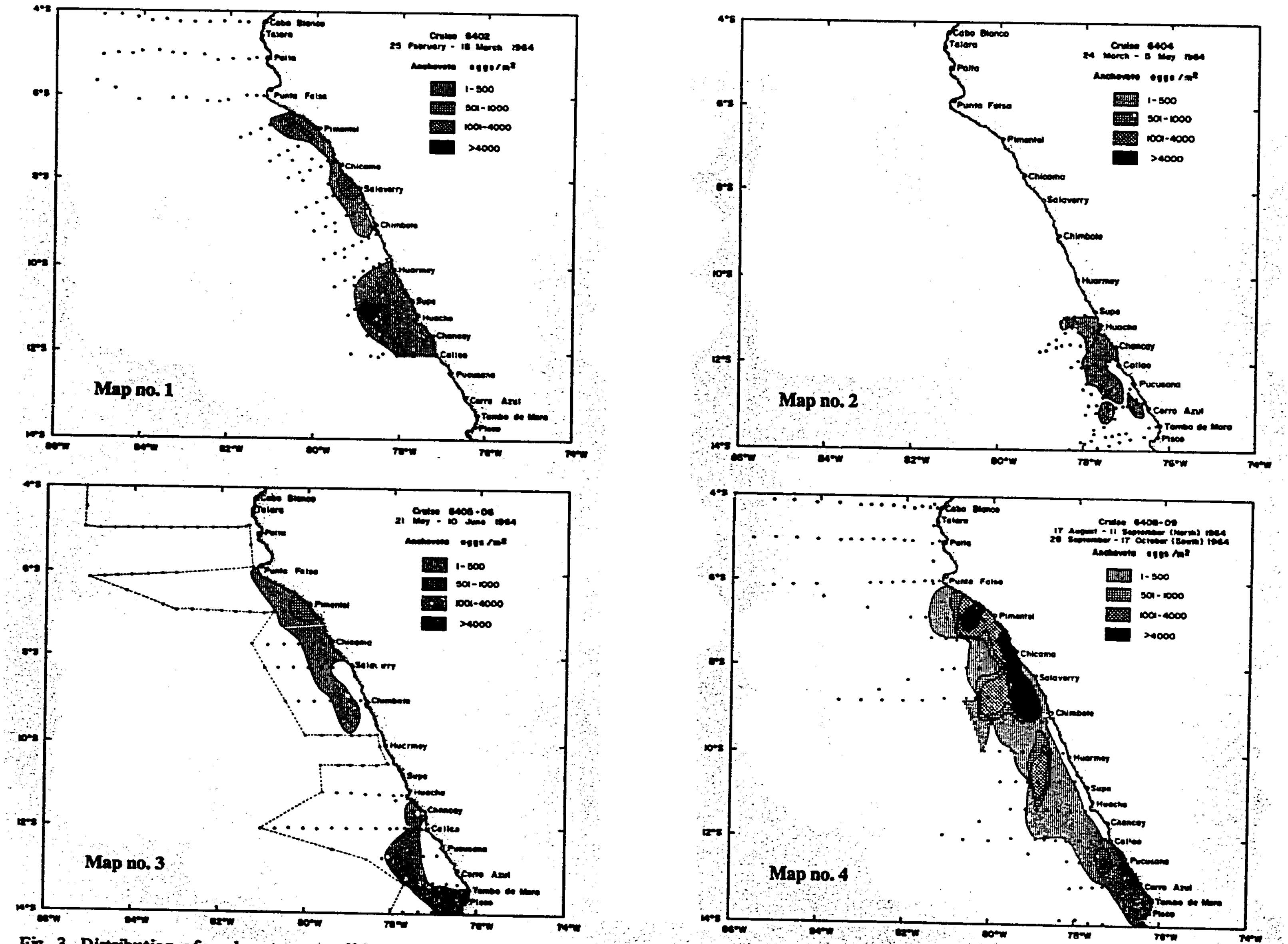

Fig. 3. Distribution of anchoveta eggs off Peru during four surveys conducted in 1964 (see Table 3 for egg standing stock estimates based on maps 1 to 4).

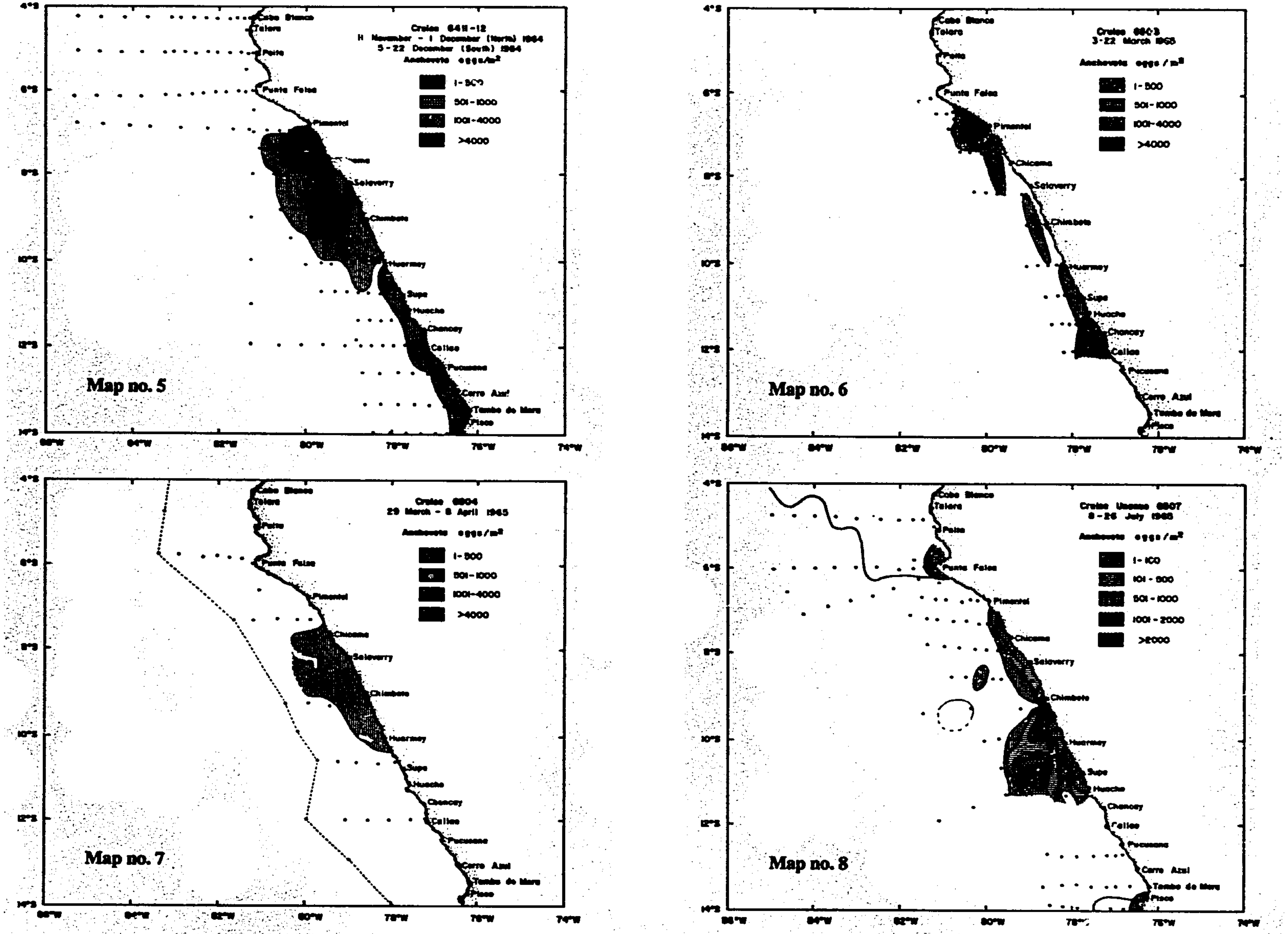

Fig. 4. Distribution of anchoveta eggs off Peru during four surveys conducted in 1964 and 1965 (see Table 3 for egg standing stock estimates based on maps 5 to 8).

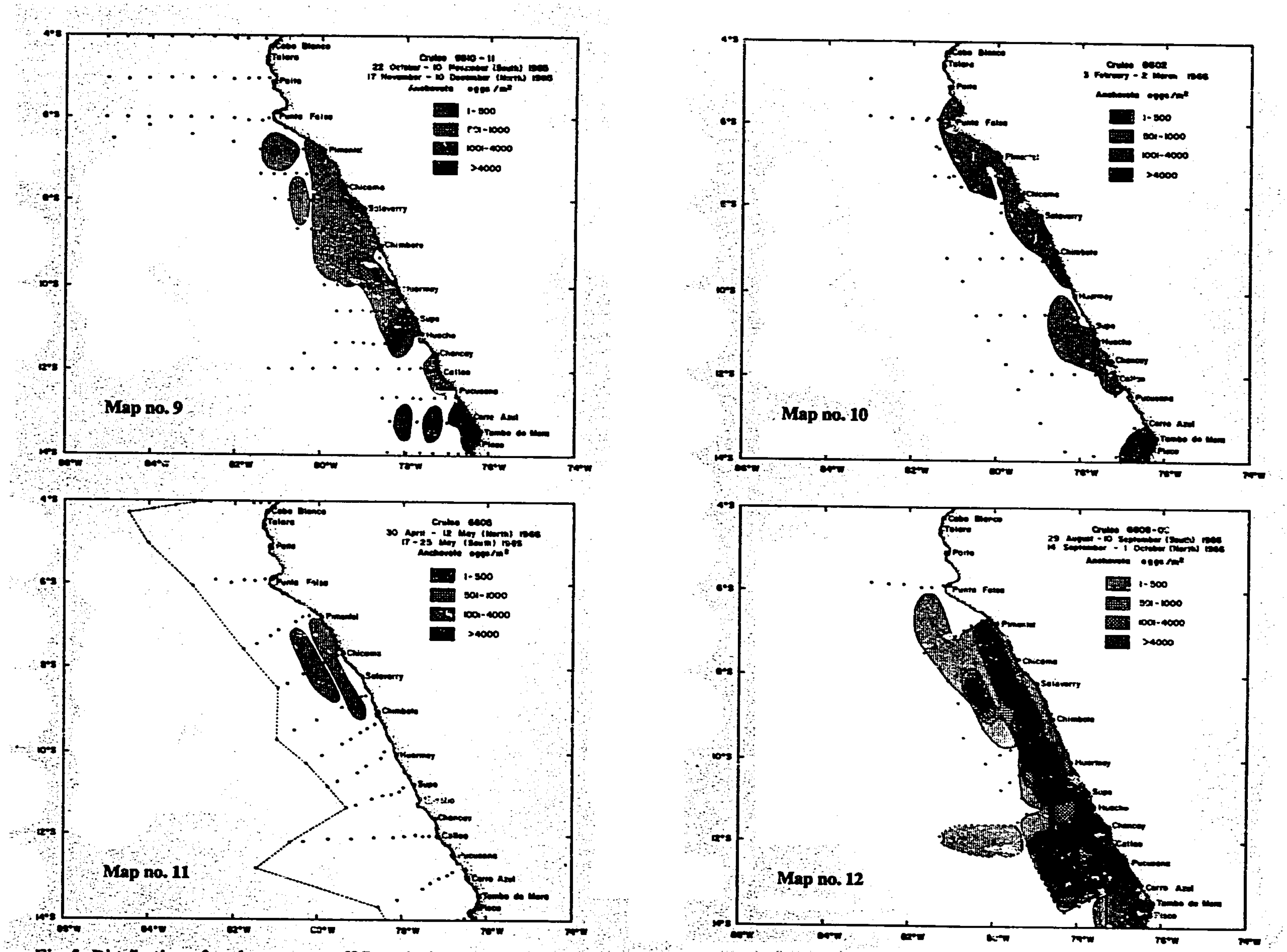

Fig. 5. Distribution of anchoveta eggs off Peru during four surveys conducted in 1965 and 1966 (see Table 3 for egg standing stock estimates based on maps 9 to 12).

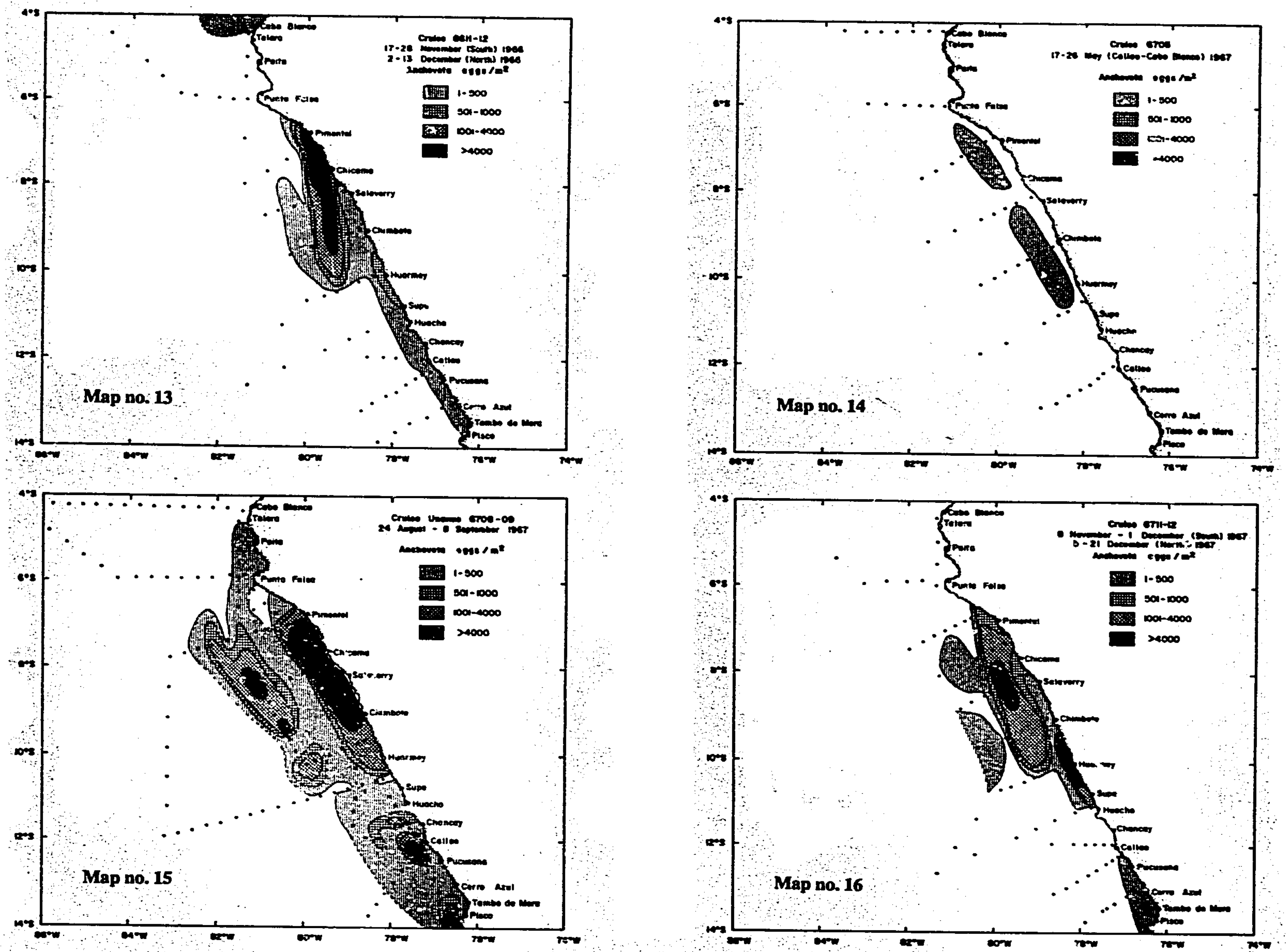

Fig. 6. Distribution of anchoveta eggs off Peru during four surveys conducted in 1966 and 1967 (see Table 3 for egg standing stock estimates based on maps 13 to 16).

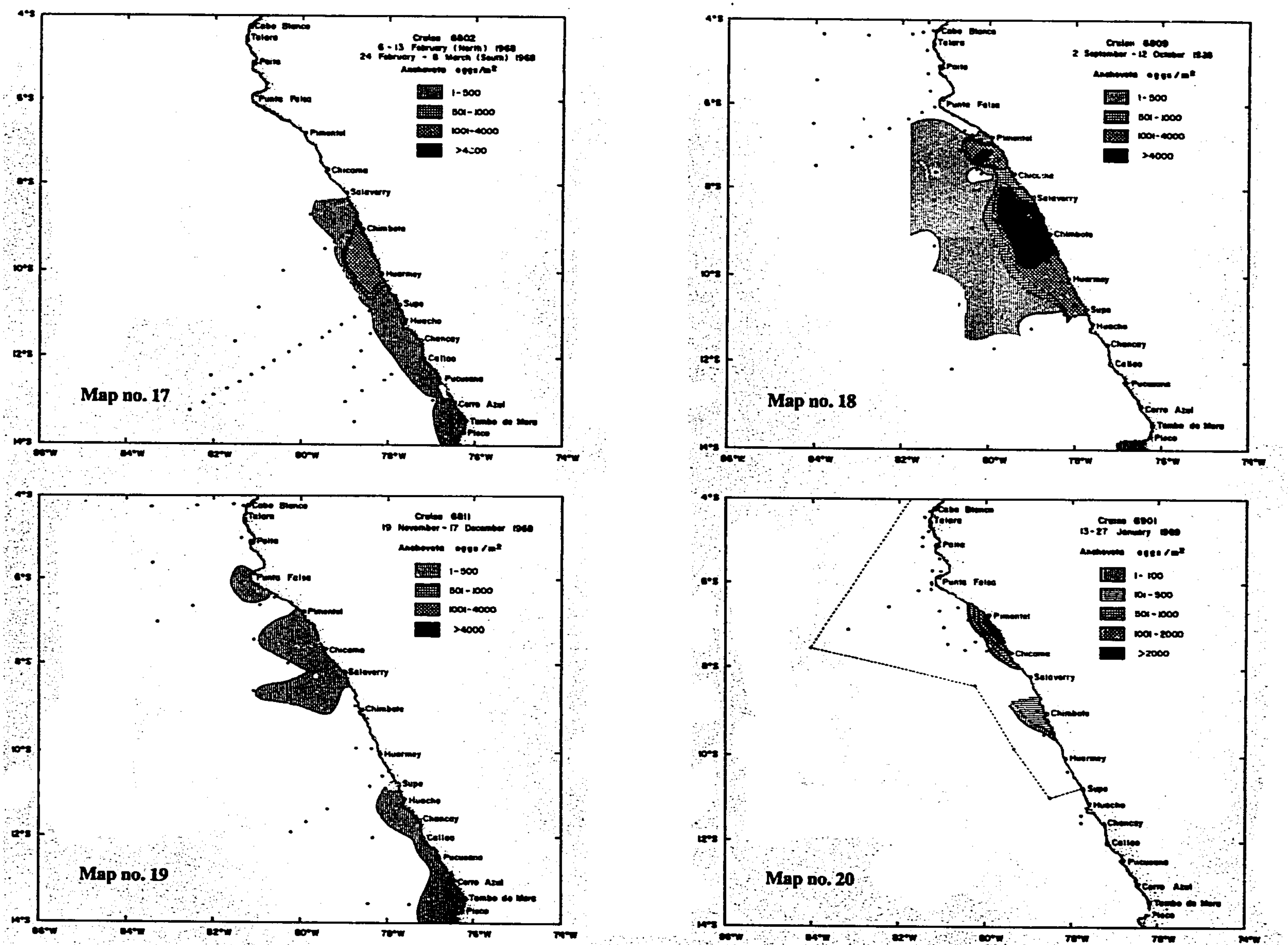

Fig. 7. Distribution of anchoveta eggs off Peru during four surveys conducted in 1968 and 1969 (see Table 3 for egg standing stock estimates based on maps 17 to 20).

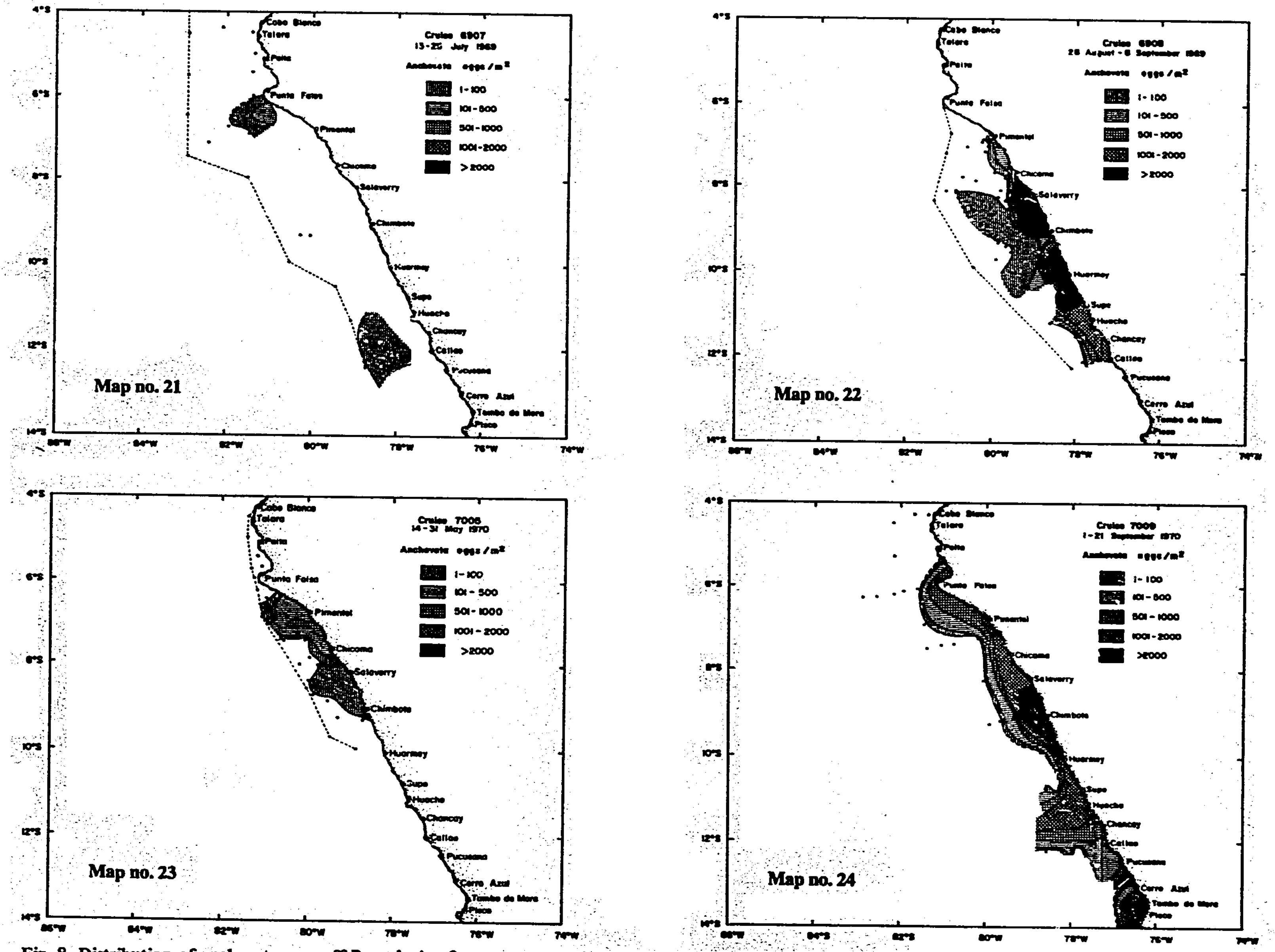

Fig. 8. Distribution of anchoveta eggs off Peru during four surveys conducted in 1969 and 1970 (see Table 3 for egg standing stock estimates based on maps 21 to 24).

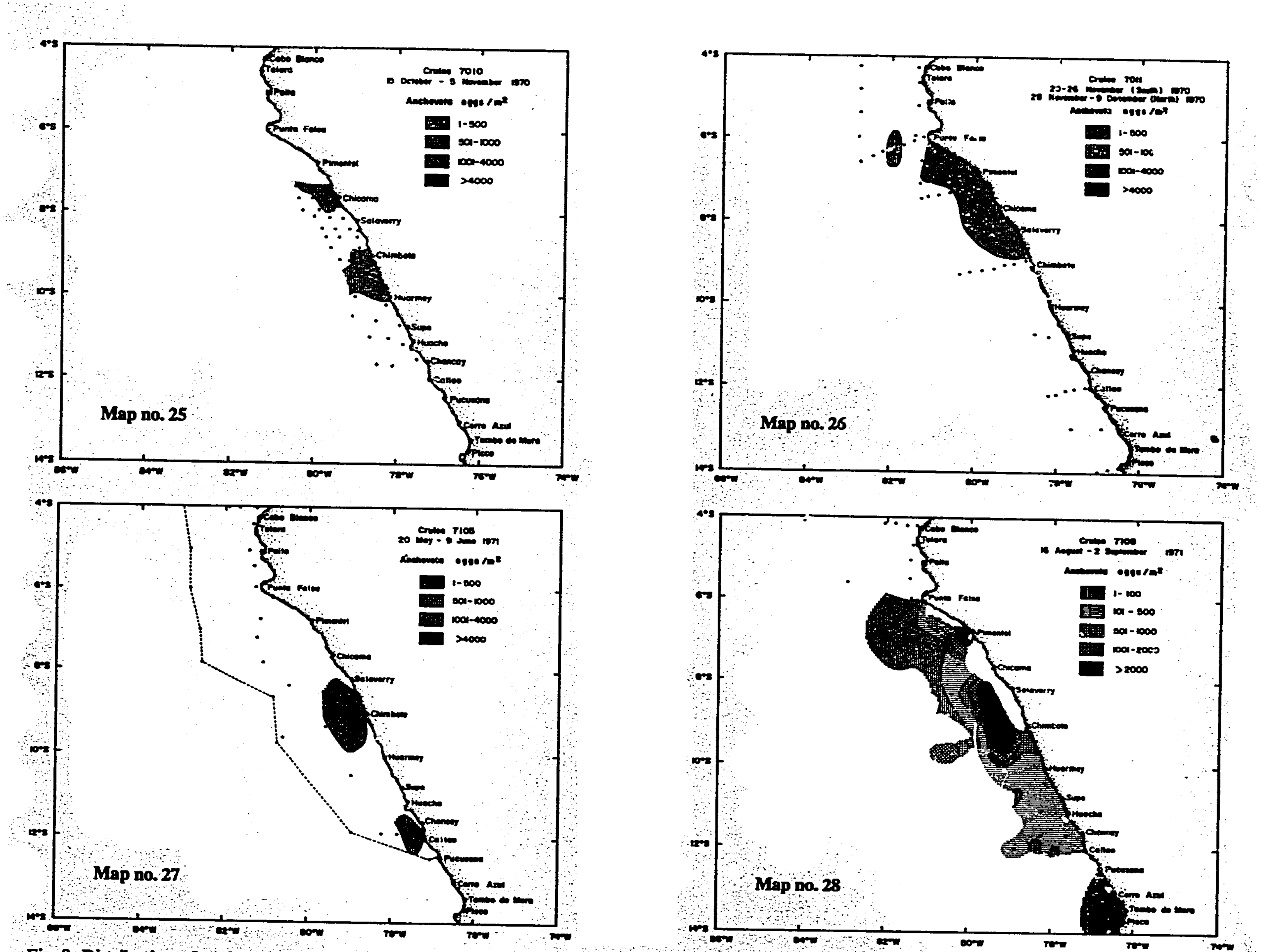

Fig. 9. Distribution of anchoveta eggs off Peru during four surveys conducted in 1970 and 1971 (see Table 3 for egg standing stock estimates based on maps 25 to 28).

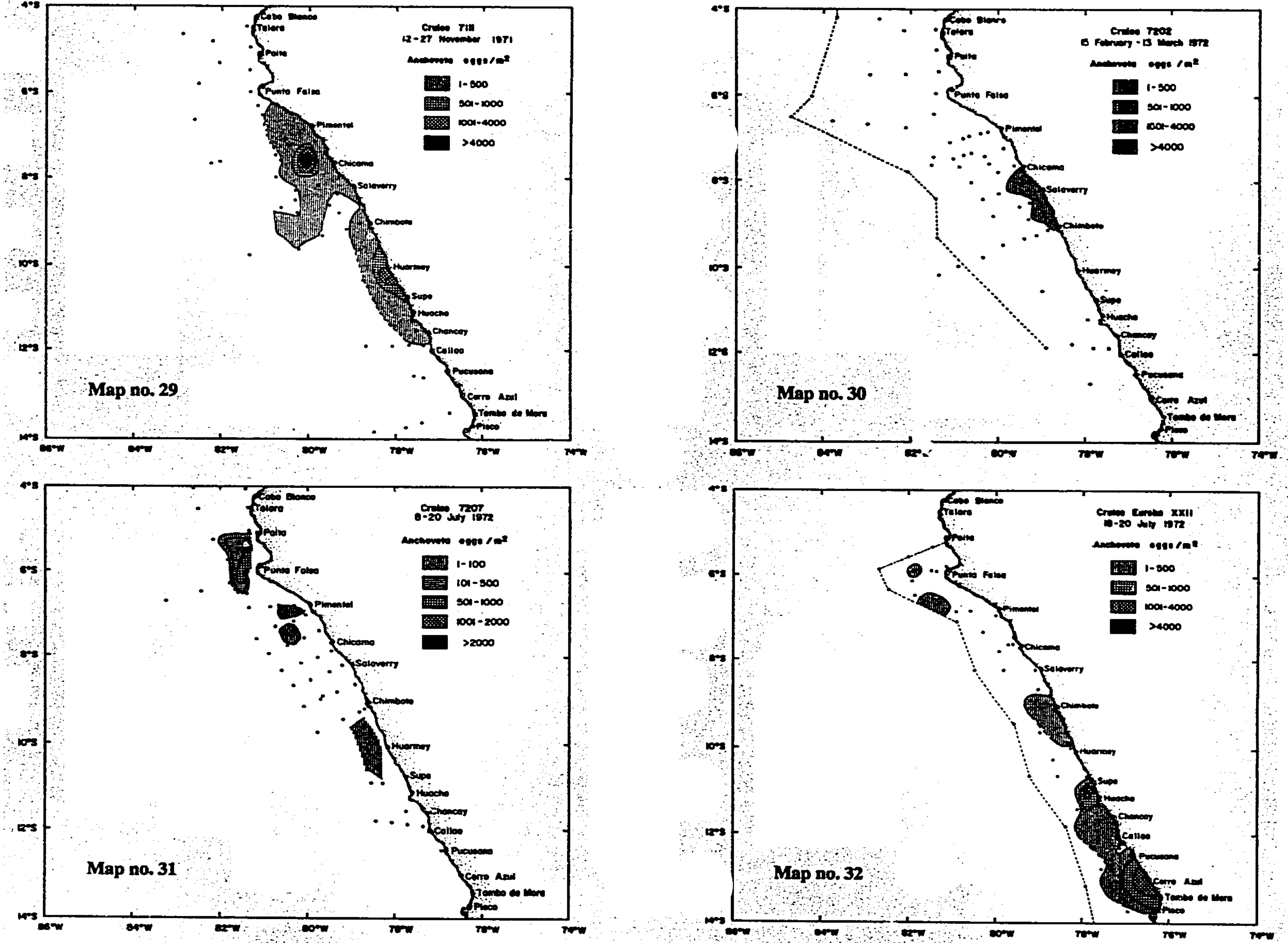

Fig. 10. Distribution of anchoveta eggs off Peru during four surveys conducted in 1971 and 1972 (see Tables 3 and 4 for egg standing stock estimates based on maps 29 to 32).

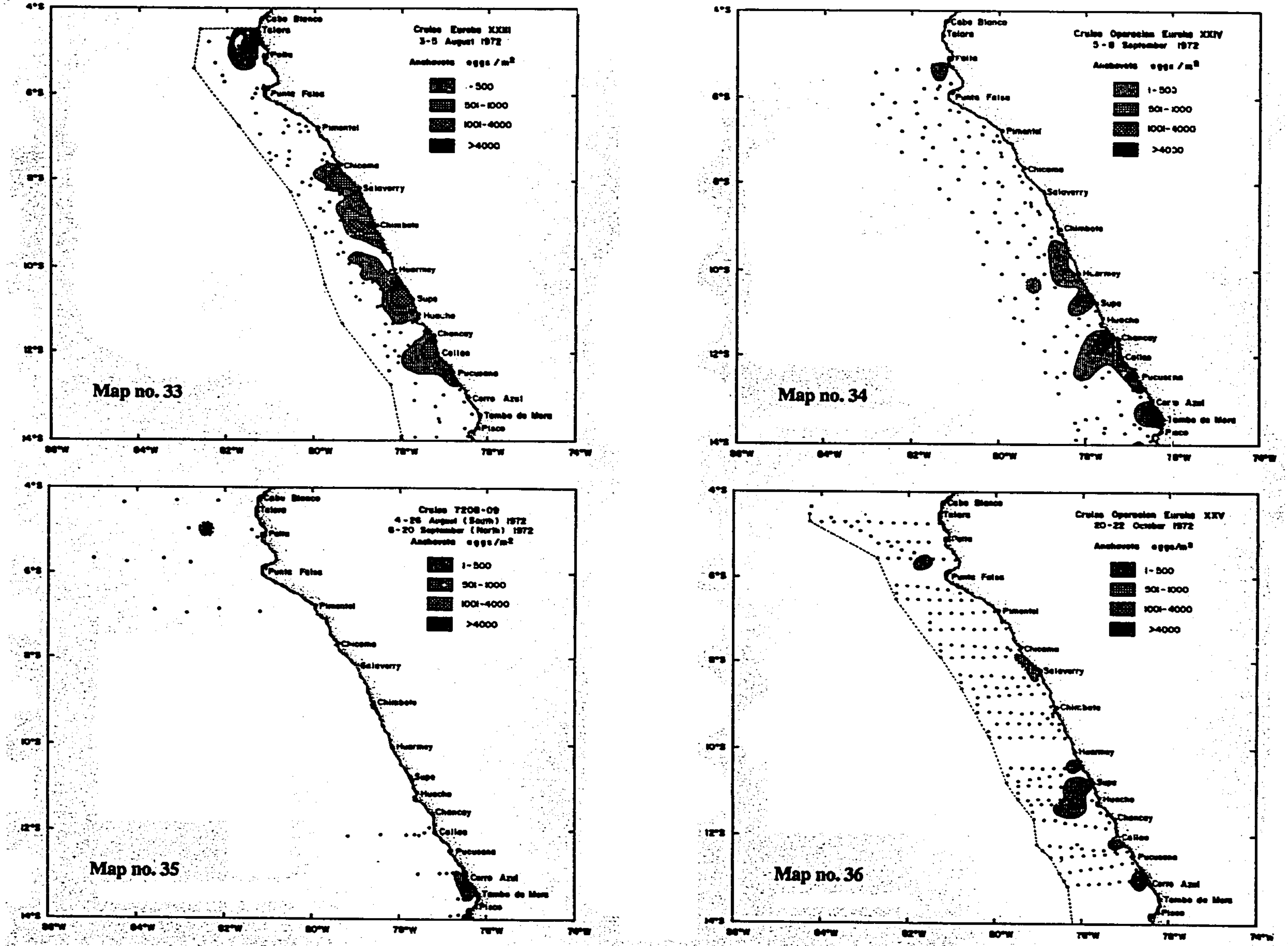

Fig. 11. Distribution of anchoveta eggs off Peru during four surveys conducted in 1972 (see Tables 3 and 4 for egg standing stock estimates based on maps 33 to 36).

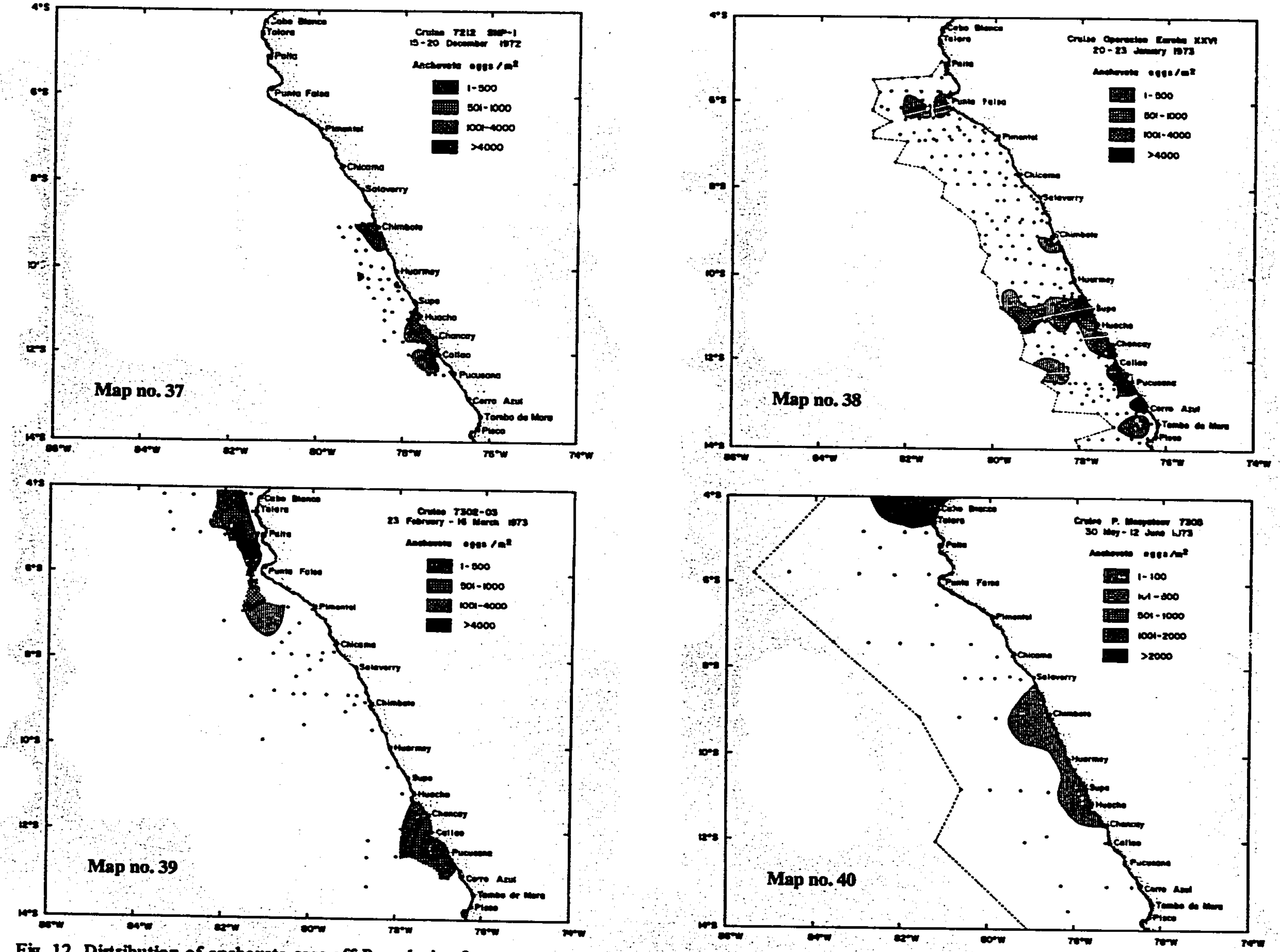

Fig. 12. Distribution of anchoveta eggs off Peru during four surveys conducted in 1972 and 1973 (see Tables 3 and 4 for egg standing stock estimates based on maps 37 to 40).

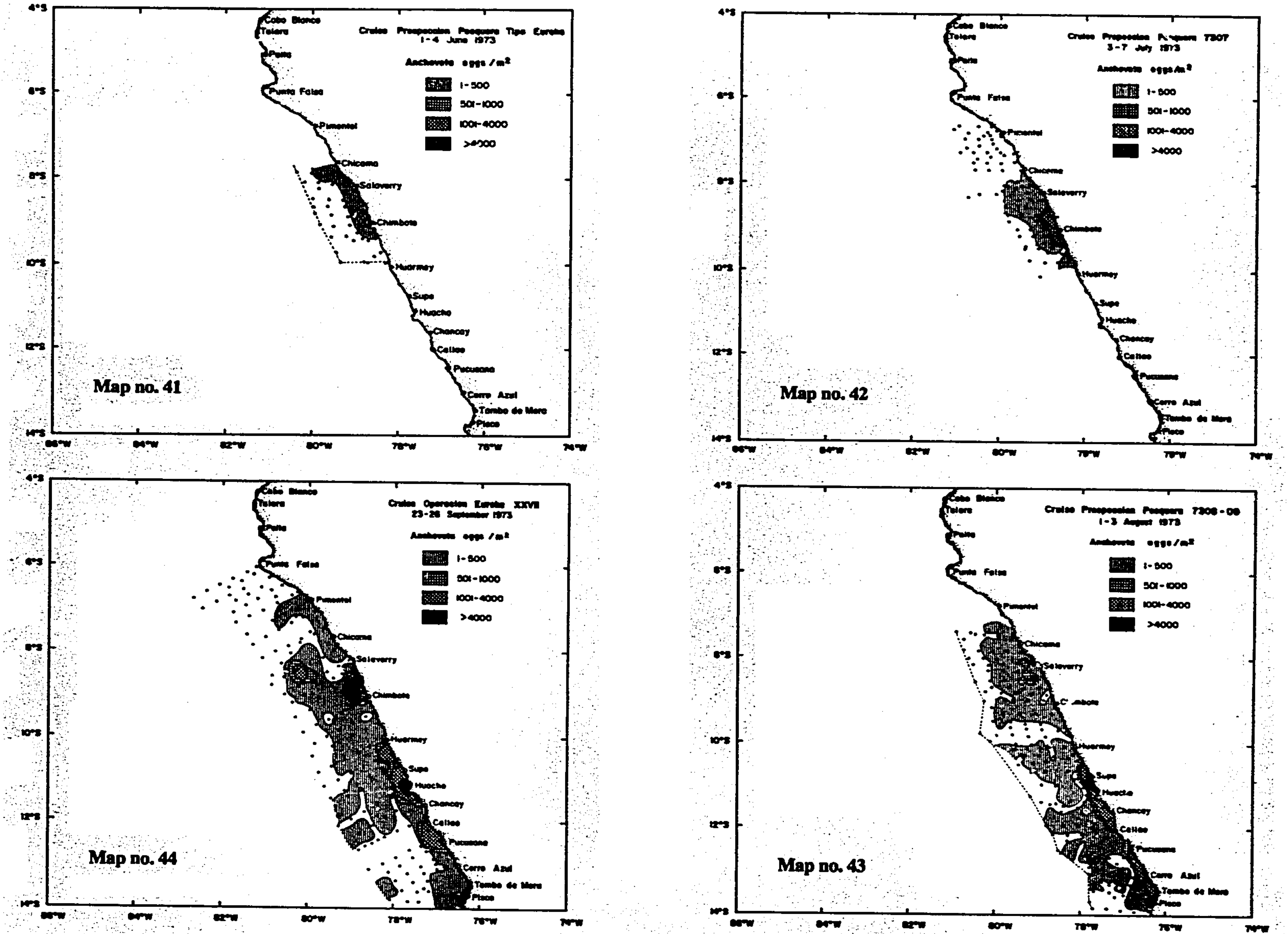

Fig. 13. Distribution of anchoveta eggs off Peru during four surveys conducted in 1973 (see Tables 3 and 4 for egg standing stock estimates based on maps 41 to 44).

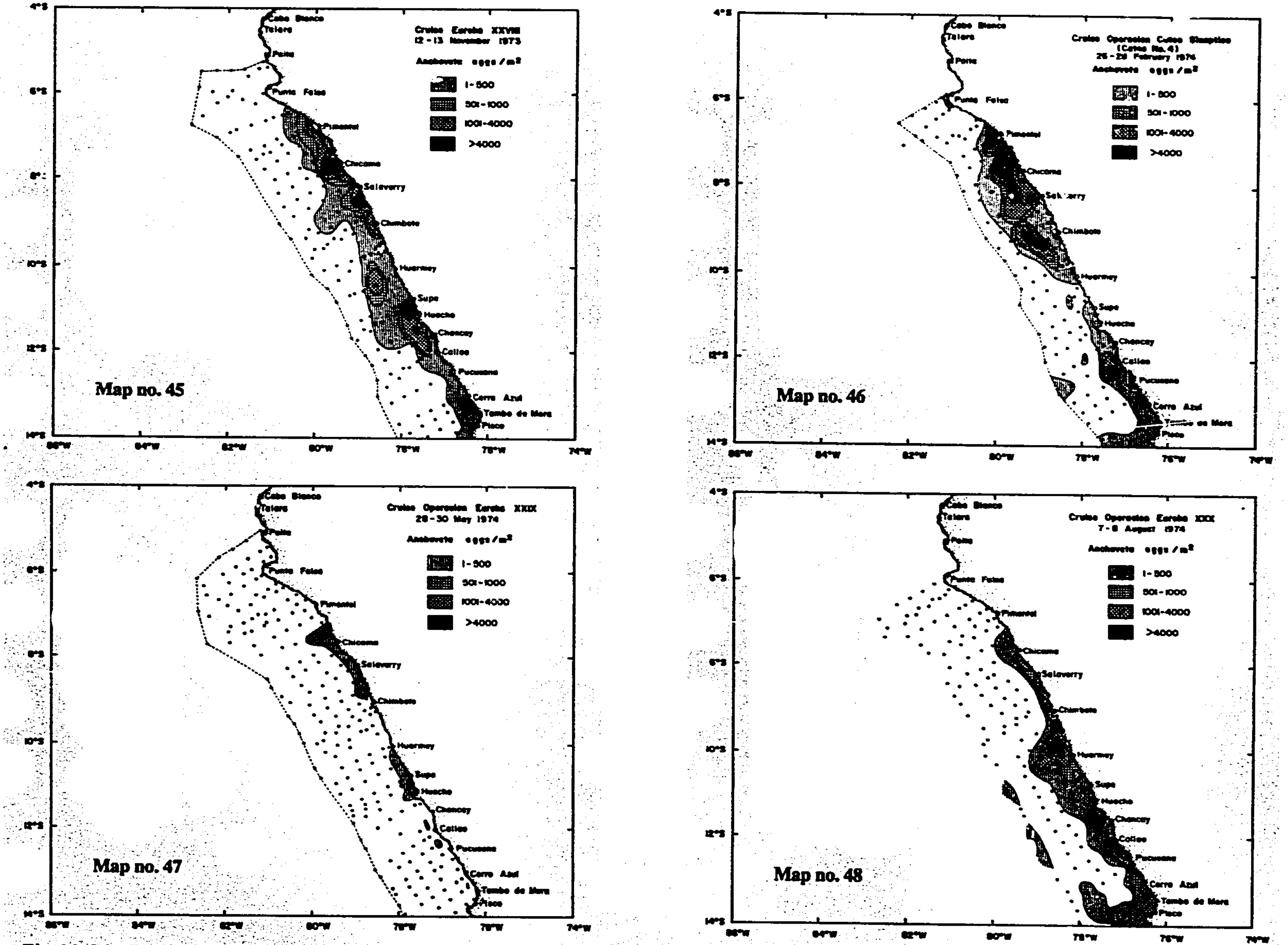

Fig. 14. Distribution of anchoveta eggs off Peru during four surveys conducted in 1973 and 1974 (see Table 3 for egg standing stock estimates based on maps 45 to 48).

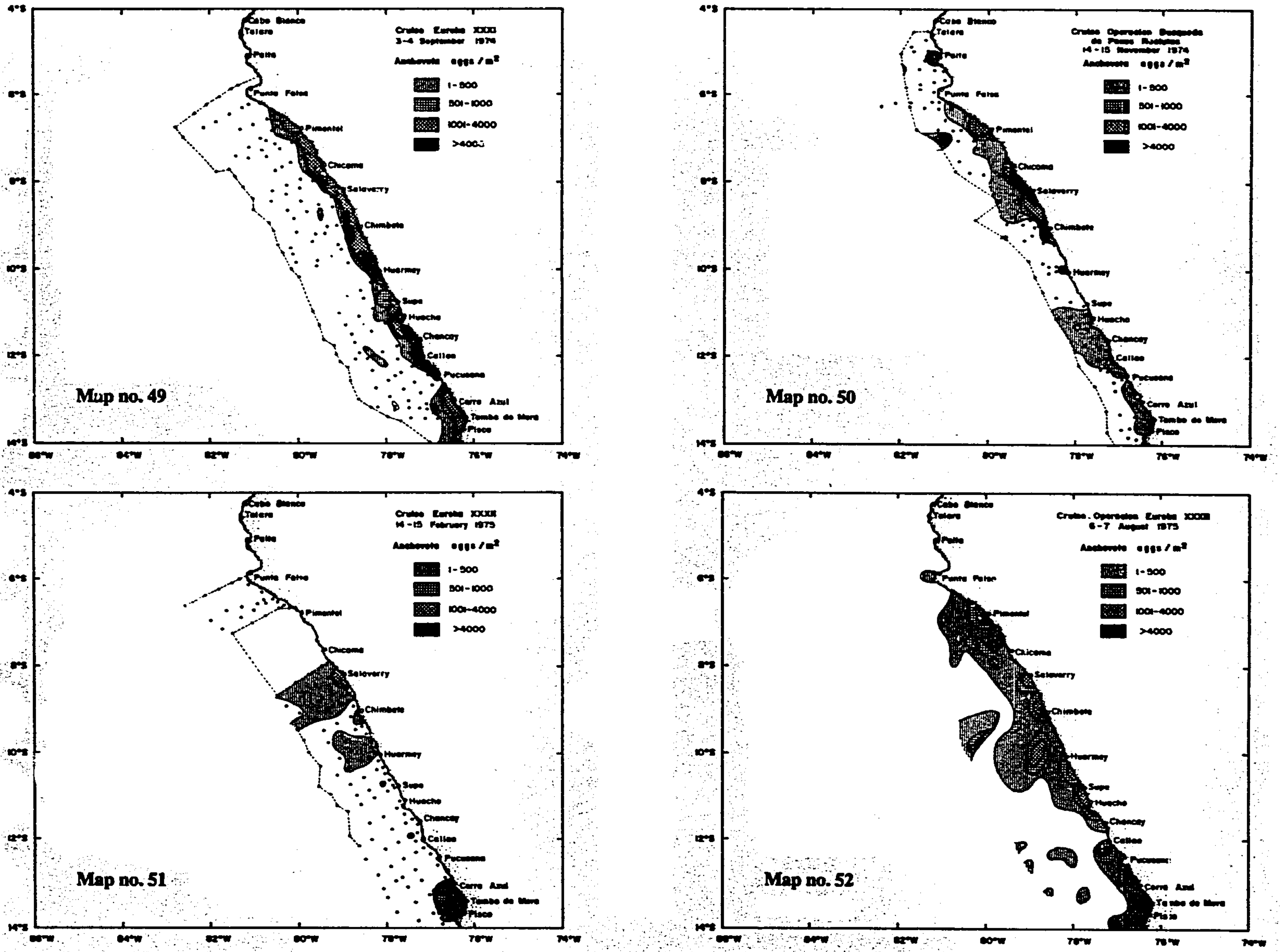

Fig. 15. Distribution of anchoveta eggs off Peru during four surveys conducted in 1974 and 1975 (see Table 3 for egg standing stock estimates based on maps 49 to 52).

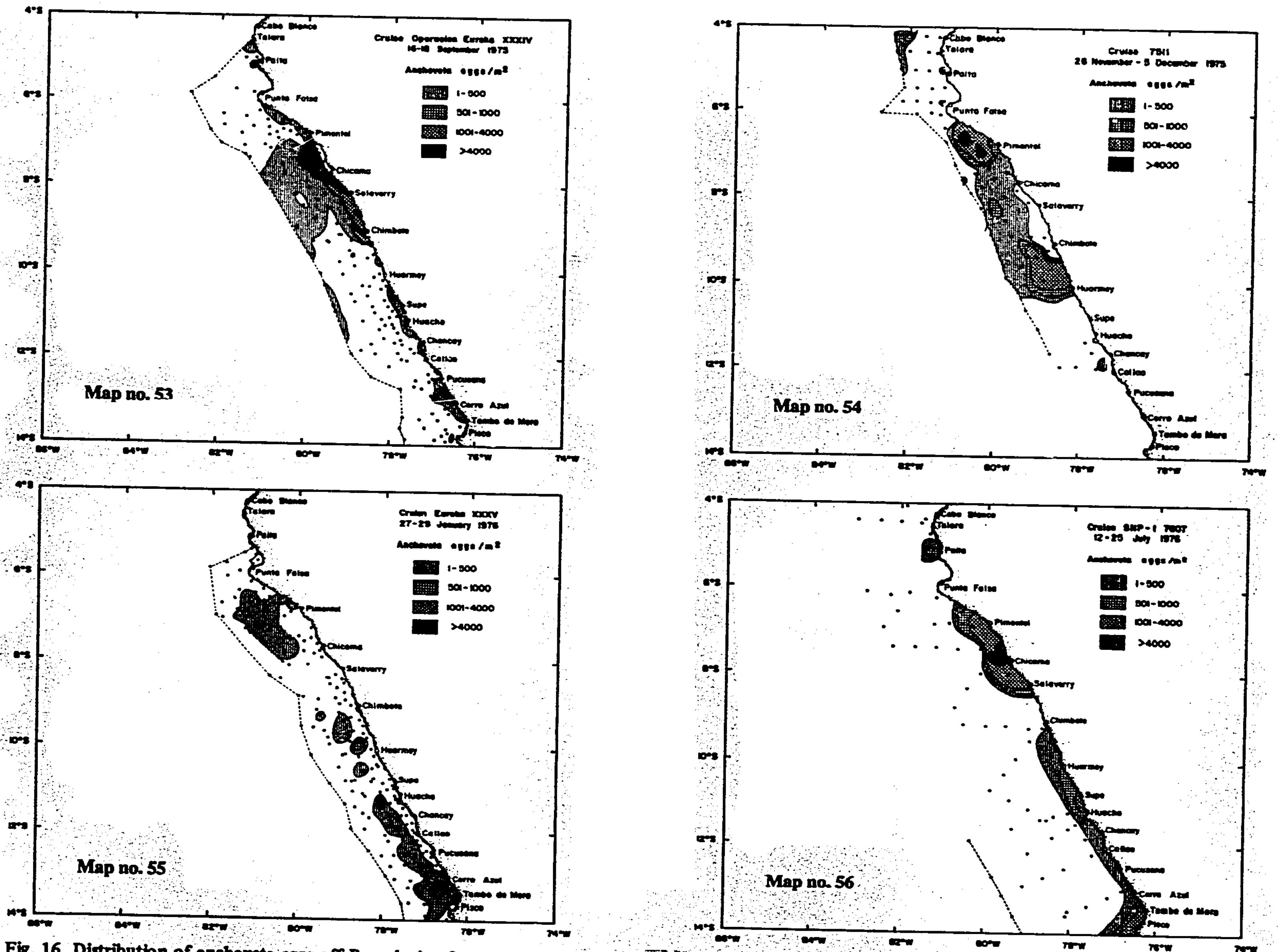

Fig. 16. Distribution of anchoveta eggs off Peru during four surveys conducted in 1975 and 1976 (see Table 3 for egg standing stock estimates based on maps 53 to 56).

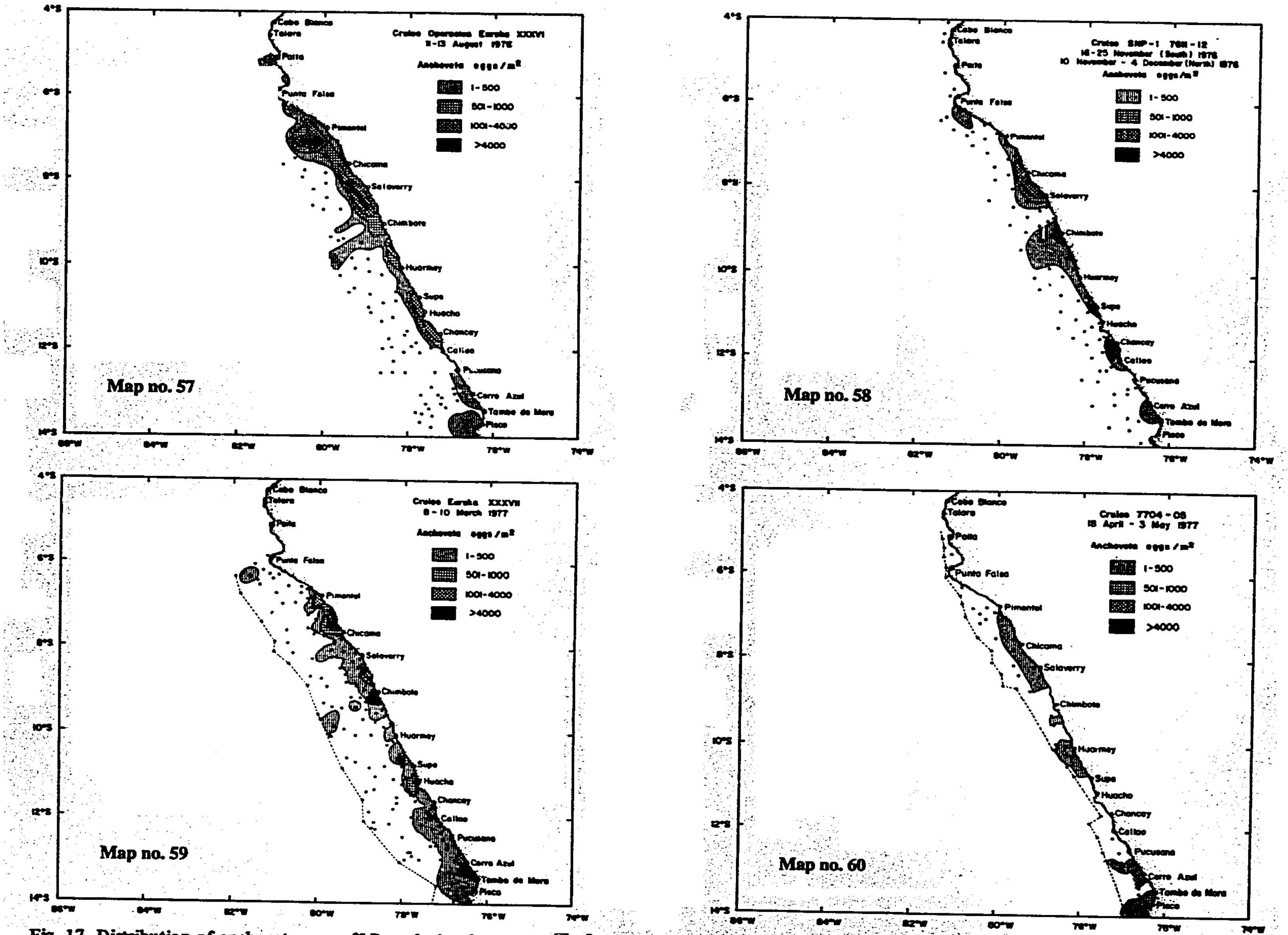

Fig. 17. Distribution of anchoveta eggs off Peru during four surveys conducted in 1976 and 1977 (see Table 3 for egg standing stock estimates based on maps 57 to 60).

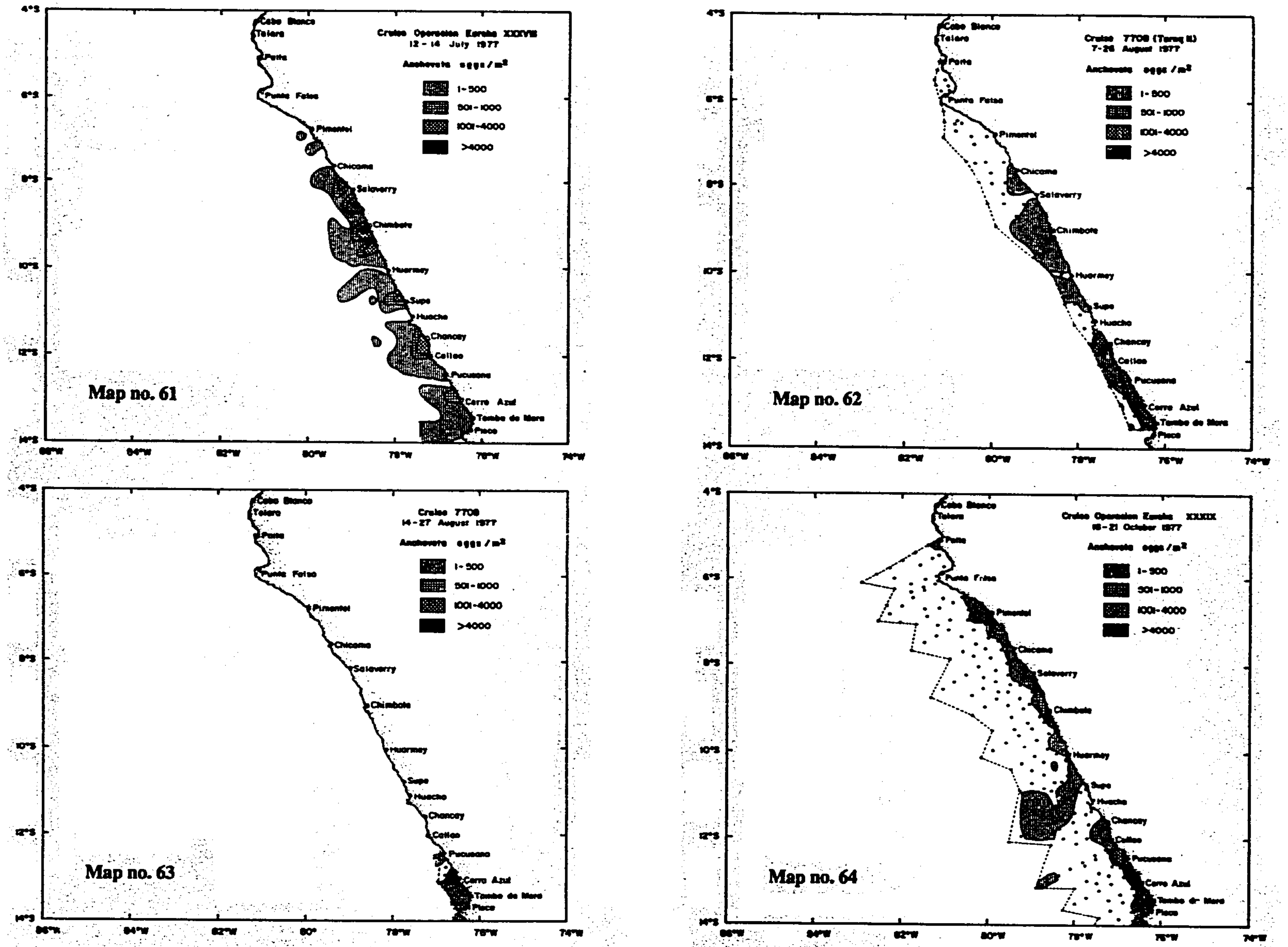

Fig. 18. Distribution of anchoveta eggs off Peru during four surveys conducted in 1977 (see Tables 3 and 4 for egg standing stock estimates based on maps 61 to 64).

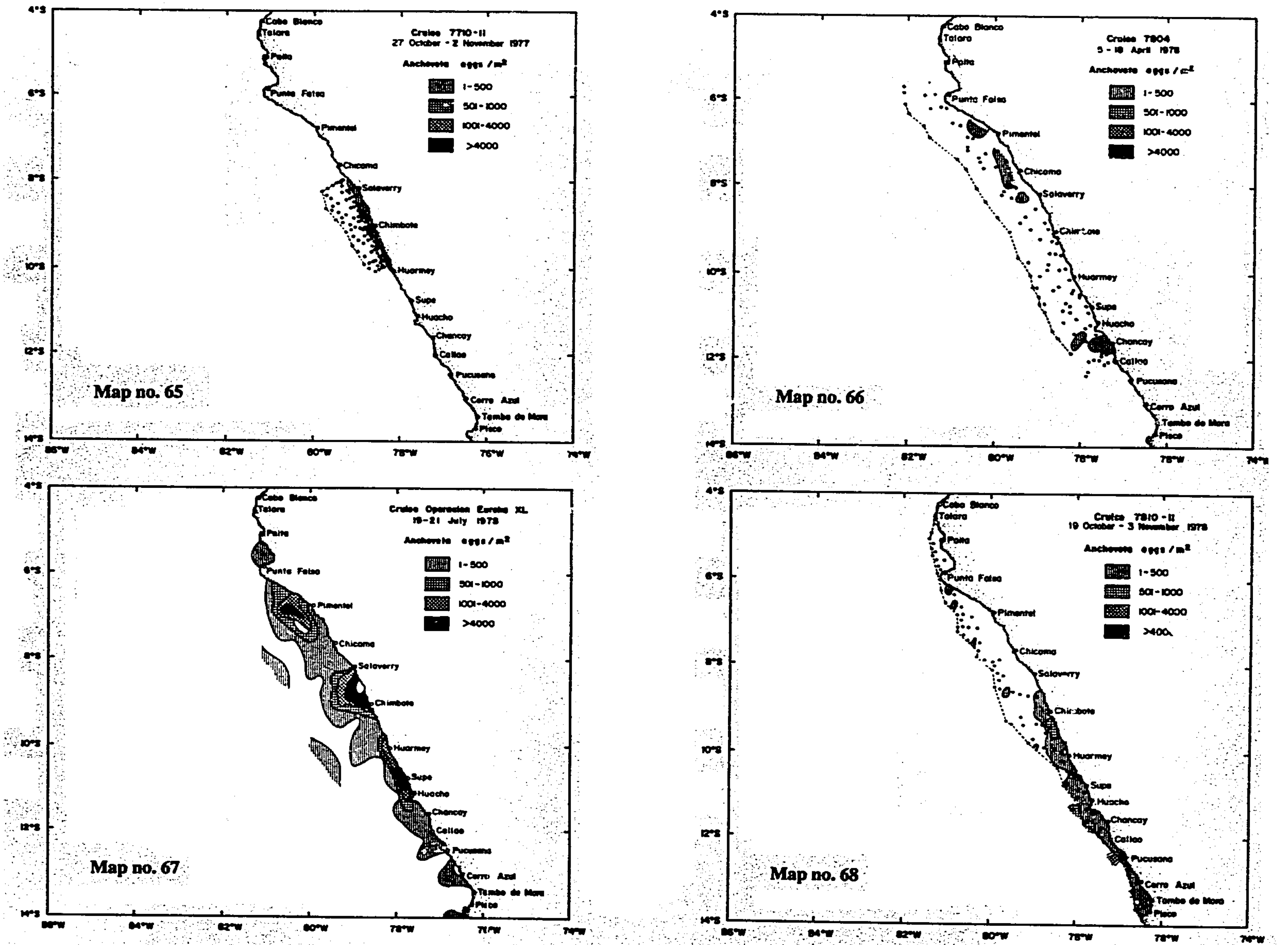

Fig. 19. Distribution of anchoveta eggs off Peru during four surveys conducted in 1977 and 1978 (see Tables 3 and 4 for egg standing stock estimates based on maps 65 to 68).

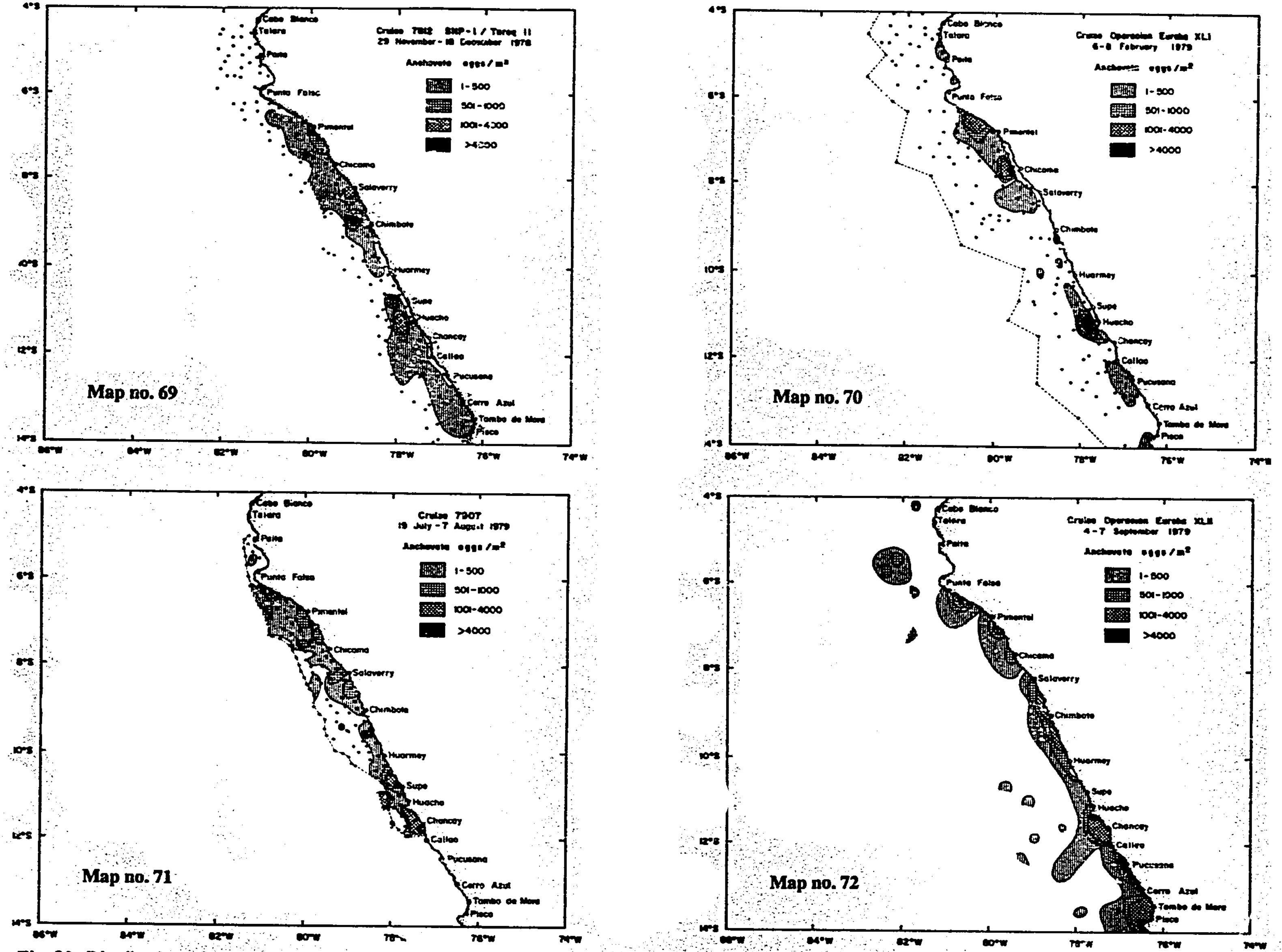

Fig. 20. Distribution of anchoveta eggs off Peru during four surveys conducted in 1978 and 1979 (see Table 3 for egg standing stock estimates based on maps 69 to 72).

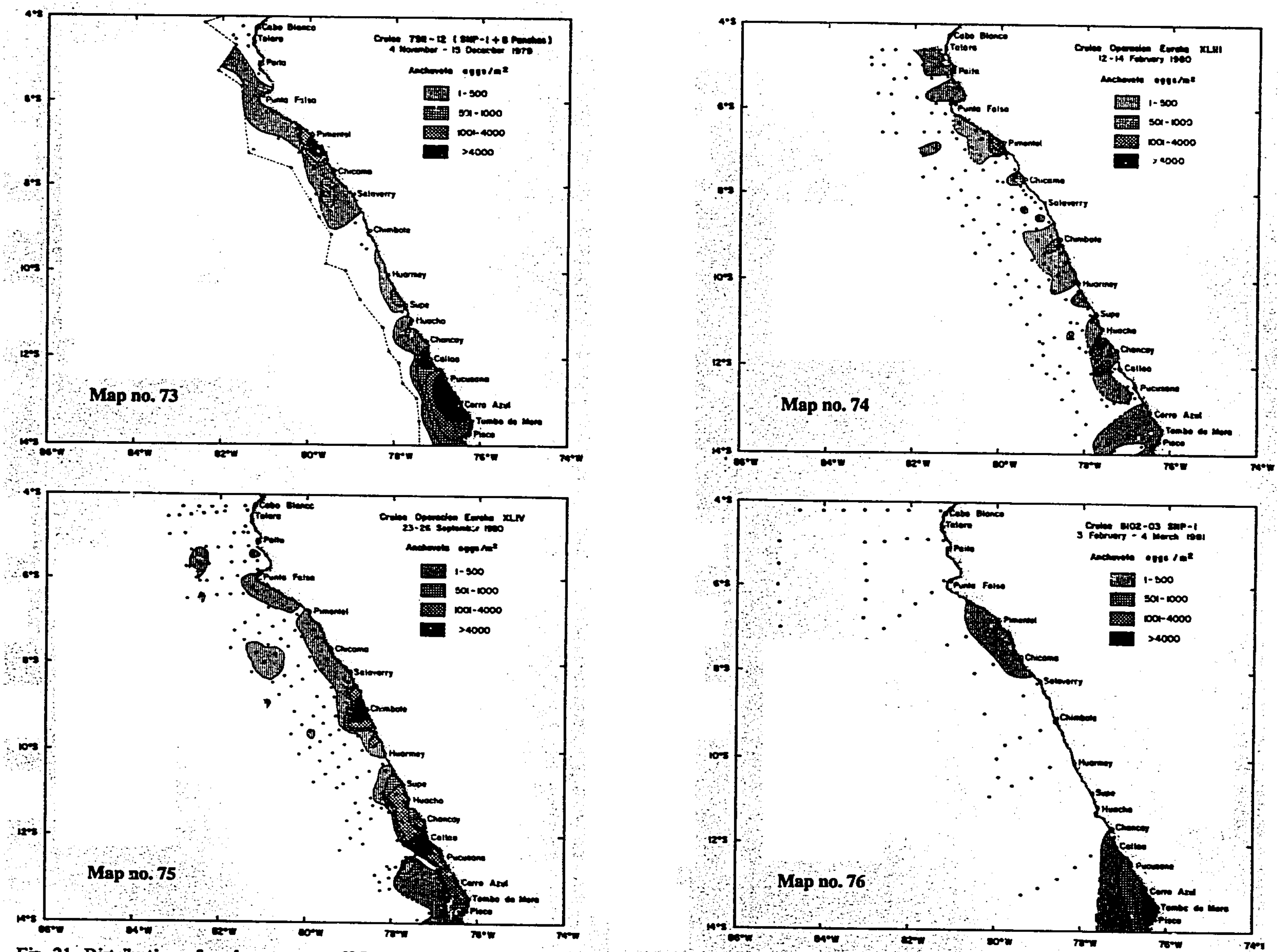

Fig. 21. Distribution of anchoveta eggs off Peru during four surveys conducted in 1979, 1980 and 1981 (see Table 3 for egg standing stock estimates based on maps 73 to 76).

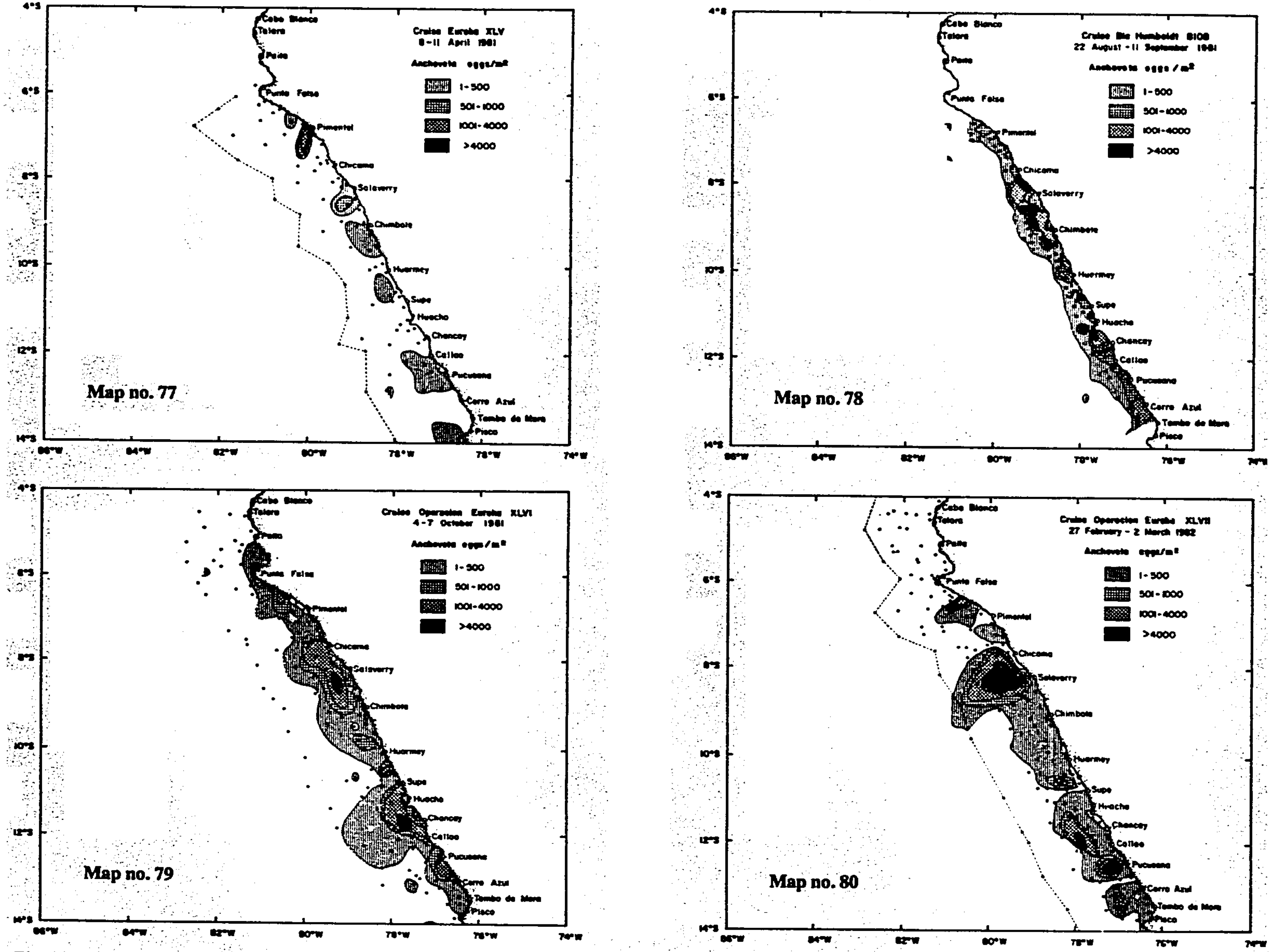

Fig. 22. Distribution of anchoveta eggs off Peru during four surveys conducted in 1981 and 1982 (see Table 3 for egg standing stock estimates based on maps 77 to 80).

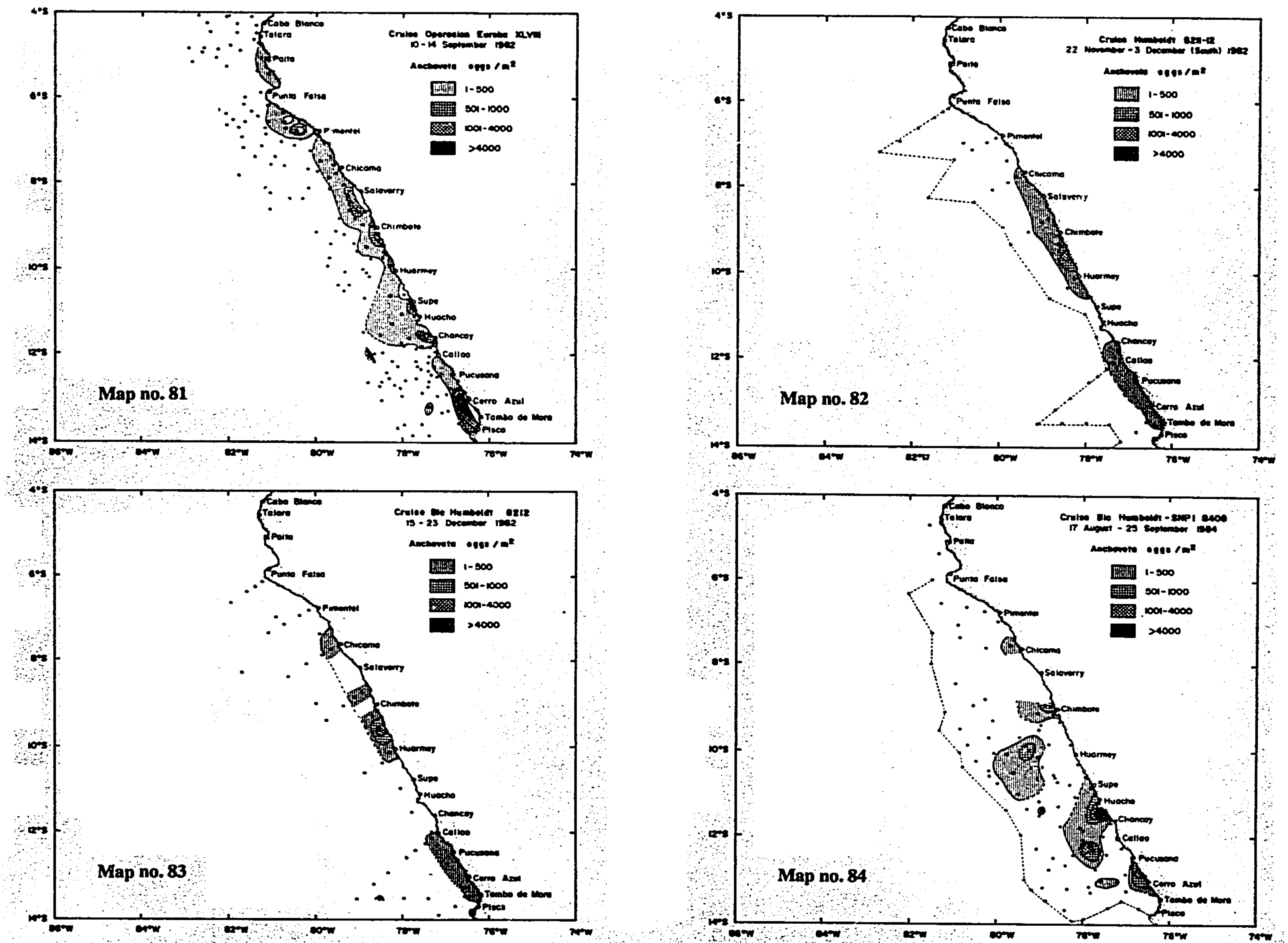

Fig. 23. Distribution of anchoveta eggs off Peru during four surveys conducted in 1982 and 1984 (see Tables 3 and 4 for egg standing stock estimates based on maps 81 to 84).

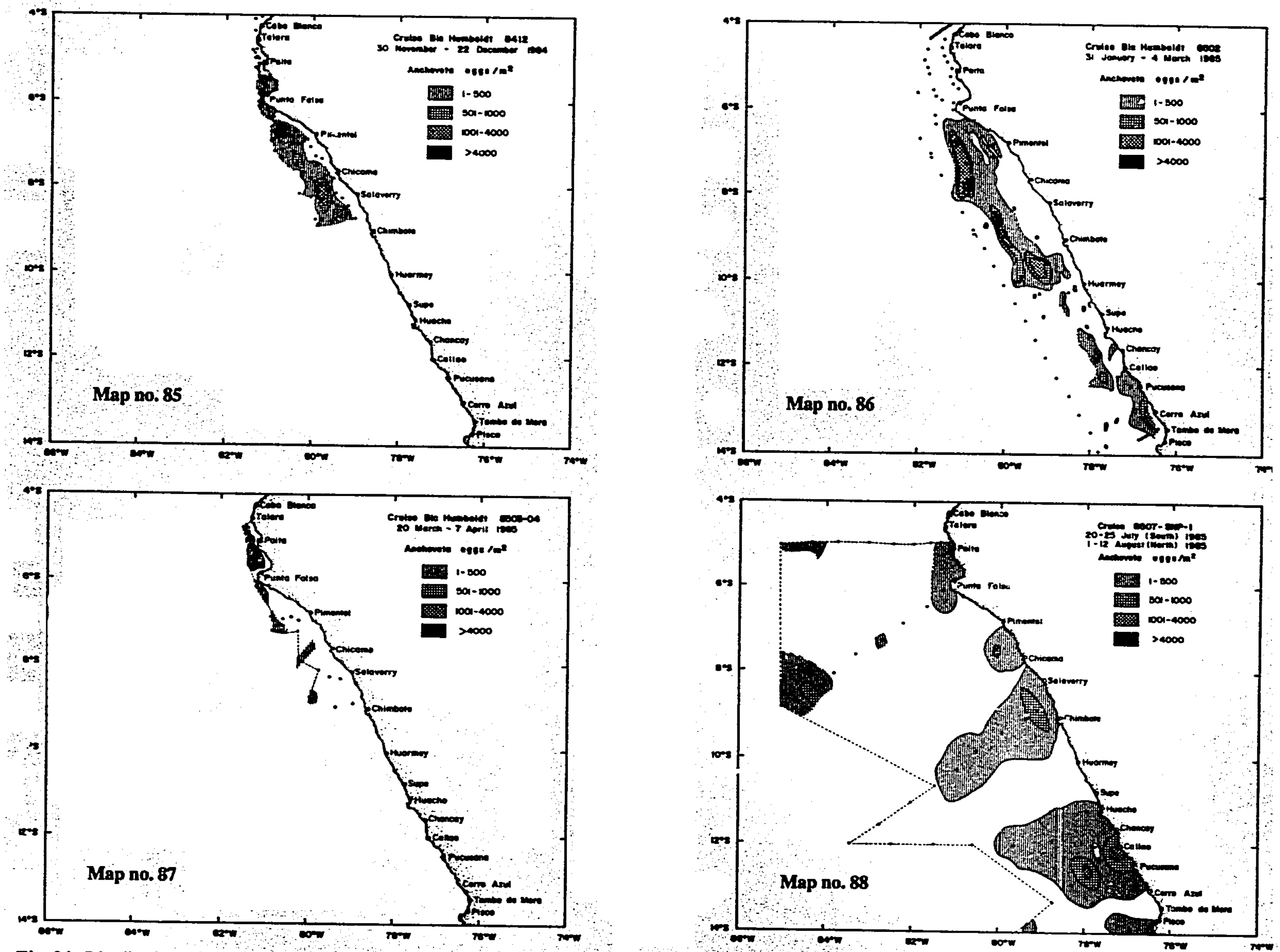

Fig. 24. Distribution of anchoveta eggs off Peru during four surveys conducted in 1984 and 1985 (see Table 3 for egg standing stock estimates based on maps 85 to 88).

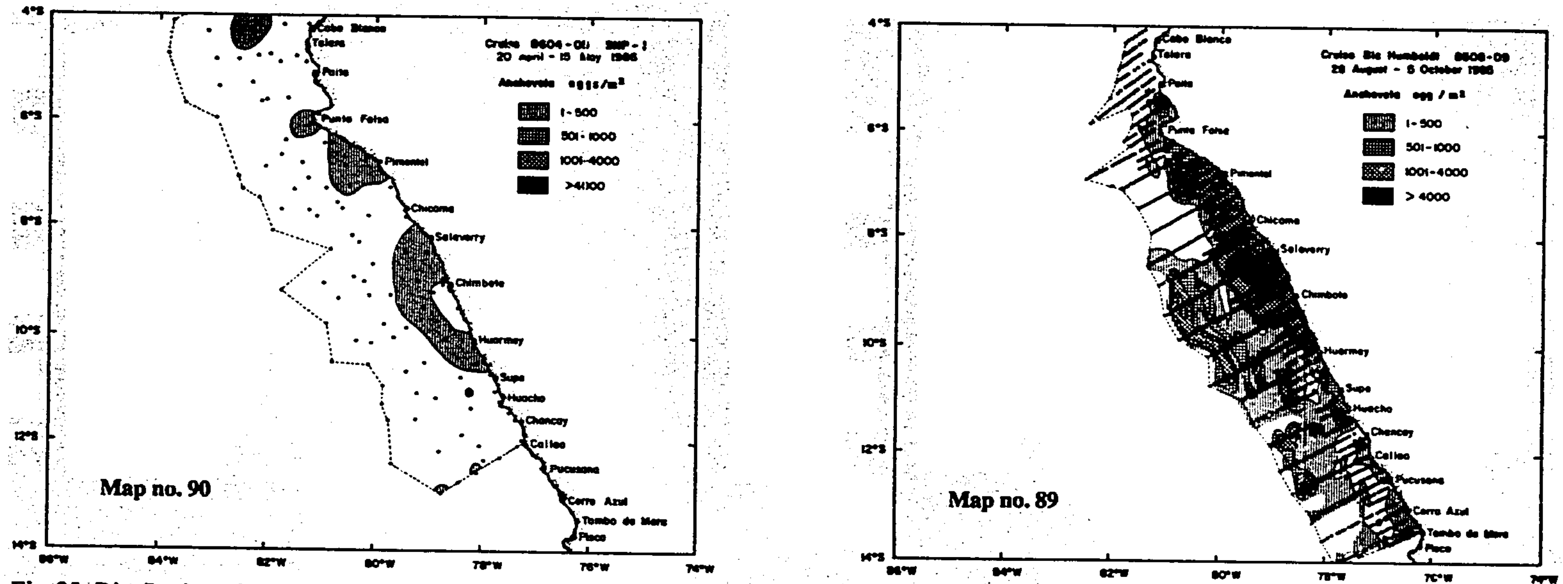

Fig. 25. Distribution of anchoveta eggs off Peru during four surveys conducted in 1985 and 1986 (see Table 3 for egg standing stock estimates based on maps 89 and 90).

Monthly Population Size of Three Guano Bird Species off Peru, 1953 to 1982

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TOVAR, H., V. GUILLEN and M.E. NAKAMA. 1987. Monthly population size of three guano bird species off Peru, 1953 to 1982, p. 208-218. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

Monthly population size estimates of three species of fish eating, guano-producing birds (cormorant: *Phalacrocorax bougainvillii*; booby: *Sula variegata* and pelican: *Pelecanus thagus*) were obtained, based on planimetric analyses of over 10,000 maps of their distribution on guano islands and points along the coast of Peru, for the years 1953 to 1982. These data allow for a much more detailed description of the interactions between the bird populations and their environment than had hitherto been the case and a preliminary discussion of such interactions is given, with emphasis on the combined effects of the anchoveta fishery off Peru and successive El Niño events.

Introduction

Of the many species of seabirds living along the Peruvian coast, on islands and "points" (i.e., small peninsulas), three, the cormorant (*Phalacrocorax bougainvillii* L., Family Phalacrocoracidae), the booby (*Sula variegata* Tschudi, Family Sulidae) and the pelican (*Pelecanus thagus* Molina, Family Pelecanidae) are the most conspicuous (Fig. 1). They are also the three species known as "guano birds" whose feces, known as "guano" (i.e., "guano de islas") were used in early, pre-Inca times, as fertilizer in agriculture. Garcilaso de la Vega (1539-1616) in his "Royal Commentaries" mentions that the Incas, following their conquest of the people along the Peru coast, explicitly protected the guano birds, and imposed the death sentence on those reported to have disturbed them, particularly during their reproductive season.

Following the Spanish conquest, the agricultural infrastructure built and/or improved by the Incas was left to decay, and gold and silver mining developed. According to Maisch (1946) the extraction of accumulated guano started again only in the mid-1840s. This extraction was totally uncontrolled, and led to rapid depletion of the guano accumulations. Thus, for example, on the Chincha Islands, 95% of the accumulated 12 million tonnes of guano were removed between 1853 and 1913.

The Compania Administradora del Guano (CAG) took over the administration of the guano islands and points in 1909, and later implemented the recommendation of Forbes (1914) who, after examination of all guano deposits along the Peruvian coast, suggested a series of protective measures such as the deployment of guards, the protection of nests and the rotation of the crews exploiting the deposits.

Following Gamarra (1964a, 1964b), six periods may be identified with regard to the guano resources and their exploitation:

i) first period - Inca times, when the birds reached their climax, being totally protected;
ii) second period - for which there is no information, except for the representation of birds on ceramics and textile of the time;

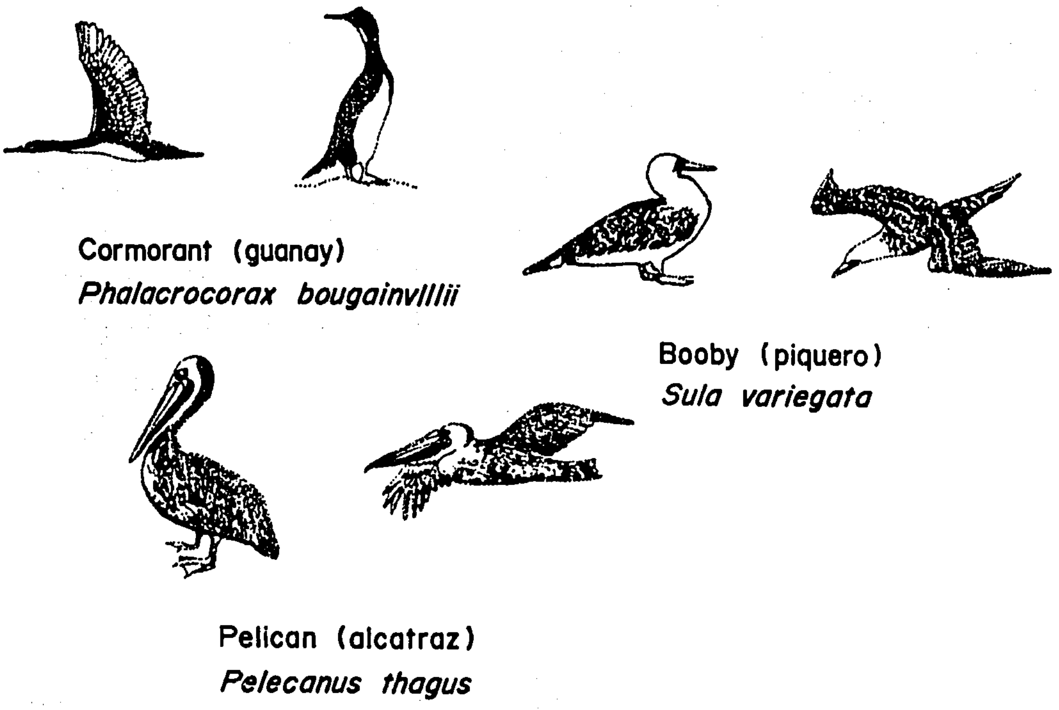


Fig. 1. The three main species of fish-eating birds of the Peruvian upwelling ecosystem (Spanish names in brackets).

iii) third period - immediately following the Spanish conquest during which the knowledge of the usefulness of guano receded, and hence the birds ceased to be protected;
iv) fourth period - starting about 1844 when, the importance of guano (for export markets) being apparent, the exploitation of guano expanded rapidly and included the use of dynamite to loosen up hardened layers of deposits without consideration to the birds. This started a regressive process which considerably reduced the bird populations which were at the time only viewed as interfering with the extraction activities;
v) fifth period - starting in 1909 when the CAG was created, with the specific purpose of regulating the guano industry. The CAG initiated measures based on scientific studies and its work has been described as the greatest effort ever made for the protection of any (wild) animal species in the world (see e.g., CAG 1946, 1955, 1958);
vi) sixth period - starting in the mid-1950s, this period saw the development of the anchoveta fishery and the decline of the anchoveta stocks which provide the bulk of the food of guano birds (Gamarra 1941). This period is characterized by a collapse of the bird populations and a large change in the relative abundance of the three species discussed here (Tovar 1983 and see below).

This paper presents monthly population estimates for the years 1953 to 1982 from Isla Terra Lobos de Tierra in the north to Isla Ballestras in the south (Table 1, Fig. 2). Because of our limitations to islands and points not farther south than 14°S, population estimates are not directly comparable with those in earlier papers (e.g., Tovar 1983), although the general trends certainly are.

Materials and Methods

Forms (maps) of islands and points, onto which guards had, for each month separately, graphed the distribution of each bird colony were used (e.g., Fig. 3). Managing the guano islands and points, and the bird colonies thereon from 1909 onwards was the duty of the CAG (see above). From 1964 to 1968, the role of the CAG was perfomed by the Corporacion Nacional de

Table 1. Summary of information on the guano islands (I) and capes (P) of the Peruvian coast considered in this contribution.

No.	Name	Latitude (South)	Longitude (West)	Area (km^2)
1	I. Lobos de Tierra	06° 27′	80° 50′	14.26
2	I. Lobos de Afuera	06° 55′	80° 41′	2.36
3	I. Macabi	07° 48′	79° 30′	0.08
4	I. Guañape Norte	08° 32′	78° 58′	0.35
5	I. Guañape Sur	08° 32′	78° 58′	0.26
6	I. Chao	08° 46′	78° 49′	0.15
7	I. Corcovado	08° 50′	78° 18′	0.04
8	I. Santa	09° 02′	78° 41′	1.42
9	I. Blanca Norte	09° 08′	78° 38′	2.28
10	I. Ferrol Norte	09° 10′	78° 38′	0.24
11	I. Tortugas	09° 29′	78° 29′	0.61
12	P. Culebras	09° 57′	78° 15′	0.56
13	P. Colorado	10° 30′	77° 58′	0.18
14	P. Litera	10° 35′	77° 52′	0.82
15	I. Don Martin	11° 02′	77° 41′	0.16
16	P. Salinas	11° 17′	77° 38′	0.91
17	I. Huampanu y Chiquitanta	11° 20′	77° 43′	0.02
18	I. Mazorca	11° 23′	77° 45′	0.12
19	I. Pescadores	11° 47′	77° 16′	0.16
20	I. Isleta	11° 48′	77° 13′	0.07
21	I. La Cruz (San Lorenzo)	12° 05′	77° 15′	0.06
22	I. Palominos	12° 08′	77° 13′	0.11
23	I. Cavinzas	12° 08′	77° 13′	0.11
24	I. Pachacamac	12° 19′	76° 55′	0.24
25	I. Asia	12° 48′	76° 38′	0.71
26	I. Chincha Norte[a]	13° 39′	76° 24′	0.64
27	I. Chincha Centro	13° 39′	76° 24′	0.66
28	I. Chincha Sur[b]	13° 39′	76° 24′	0.27
29	I. Ballestas	13° 44′	76° 44′	0.32

[a] See Fig. 4.
[b] See Fig. 3.

Table 2. Mean densities of guano birds in colonies.

	Number of birds per m^2		
	Cormorant	Booby	Pelican
Reproducing adults (with nests)	7	5	3
Nonreproducing adults	15	5	3
Chicks	10	5	4

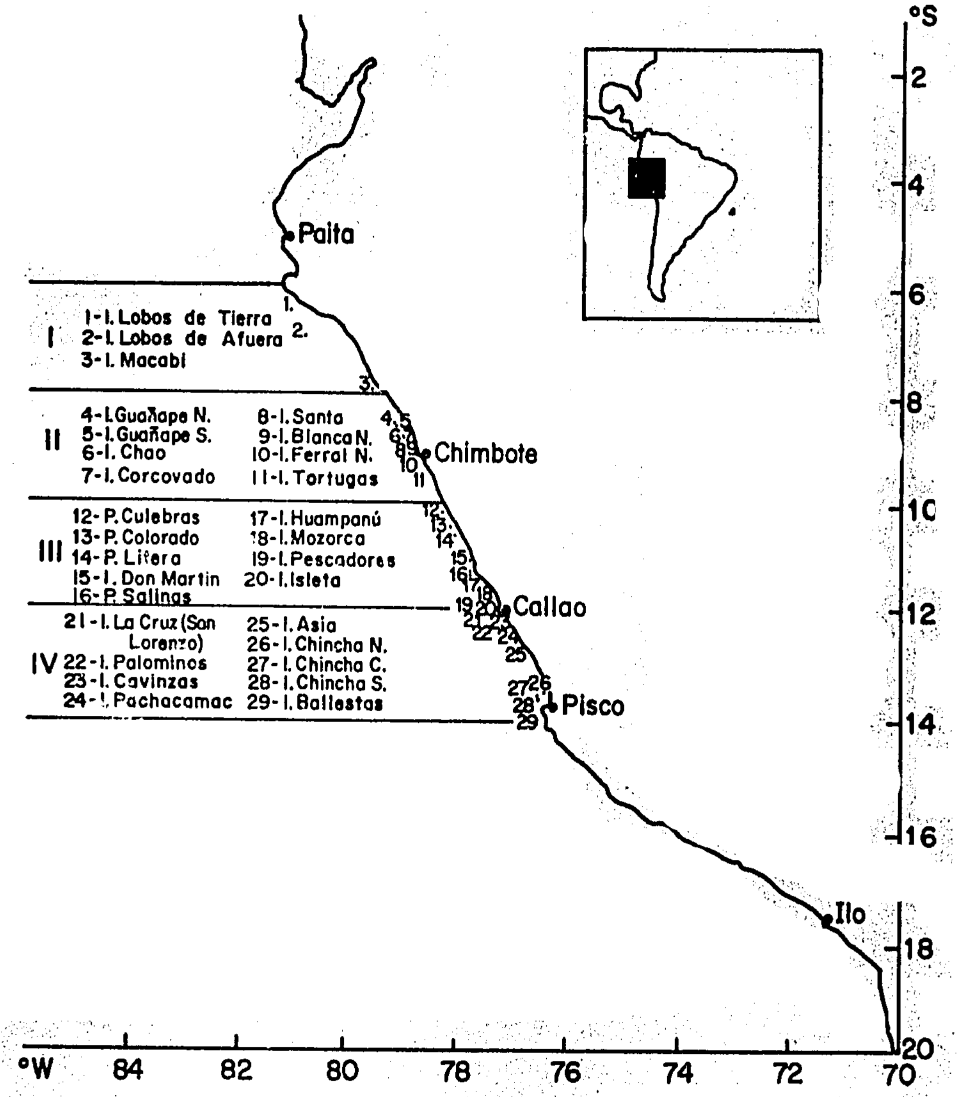
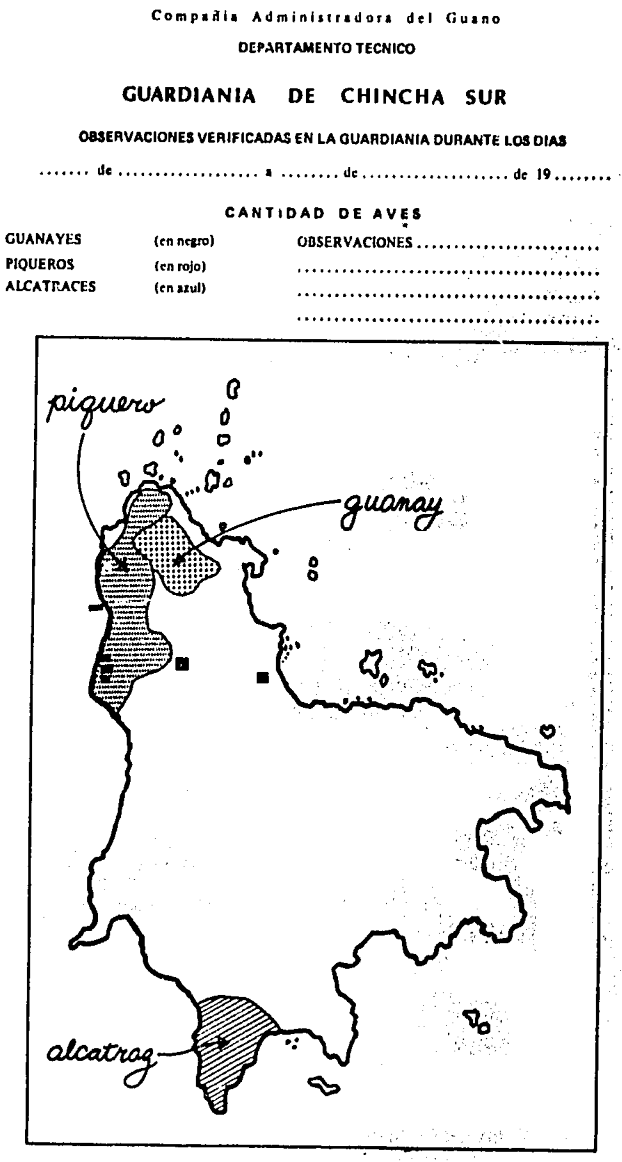


Fig. 2. Location of guano islands and points along the Peruvian coast (islands and points outside of 4-14°S not considered).

Fertilizantes (CONAFER). From 1970 to 1974, the management of the guano resources became the perogative of the Servicio Nacional de Fertilizantes (SENAFER); from 1976 to date, the guano resources have been managed by Pesca Peru Fertilizantes. All maps used here were obtained from the latter, which inherited the archives of its predecessors. Altogether, 10,080 maps were analyzed, covering the 360 months from January 1953 to December 1982. Of these, only 336 maps corresponding to the 1957 El Niño, had been previously reported upon by Tovar and Garcia (1982). A few more maps covering August 1971 to April 1976 were analyzed by Tovar and Galarza (1983). Thus, the overwhelming part of the materials reported upon here is new.

A planimeter was used to estimate for each month and island (or point) the surface area covered by the different stages (nonreproducing adult, reproducing adult, chick) of the three species in question (see Fig. 3 for a first example).

The empirically estimated densities in Table 2 were used to obtain, for each estimate of an area covered by birds, the corresponding population estimate. Note that the use of a mean density is justified due to the opposite tendencies of guano birds to both crowd themselves (to reduce predation), and to keep a minimum distance from each other (as determined by the birds' ability to peck at each other).



Compañía Administradora del Guano
DEPARTAMENTO TECNICO

GUARDIANIA DE CHINCHA SUR

OBSERVACIONES VERIFICADAS EN LA GUARDIANIA DURANTE LOS DIAS
.... de .... a .... de .... de 19........

CANTIDAD DE AVES

GUANAYES (en negro) OBSERVACIONES..........................
PIQUEROS (en rojo) ....
ALCATRACES (en azul) ....
....

Fig. 3. Example of map partly completed by the guard of Chincha Sur Island on the 10th of January 1962 at 3 p.m. (see Table 1 for location). The color codes, i.e., black for cormorants (guanay), red for boobies (piquero) and blue for pelicans (alcatraz) were here replaced by different shading patterns.

Data Interpolation

Interpolations were necessary for various islands (or points) and month, mainly because original graphs had been lost. Thus e.g., for the case:

month	January	February	March	April
population	5,000	no data	no data	2,000

we used the linear interpolation:

i) 5,000 - 2,000 = 3,000
ii) 3,000 / 3 = 1,000
iii) 2,000 + 1,000 = 3,000 (March)
iv) 3,000 + 1,000 = 4,000 (February)

As it turned out, interpolating missing data was never necessary for all islands and points in the same month and hence months with interpolated values have not been distinguished from months without such values when computing overall population sizes from 6 to 14oS.

Computational Example

The Chincha Sur bird colonies (Fig. 4) demonstrate the planimetric method used for estimation of bird population sizes.

In September 1974, the birds did not reproduce, hence the maps showing the distribution of reproducing adults with nests and chicks are empty. The planimeter conversion factor for Chincha Norte Island was computed as 81.5. Hence we have:

number of cormorants = $0.019 \cdot 81.5 \cdot 15 = 232{,}275$
number of boobies = $0.088 \cdot 81.5 \cdot 5 = 358{,}600$
number of pelicans = $0.050 \cdot 81.5 \cdot 3 = 122{,}250$

where 0.019, 0088 and 0.05 are relative surface areas estimated by planimetry (see Fig. 4) and 15, 5 and 3 are the empirical estimates of adult bird density taken from Table 2.

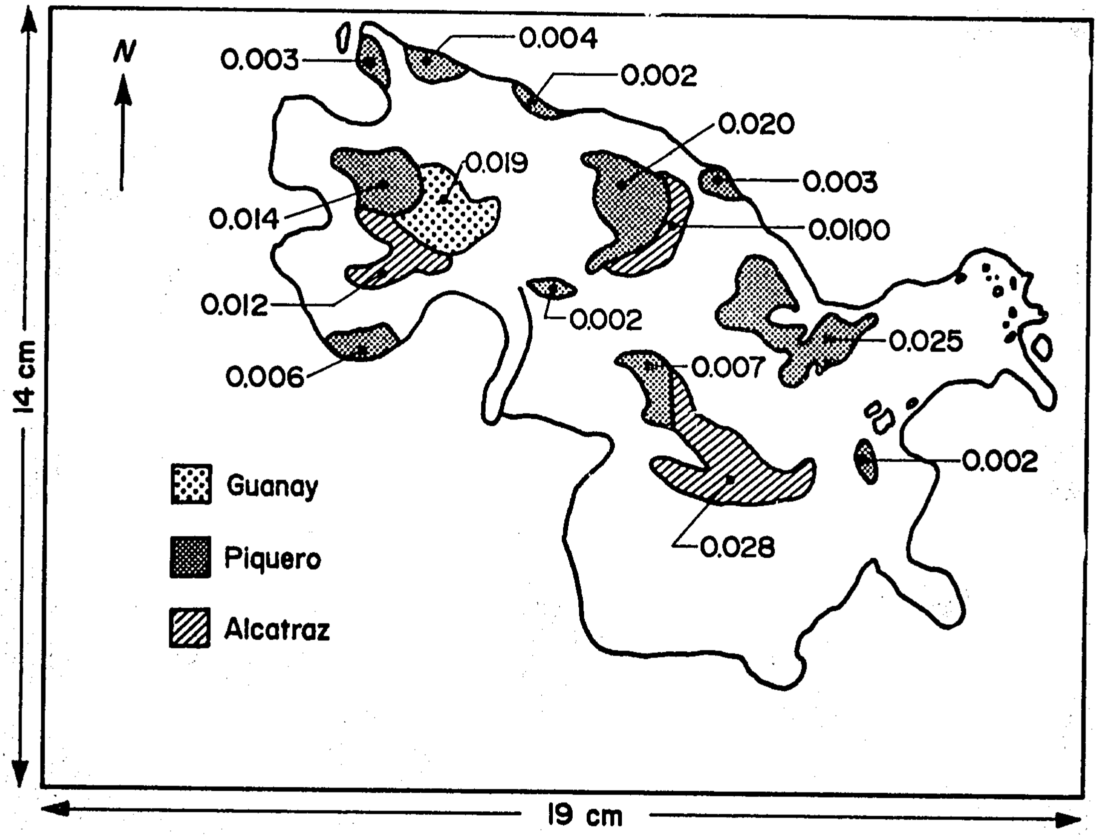


Fig. 4. Distribution of cormorants (guanay), boobies (piquero) and pelicans (alcatraz) on Chincha Norte Island (see Table 1) in September 1974, with relative areas estimated by planimetry. The sums of the relative area are 0.019, 0.088 and 0.050 for cormorants, boobies and pelicans, respectively (see text).

Results and Discussion

Areas Inhabited by Seabirds

From 1909 to 1945, there were 36 guardposts (*guardianas*) on islands and points along the Peruvian coast, 23 of which were on islands.

From 1945 on, the protection of the birds resulted in the expansion of their populations, requiring the establishment of new posts, especially on points which represent second-choice breeding locations compared to islands. As these colonies were frequently disturbed by people and animals (especially by the fox *Dusycyon sechurae*), the sites were isolated by walls of up to 3 m high. This intervention, which caused a further increase in bird population led to a maximum in 1955 of 52 guardposts along the Peruvian coast. However the expansion of the anchoveta purse seine fishery, which started in the early 1950s and the 1957 El Niño led to a decrease in the number of points used for breeding by the birds and hence to a decline of the number of guardposts to 45 in 1964. Urban sprawl and the further decline of the bird population led to more points and islands becoming free of seabirds. In 1982, only 26 islands and 12 points from 6 to 18ºS were still used by the birds.

Absolute Population Sizes of Guano Birds

Previous reports of the population of guano birds along the coast of Peru have been presented for various, relatively short periods by Vogt (1942), Jordan (1959, 1961, 1963, 1964), Gamarra (1964a, 1964b), Jordan and Fuentes (1966), Galarza (1968), Fuentes (1969) and Tovar (1978, 1983).

Tables 3, 4 and 5 present population estimates for cormorants, boobies and pelicans respectively. Fig. 5 presents the same data as time series.

Table 3. Population (in millions) of adult cormorants off Peru (6 to 14ºS, 1953 to 1982).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	14.53	13.58	10.76	9.54	8.99	14.24	11.75	12.18	16.11	19.17	17.81	17.20
1954	14.98	14.87	14.22	20.22	26.35	30.12	26.39	26.81	26.31	20.12	22.39	12.52
1955	13.76	16.22	12.41	16.70	22.70	28.23	28.35	33.50	29.50	18.55	16.16	13.60
1956	11.32	10.73	15.86	21.35	20.26	24.38	25.37	23.09	20.70	18.26	12.42	9.63
1957	14.17	13.21	8.80	6.47	5.97	7.93	4.75	3.17	9.09	14.50	13.06	8.46
1958	3.07	3.30	5.76	6.46	9.19	6.31	0.89	10.07	10.77	9.55	5.74	4.88
1959	5.06	5.75	11.23	14.72	14.60	18.06	16.98	12.50	12.11	7.48	7.88	8.31
1960	9.91	7.95	13.44	11.01	10.87	13.47	13.04	9.74	10.94	10.23	10.85	10.08
1961	7.92	10.63	11.16	8.85	13.05	14.71	18.92	23.34	16.55	12.38	13.39	11.18
1962	9.41	9.83	9.98	11.29	14.38	22.81	20.21	16.67	14.07	10.33	9.85	7.69
1963	9.38	12.04	11.74	12.94	20.56	9.24	8.51	8.76	7.39	10.94	10.32	8.38
1964	10.11	8.19	13.76	10.08	26.01	18.66	14.18	12.33	13.88	14.21	9.60	8.24
1965	8.65	6.58	9.12	6.36	2.55	4.10	2.78	0.87	0.38	1.15	2.20	1.56
1966	2.36	2.13	1.61	2.57	1.43	2.14	2.21	3.91	3.62	2.15	1.57	1.58
1967	1.83	1.43	2.05	2.02	4.40	3.25	2.53	4.55	5.23	2.68	1.94	1.88
1968	2.52	2.68	2.20	2.88	3.55	4.04	3.60	4.16	3.24	2.38	2.32	2.23
1969	2.06	1.99	1.62	1.82	1.47	0.80	1.15	2.06	3.51	2.39	2.46	1.55
1970	1.35	1.60	1.87	1.84	2.00	3.04	3.52	3.08	2.23	1.82	1.27	1.41
1971	1.90	1.84	1.89	3.23	3.17	4.68	4.29	3.86	2.70	3.63	2.62	2.38
1972	2.37	3.13	3.08	0.65	0.50	0.29	0.14	0.08	0.09	0.99	1.26	0.43
1973	0.76	1.24	0.62	0.70	0.94	1.08	0.95	0.54	0.52	0.26	0.39	0.44
1974	0.41	0.66	0.74	0.54	0.70	1.06	1.32	1.43	0.56	0.53	0.50	0.62
1975	0.43	0.62	0.85	0.90	1.19	1.08	1.63	1.29	1.21	1.31	1.04	0.85
1976	0.50	0.55	1.23	1.08	0.94	0.90	0.83	0.98	1.14	0.82	0.66	1.02
1977	1.06	1.06	0.70	0.99	1.04	1.35	1.38	1.51	1.14	1.08	1.22	1.08
1978	0.81	0.73	0.98	1.36	1.18	1.69	1.03	1.51	1.01	1.04	1.04	0.93
1979	1.17	2.18	1.56	2.63	2.43	1.99	2.11	1.61	1.51	1.39	1.20	1.41
1980	1.33	1.25	1.61	2.14	2.20	2.35	2.52	2.40	2.24	2.15	2.05	2.76
1981	2.49	2.73	2.38	2.06	3.93	3.11	3.03	2.72	2.34	2.65	2.90	2.98
1982	2.22	2.36	2.15	3.25	2.47	5.25	4.68	4.48	3.59	4.08	1.76	1.34

As might be seen from Fig. 5, the cormorant population, increased from about 10 million in 1953 up to values above 30 million in 1955, then began to decline down to values between 1.3 and 5.3 million in 1982. Table 6 suggests that this downward trend was intensified by the 1982-1983 El Niño.

Fig. 5 shows that despite the decline of their population, the boobies were not as strongly affected by the successive El Niño and the fishery (see also Fig. 6).

The pelicans had, throughout, the lowest population sizes, starting the time series with 0.1-0.7 million in 1953. The reduction of the pelican population was not caused only by starvation-induced mortality. Rather, a large number of pelicans migrate southward during periods of food

Table 4. Population (in millions) of adult boobies off Peru (6 to 14°S, 1953 to 1982).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	3.06	2.68	2.36	2.04	1.35	1.42	1.28	0.94	1.50	2.30	2.13	2.84
1954	2.51	2.24	2.09	2.07	2.11	2.12	2.79	2.32	2.31	2.61	2.83	2.79
1955	3.21	2.61	2.86	3.21	2.78	2.60	2.40	2.54	2.34	3.09	2.38	2.52
1956	3.20	3.16	2.43	2.92	2.44	1.73	2.23	2.69	1.93	2.48	3.27	4.22
1957	3.20	2.32	2.55	1.35	0.82	0.25	0.16	0.25	0.70	1.52	1.74	0.98
1958	0.89	0.73	0.80	1.02	1.15	2.57	1.17	0.50	1.08	1.11	1.69	1.41
1959	1.48	1.41	1.90	1.82	1.27	1.32	1.16	1.18	1.36	1.29	1.74	1.53
1960	1.71	1.79	1.21	1.32	1.59	1.28	1.68	1.49	2.56	2.46	2.66	1.90
1961	2.02	1.94	1.73	1.34	1.63	1.62	1.95	1.41	1.72	1.80	2.08	2.32
1962	2.18	2.28	2.28	1.58	1.46	1.89	1.71	1.37	1.42	2.16	3.21	2.38
1963	2.69	2.53	1.75	1.49	1.55	1.58	1.28	1.37	1.35	0.97	1.71	2.10
1964	1.48	1.84	2.19	1.60	1.72	1.65	1.65	2.09	1.16	2.25	2.35	2.62
1965	2.36	3.21	2.62	1.74	0.45	0.44	0.39	0.28	0.19	0.51	0.80	0.77
1966	1.57	0.95	0.78	1.20	1.45	1.62	1.23	1.00	1.16	0.96	0.69	1.04
1967	1.11	1.20	1.10	0.84	1.07	0.67	0.88	1.41	1.55	0.95	0.68	0.99
1968	1.64	1.53	1.14	0.74	0.82	0.71	0.96	1.02	1.32	1.20	1.30	1.51
1969	1.64	1.93	1.63	1.84	1.34	1.42	1.00	1.33	0.98	0.77	0.97	0.73
1970	1.26	1.36	1.48	1.39	1.00	1.51	1.43	1.31	1.13	1.20	1.31	1.18
1971	1.30	2.17	1.30	1.39	1.32	1.70	1.81	1.24	1.42	1.48	1.37	1.47
1972	1.79	2.11	1.41	0.33	0.33	0.29	0.30	0.43	0.42	0.48	0.40	0.86
1973	0.81	1.17	1.22	0.83	0.82	0.83	0.71	0.63	0.74	0.86	1.06	1.17
1974	1.13	1.32	1.58	1.18	1.56	1.04	1.14	1.49	1.46	1.43	1.33	1.23
1975	1.19	1.64	1.51	1.82	1.40	1.09	1.67	0.95	0.97	1.31	1.42	1.28
1976	1.76	1.95	1.80	1.43	0.88	0.78	1.12	0.97	1.21	1.33	1.58	1.25
1977	1.64	1.81	1.82	1.74	2.08	1.32	1.24	0.90	0.84	1.01	1.63	2.37
1978	1.81	1.82	2.17	2.66	2.21	2.99	2.25	2.05	2.44	2.50	2.59	2.42
1979	1.69	2.11	2.22	1.75	1.41	1.55	1.94	1.56	1.80	1.83	1.89	1.86
1980	1.59	1.53	1.87	1.67	1.72	1.27	1.68	1.64	1.72	1.79	1.82	2.18
1981	1.74	1.69	1.94	1.83	2.60	2.04	1.92	2.19	1.92	1.76	1.96	1.92
1982	1.78	1.60	2.60	1.97	1.84	2.43	2.78	1.86	1.73	1.19	0.93	1.19

scarcity off northern/central Peru, while weaker specimens are often caught on beaches by people and eaten.

For all species, the fluctuation of population suggests a succession of partial recoveries following El Niño-induced crashes which were intensified by the reduction of the anchoveta induced by the purse seine fishery (see Table 6).

Changes in Relative Abundance

Fig. 6 shows on an annual basis the changes in the relative abundance of cormorants, boobies and pelicans from 1953 to 1982 (see Table 6 for data pertaining to 1983). As might be seen, the major change is that the cormorants, being far more specialized on anchoveta than both boobies and pelicans (see Tovar and Galarza 1984; Muck and Pauly, this vol.) lost their overwhelming dominance over the latter two species, a trend which was intensified by the 1982-1983 El Niño.

Relationship Between Environmental and Guano Population Fluctuations

Earlier authors commenting on the causes of mass mortalities in guano birds disagreed as to the relative impact of epizootic diseases and simple starvation due to a decline of fish biomass (Lavalle 1912, 1917; Ballen 1924, 1925; Murphy 1931; Stiglich 1931; Torrico 1933; Vogt 1940; La Rosa Llosa and Ramos Saco 1949; Avila 1953).

More recent work (Jordan 1964; Tovar and Garcia 1982; Tovar and Galarza 1983; Tovar and Cabrera 1985) have vindicated those who suggested that lack of food is the ultimate cause

Table 5. Population (in millions) of adult pelicans off Peru (6 to 14°S, 1953 to 1982).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	0.42	0.66	0.64	0.18	0.14	0.11	0.10	0.08	0.08	0.41	0.76	0.69
1954	0.59	0.72	0.67	0.45	0.45	0.36	0.29	0.31	0.21	0.31	0.41	0.52
1955	0.52	0.66	1.30	0.68	0.18	0.08	0.10	0.13	0.38	0.40	0.75	0.64
1956	0.77	1.10	0.70	0.27	0.55	0.36	0.12	0.11	0.07	0.13	0.31	0.35
1957	0.32	0.28	0.15	0.02	0.06	0.08	0.04	0.02	0.15	0.16	0.18	0.22
1958	0.13	0.12	0.09	0.24	0.28	0.24	0.16	0.19	0.39	0.24	0.20	0.19
1959	0.28	0.63	0.33	0.85	0.75	0.41	0.13	0.40	0.35	0.29	0.22	0.49
1960	0.41	0.26	0.13	0.33	0.34	0.35	0.55	0.53	0.44	0.40	0.33	0.22
1961	0.23	0.24	0.21	0.20	0.48	0.41	0.11	0.12	0.29	0.45	0.32	0.34
1962	0.45	0.34	0.23	0.15	0.19	0.10	0.10	0.11	0.22	0.34	0.42	0.31
1963	0.30	0.46	0.59	0.77	0.47	0.19	0.15	0.11	0.06	0.06	0.06	0.14
1964	0.15	0.27	0.38	0.12	0.27	0.02	0.14	0.10	0.14	0.11	0.33	0.61
1965	0.81	0.45	0.54	0.60	0.47	0.18	0.08	0.05	0.04	0.08	0.15	0.14
1966	0.24	0.08	0.14	0.15	0.23	0.18	0.15	0.15	0.23	0.33	0.22	0.39
1967	0.52	0.40	0.38	0.35	0.60	0.12	0.13	0.32	0.76	0.20	0.13	0.17
1968	0.47	0.37	0.43	0.23	0.27	0.16	0.20	0.30	0.32	0.26	0.25	0.31
1969	0.24	0.20	0.22	0.18	0.07	0.10	0.09	0.15	0.12	0.12	0.17	0.14
1970	0.18	0.18	0.21	0.25	0.23	0.25	0.22	0.16	0.23	0.33	0.12	0.09
1971	0.12	0.13	0.09	0.23	0.16	0.31	0.18	0.24	0.10	0.20	0.22	0.19
1972	0.24	0.23	0.32	0.16	0.23	0.12	0.12	0.15	0.14	0.16	0.12	0.19
1973	0.15	0.32	0.18	0.38	0.11	0.12	0.18	0.10	0.12	0.19	0.27	0.21
1974	0.26	0.29	0.36	0.13	0.19	0.05	0.06	0.06	0.24	0.37	0.27	0.09
1975	0.10	0.21	0.15	0.13	0.10	0.03	0.06	0.04	0.08	0.06	0.05	0.07
1976	0.06	0.12	0.16	0.25	0.10	0.08	0.04	0.08	0.09	0.08	0.11	0.10
1977	0.11	0.20	0.13	0.11	0.08	0.03	0.04	0.12	0.09	0.11	0.12	0.27
1978	0.23	0.23	0.51	0.46	0.35	0.28	0.13	0.18	0.23	0.12	0.20	0.19
1979	0.28	0.34	0.23	0.19	0.27	0.23	0.20	0.25	0.34	0.38	0.41	0.23
1980	0.15	0.14	0.26	0.17	0.30	0.17	0.11	0.08	0.15	0.16	0.21	0.27
1981	0.16	0.13	0.11	0.14	0.21	0.22	0.07	0.07	0.09	0.18	0.21	0.14
1982	0.16	0.18	0.22	0.16	0.19	0.23	0.16	0.16	0.18	0.10	0.10	0.13

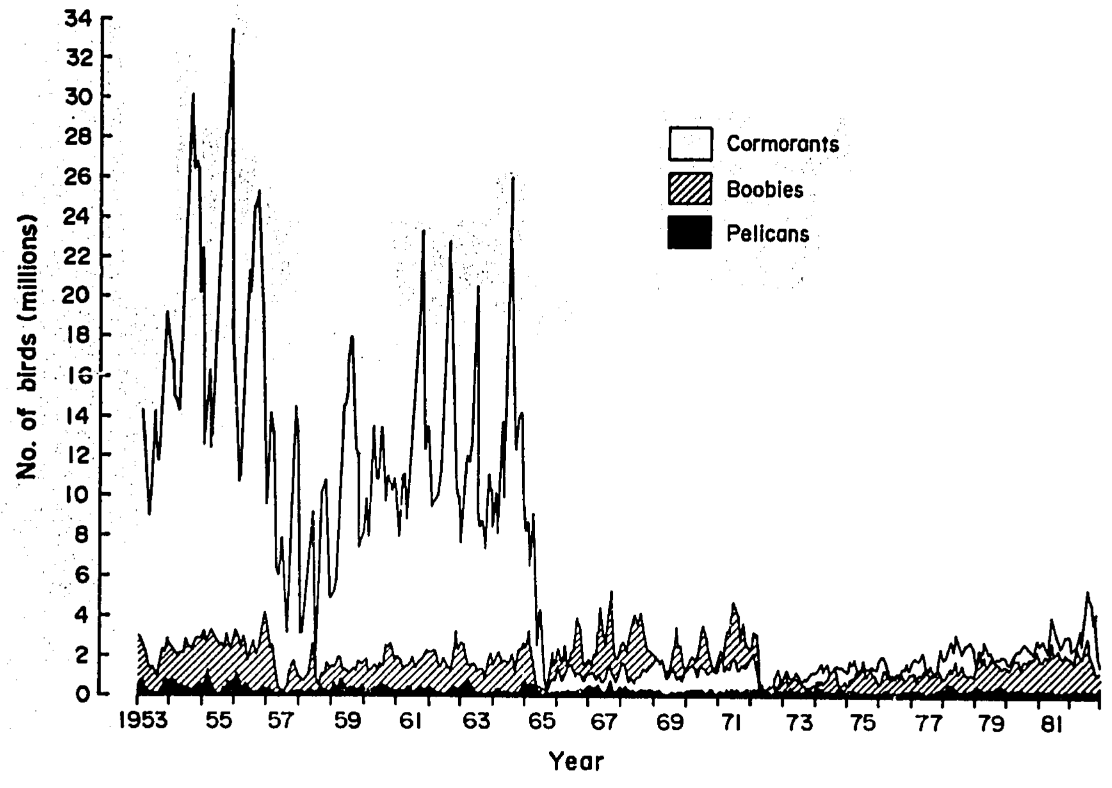


Fig. 5. Monthly fluctuations of the population of the three major seabird species off Peru (4-14°S), 1953 to 1982.

Table 6. Changes in guano bird populations between 6 and 14°S off Peru following El Niño 1982/82, (adapted from data in Tovar and Cabrera 1984).

Month	Bird population (millions) Cormorants	Boobies	Pelicans
Jul 1982	4.68	2.78	0.16
Dec 1982	1.34	1.19	0.13
Mar 1983	0.91	0.28	0.16
May 1983	0.23	0.15	0.23
Jun 1983	0.11	0.05	0.08
Jul 1983	0.19	0.08	0.08

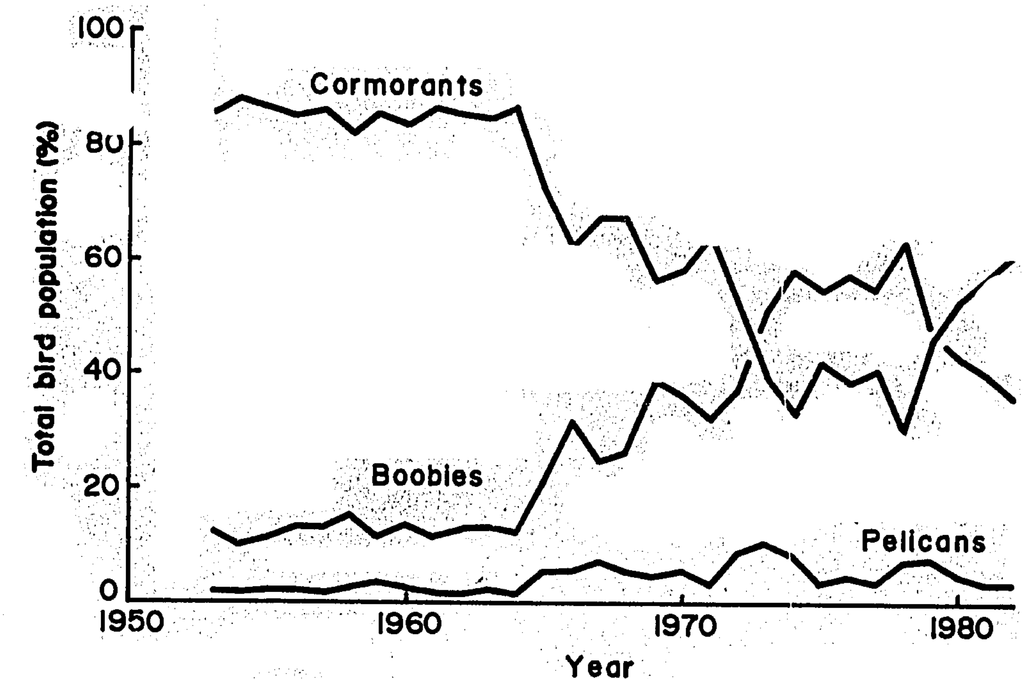


Fig. 6. Relative abundance of the three guano birds considered in this study, 1953 to 1982. Note gradual decline of the importance of cormorants and the small increase of pelicans (see also text).

for the mass mortalities of guano birds observed so far, and this is also confirmed by the present study, which shows that there is, for every El Niño event off Peru, a corresponding decline of guano bird numbers. The fishery thus affects the guano bird populations, by reducing their food base before, during and after an El Niño event, and this indeed has been assumed by Muck and Pauly (this vol.) who, based on the population estimates presented in this contribution, proceeded to estimate the amount of anchoveta eaten, from 1953 to 1982 by Peruvian guano birds.

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Monthly Anchoveta Consumption of Guano Birds, 1953 to 1982*

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Abstract

Anchoveta consumption by Peruvian guano birds (*Phalacrocorax bougainvillii, Sula variegata, Pelecanus thagus*) was estimated for the period 1953 to 1982 for the area 4-14°S latitude using an analytical consumption model and monthly seabird population estimates based on field counts. Highest estimates were obtained for 1955-1956 with about 2 million metric tonnes (t) per year of anchoveta being consumed by the guano birds. Due to the continuous decline of the guano bird populations, their anchoveta consumption dropped to values of less than 20,000 t at the beginning of the 1970s and an average of around 30,000 t between 1970 and 1982.

Population decline of guano birds is most probably caused by reduced anchovy availability, a consequence of the combined effects of the heavy anchovy fishery and El Niño-related periods of low food vulnerability.

Introduction

In the Peruvian upwelling ecosystem guano birds are probably the species most dependent on anchoveta (*Engraulis ringens*) as a food resource and the most conspicuous competitors for the anchoveta fishery.

This competition is particularly visible when one compares the range of anchoveta sizes consumed by cormorants and boobies with the size distribution of the Peruvian purse seine fishery (see Figs. 1 and 2). That this size overlap is neither confined to Peru, nor to these two guano bird species is illustrated by Fig. 3, showing an even more pronounced overlap between the anchovy (*E. mordax*) size distribution in the California purse seine fishery and in regurgigated food bolus of the brown pelican (*Pelecanus occidentalis californicus*), a close relative of the pelican occurring off Peru (earlier taxonomies in fact saw *P. thagus* as a subspecies of *P. occidentalis*, just as *P. occidentalis californicus* is).

Periods of high anchoveta biomass have thus usually also been periods of high abundance of cormorants (*Phalacrocorax bougainvillii*), gannets (*Sula variegata*) and pelicans (*Pelecanus thagus*) which are the principal species of so-called guano birds (see Tovar et al., this vol.).

Their excrements (Spanish *guano*) are of economical importance as fertilizer and, in the past, for gunpowder production. Following the 1972 anchoveta collapse due to overexploitation and unfavorable oceanographic conditions, the guano birds became reduced to around 20% of their former population size (of 24 million in 1954-1955).

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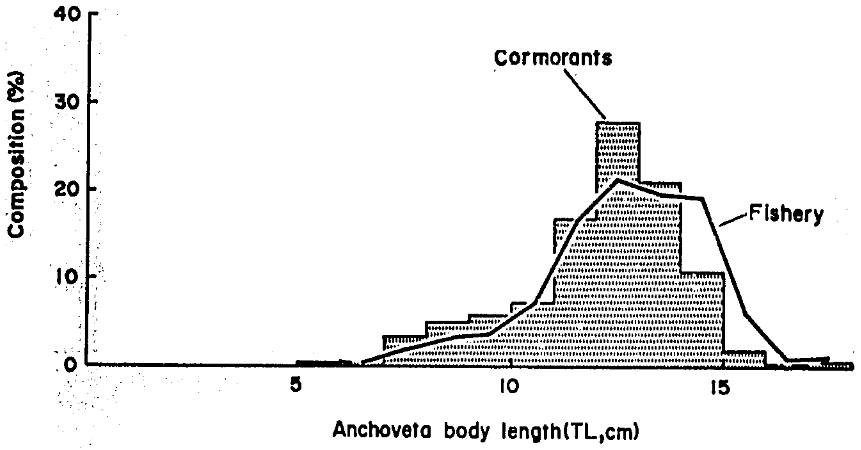

Fig. 1. Relationship between reconstructed % size composition of anchoveta in cormorant food bolus and size-frequency distribution in the fishery, June 1954 to June 1958 (adapted from data in Jordan 1959, Fig. 5).

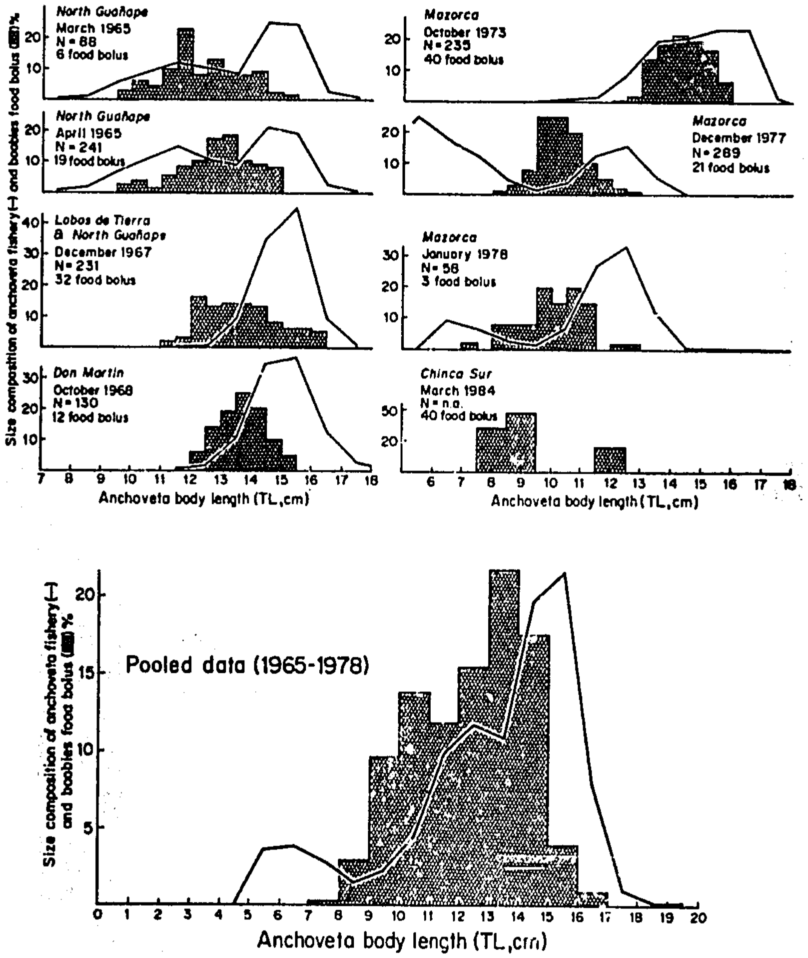

Fig. 2. Relationship between the reconstructed % size composition in booby food bolus and the size-frequency composition of the northern/central Peruvian anchoveta fishery (based on H. Tovar, IMARPE, pers. comm.; data for Chinca Sur Island are from Fuertes 1985).

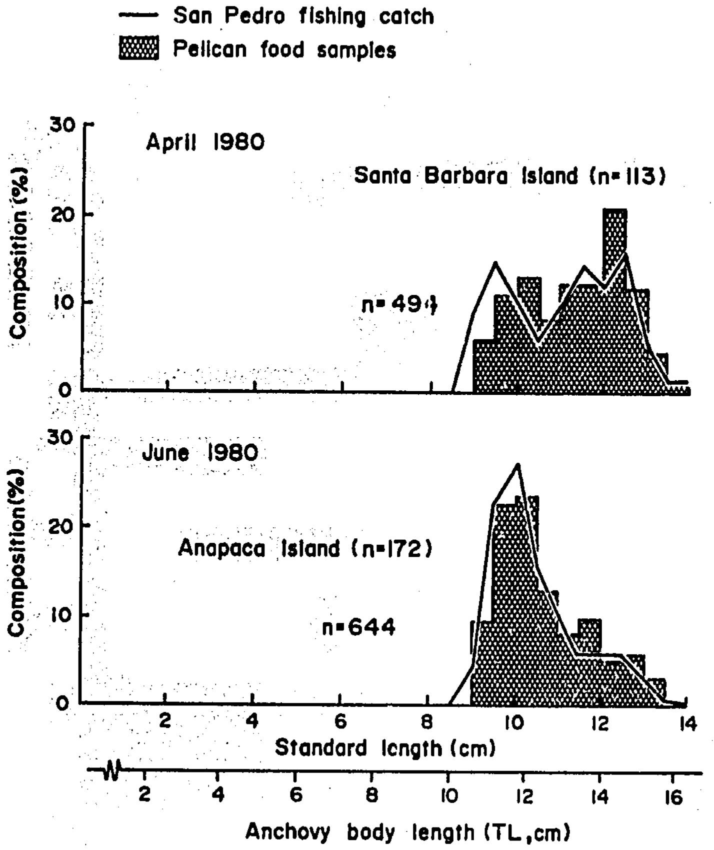

Fig. 3. Relationship between reconstructed % size composition of northern anchovy in pelican food bolus and size-frequency distribution in the California purse seine fishery (adapted from Sunada et al. 1981).

Furness (1982) using data of Schaefer (1970) suggests that, between 1961 and 1965, guano birds were consuming annually 17% of the total Peruvian anchoveta biomass. Jordan (1967) estimated that the annual anchoveta consumption between 1961 and 1963 was around 45% of the total annual anchoveta catch; similar figures are given in Murphy (1972).

It is the aim of this paper to present monthly estimates of anchoveta consumption by guano birds for the period 1953 to 1982 and to relate this consumption to the fishery and environmental conditions such as El Niño events.

Materials and Methods

Anchoveta consumption was calculated using (i) monthly biomass data for the three guano bird species (based on the abundance data for juveniles and adults given in Tovar et al., this vol.), (ii) "possible" consumption rates (based on the guano birds' body weights and on metabolic considerations) and (iii) anchoveta availability to guano birds.

Abundance data were converted to biomass by multiplying with the birds' average body weight, given in Table 1.

A large body of literature on daily consumption rates based on metabolic equations, stomach contents analysis, feeding experiments and guano production exists for guano birds (Table 2). These data, plotted against body weight, suggest that specific differences can be neglected, and that the daily food consumption is a logarithmic function of body weight and of the analytic method (see Fig. 4).

The metabolic equations - which result in notable lower values - were used to calculate consumption rates corresponding to the daily energy expenditures (DEE, see Wiens and Scott

Table 1. Feeding behavior, body weight and daily ration for the main Peruvian guano bird species.

Species	Feeding method^a	Maximum depth of foraging (m)	Foraging period	Adult weight (kg)^d	Daily ration (% body weight)	% anchovy in diet
Pelecanus thagus	piracy, surface seizing, surface plunging	2.0^a	day and night^{b,c}	5.9-7.8 mean 6.68	11.2^e 10.1^f	>80^b
Sula variegata	deep plunging	5.0^a 15.0^b	dawn-sunset^b	1.2-1.4 mean 1.28	27.4^e 16.3^f	>80^b
Phalacrocorax bougainvillii	pursuit diving	12.0^b 15.0^a	dawn-sunset^b	1.7-2.2 mean 1.94	23.3^e 14.7^f	96^{b,g}

[a] In Duffy (1980) after Ashmole (1971)
[b] Jordan (1967)
[c] Vogt (1942)
[d] H. Tovar (IMARPE, pers. comm.)
[e] from equation (1)
[f] from equation (2)
[g] Avila (1954)

Table 2. Estimates of fish consumption in three genera of fish-eating birds *(Phalacrocorax, Sula* and *Pelecanus).*

Species	Area	Adult weight (kg)	Daily consumption (% body weight)	Reference and remarks
I) CORMORANTS				
Phalacrocorax africanus	Zimbabwe	0.62	39.4	Junor (1965), feeding experiments with immature birds.
P. auritus	n.a.	3.0	17.0	Hutchinson (1950)
P. bougainvillii	Peruvian coast	1.80	14.4	
			15.1	
			16	Laugksch and Duffy (1984), see below
			16.3	
P. bougainvillii	Peruvian coast	2.07	21.5	Jordan (1959, 1967), based on regurgitated food bolus and stomach contents analysis. Body weight from Hutchinson (1950).
P. bougainvillii	Peruvian coast	2.00	23.7	Avila (1954), based on guano production.
P. capensis	South Africa	1.22	12.4	Furness and Cooper (1982) (see below)
P. capensis	South Africa	1.22	16.8^a	Laugksch and Duffy (1984), adjusted for reproductive and other costs, using metabolic equations of: (a) Lasiewski and Dawson (1967), (b) Aschoff and Pohl (1970), (c) Kendeigh et al. (1977), (d) Walsberg (1983).
			16.8^b	
			17.7^c	
			18.2^d	
P. carbo	Sri Lanka	2.10	16.4	Winkler (1983) metabolic equation not adjusted for reproductive and other costs.
P. carbo	Yugoslavia	5.00	32.0	Apostolski and Matvejev (1955), no information on method available; these authors refer to "Riesenvögel", i.e., giant birds, for which the upper limits of weights in Palmer (1962) was used.
P. carbo lucidus	Zimbabwe	1.97	22.2	Junor (1965) see above.
P. fuscicolli	Sri Lanka	0.93	18.4	Winkler (1983) see above
P. niger	South Africa	0.58	20.2	Winkler (1983)
P. penicilatus	British Columbia	2.38	20.0	Robertson (1972), stomach contents analysis.
II) BOOBIES and GANNETS				
Sula capensis	South Africa	2.65	11.9	Furness and Cooper (1982), metabolic equivalents adjusted for reproductive and other costs
S. capensis	South Africa	2.65	12.4	
			13.6	
			14.4	Laugksch and Duffy (1984) see above
			14.7	
S. dactylatra	South Africa	2.16	13.1	Laugksch and Duffy (1984) see above
S. leucogaster	French Frigate Islands	1.30	15.4	Pettit et al. (1984) see below
S. sula	French Frigate Islands (N.W. of Hawaii)	1.10	24.7	Harrison and Hida (1980), stomach contents analysis.
S. sula	French Frigate Islands (N.W. of Hawaii)	1.10	14.2	Pettit et al. (1984), metabolic equations adjusted for reproductive and other costs.
S. variegata	Peruvian coast	1.28	16.4	
			16.6	Laugksch and Duffy (1984) see above
			17.4	
			17.7	
III) PELICANS				
Pelecanus onocrotalus	South Africa	9.55	8.8	Guillet and Furness (1985), metabolic equations adjusted for reproduction and other costs.
P. onocrotalus	South Africa	9.55	10.0	Din (1979), stomach contents analysis.
P. thagus	Peruvian coast	6.00	9	
			10.8	Laugksch and Duffy (1984) see above
			11.5	
			11.8	

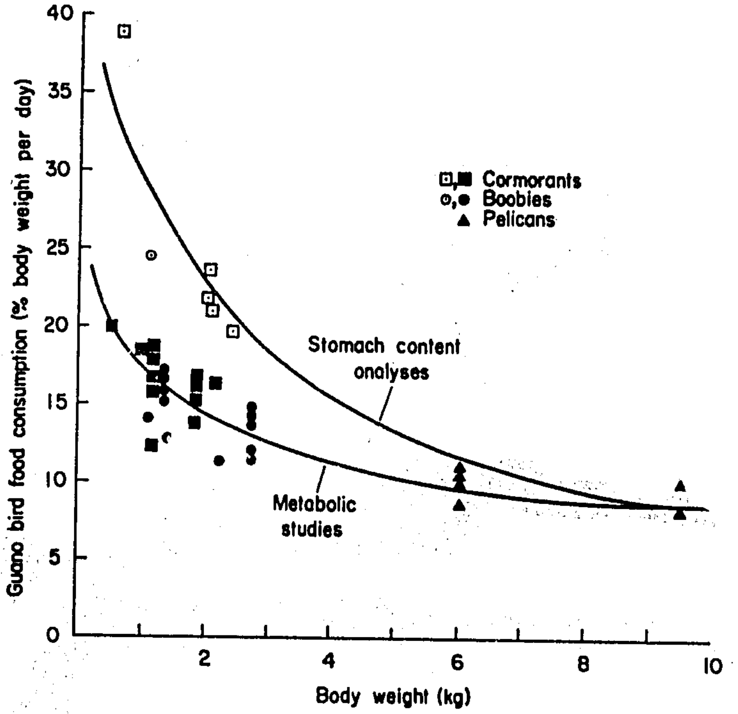

Fig. 4. Relationship between estimated food consumption and body weight in three genera of fish-eating guano birds. Note difference between line derived from stomach content analyses and line based on metabolic studies (based on data in Table 2).

1975; Schneider and Hunt 1982; Furness and Cooper 1982; Laugksch and Duffy 1984) sufficient for individual growth and egg production and for balancing, at the population level, mortality by reproduction.

The higher consumption rates derived by the other methods can be interpreted as providing rough estimates of "possible daily consumption" (PDC). Increase of population would thus occur when actual consumption ranges between DEE and PDC.

Two curves corresponding to these two consumption levels were established by regression analysis, i.e.:

Possible daily consumption

$$\text{PDC}\ \% = 29.78 - 9.77 \log_e \text{Weight} \qquad ...1)$$

Daily energy expenditures

$$\text{DEE}\ \% = 17.20 - 3.73 \log_e \text{Weight} \qquad ...2)$$

Dividing the PDC %-value by 100 and multiplying by 30 allows computation of total possible consumption for each of the three species "j" at month "i" (C_{ij}) from:

$$C_{ij} = B_{ij} \cdot \text{PDC}\%_j \qquad ...3)$$

and anchoveta consumption (Ca_{ij}) as:

$$Ca_{ij} = C_{ij} \cdot Aa_{ij} \qquad ...4)$$

where "B_{ij}" is the bird biomass for species "j" at month "i" and "Aa_{ij}" is an index (>0.1) quantifying the availability of anchoveta during month "i" to predator "j".

The availability index is calculated as the product of (i) relative anchoveta biomass (Ba_i, >0, <1), (ii) anchoveta vulnerability (Vul_{ij}, >0, <1) and (iii) an index expressing competition for anchoveta as food resource ($Comp_i$, >0, <1):

$$Aa_{ij} = Ba_i \cdot Vul_{ij} \cdot Comp_i \qquad ...5)$$

This allows taking into account the suggestions of Furness (1982) and MacCall (1982) for modelling of the Peruvian anchovy-seabird system that (i) El Niño related changes in sea temperature should affect anchoveta vulnerability to guano birds, (ii) that predation pressure from the guano birds themselves should reduce the availability of their food and that (iii) in periods following extremely high bird mortality the food supply per bird should be much greater than during the preceding period.

The estimation of anchoveta availability to the three guano species was performed as follows:

Relative anchoveta biomass. Relative anchoveta biomass at month "i" (Ba_i) has been calculated using the preliminary anchoveta biomass data in Table 3, divided by the highest annual mean of 20.8 t x 10^6, in 1967 (see Fig. 5).

Anchoveta vulnerability index. Vulnerability (Vul_{ij}) is treated as a function of the overlap between predator and prey which might be expressed through an index of vertical (i.e., depth) overlap (V) and another index for horizontal overlap (H). Also, dispersion (D) was considered, leading to:

$$Vul_{ij} = V_i \cdot H_i \cdot D_i \qquad ...6)$$

Table 3. Preliminary estimates of anchoveta biomass for the area 4-14°S (in t x 10^6), as used to compute the availability of anchoveta to the guano birds.[a]

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	13.7	18.0	17.5	19.1	18.0	18.0	14.5	11.3	13.3	17.3	22.7	18.0
1954	13.3	17.6	17.1	18.6	17.6	17.6	14.2	11.0	13.0	16.8	22.1	17.6
1955	13.1	17.3	16.8	18.3	17.3	17.3	13.9	10.8	12.8	16.6	21.7	17.3
1956	12.9	17.0	16.5	18.0	17.0	17.0	13.7	10.6	12.5	16.3	21.4	18.6
1957	15.8	16.5	16.1	17.5	16.5	16.5	13.3	10.3	12.2	15.8	20.8	16.3
1958	12.3	16.2	15.8	17.2	16.2	16.2	13.1	10.2	12.0	15.6	20.4	16.3
1959	12.1	12.1	15.2	14.5	13.9	13.3	13.9	8.5	8.5	17.5	21.4	21.4
1960	18.4	18.4	14.2	15.5	15.4	16.0	13.6	10.1	10.7	8.3	17.2	17.2
1961	16.8	16.3	13.4	17.7	15.1	16.3	9.1	6.1	11.6	17.4	19.8	18.6
1962	12.0	14.8	17.1	17.7	17.1	16.0	13.1	13.1	14.8	16.0	19.4	20.5
1963	17.1	13.7	12.0	12.5	11.2	11.2	11.5	11.8	11.9	13.8	15.0	15.2
1964	15.0	14.8	14.0	13.0	12.0	12.8	12.5	12.0	11.9	13.2	15.0	14.6
1965	15.0	14.2	15.5	16.5	17.0	17.5	16.5	17.2	17.6	17.9	19.0	21.0
1966	20.5	19.8	18.5	17.5	16.2	14.8	14.5	14.2	16.8	15.8	14.5	16.2
1967	16.5	17.2	23.0	23.0	22.8	22.2	22.0	22.0	21.8	21.2	20.0	27.8
1968	18.5	17.2	16.2	15.8	15.5	14.5	14.8	14.8	14.8	13.0	13.8	13.8
1969	13.5	12.8	13.2	11.0	11.5	11.2	12.0	12.2	13.0	12.2	14.8	15.8
1970	15.2	14.2	14.5	14.0	13.0	14.8	14.7	14.5	14.3	14.2	14.0	13.8
1971	13.8	13.7	13.5	13.4	13.3	13.2	13.0	12.9	12.7	10.6	9.3	9.0
1972	8.3	7.7	7.2	6.5	6.2	5.7	4.9	4.7	4.1	4.7	4.9	5.2
1973	5.2	5.1	5.0	5.0	4.9	4.8	4.7	4.6	4.6	4.6	4.7	4.8
1974	5.0	5.1	5.2	5.4	5.5	5.6	5.7	5.9	5.9	6.5	6.9	7.2
1975	7.2	7.0	6.8	6.7	6.6	6.5	6.4	6.2	7.2	8.2	9.8	10.6
1976	9.8	9.1	8.6	8.0	7.5	7.0	6.5	6.0	5.4	4.9	4.7	4.1
1977	3.7	2.9	3.1	3.3	3.4	3.7	3.9	4.1	4.2	4.4	4.6	4.7
1978	4.4	4.2	4.1	3.7	3.6	3.4	3.3	3.1	2.9	3.1	3.2	3.3
1979	3.3	3.4	3.2	3.0	2.8	2.7	2.4	2.3	2.1	2.0	1.7	1.6
1980	1.7	1.7	1.8	1.9	2.0	2.0	2.0	2.0	2.1	2.4	2.8	3.0
1981	2.7	2.5	2.2	2.0	1.7	1.5	1.2	1.2	1.2	1.5	1.7	2.0
1982	2.0	1.8	1.6	1.5	1.4	1.3	1.2	1.0	1.2	1.5	1.8	2.0

[a] Based on independent biomass estimates cited in Pauly, Palomares and Gayanilo (this vol.), with linear interpolation to obtain "monthly" values and backward extrapolation using standardized catch/effort data in Boerema et al. (1965) and Doucet and Einarsson (1967). *Caution:* Data in this table represent no more than educated guesses, presented here to allow replication of our results. See contribution cited above for improved estimates of monthly anchoveta biomass for 1953 to 1981.

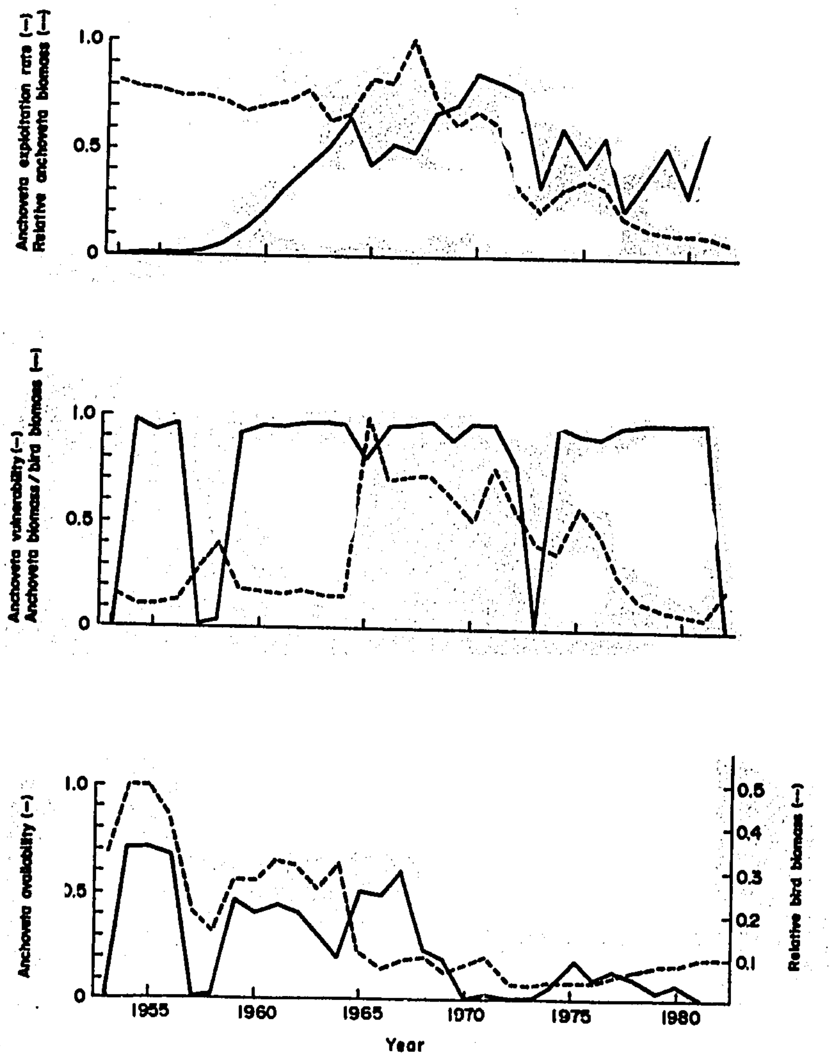

Fig. 5. Time series (annual means) of variables affecting the consumption of anchoveta by guano birds off Peru (4-14°S), 1953 to 1982 (see text for definitions and uses to which these variables were put).

Spatial overlapping and anchoveta dispersion are related to sea surface temperature. Increases in water temperature (e.g., through El Niño events) result in the dispersion of anchoveta (Furness 1982), their southward migration (Vogt 1942) and/or migration to deeper, cooler water (Schweigger 1940; Fiedler et al. 1943; Jordan and Fuentes 1966; Valdivia 1978; Johanneson and Vilchez 1980).

The data given in Table 1 on maximum foraging depth of the three bird species considered here shows that they are unable to forage at depths exceeding 15 cm. This diving capacity has evolved to correspond to the vertical distribution pattern of anchoveta school under normal conditions, for which estimates of 6-20 m, 10-30 m and 7-18 m have been presented by Clark (1954), Jordan (1967) and Guillen et al. (1969), respectively. However, during periods of high temperatures (i.e., El Niño events), anchoveta schools occur at depths of 100 m and more.

Therefore the vertical component "V_i" in equation (6) should be the most sensitive to temperature changes and therefore the key factor for vulnerability estimates.

Acoustic surveys of pelagic fishes (sardine, mackerel, horse mackerel) conducted off Peru in 1983-1984 by IMARPE were used here to establish a relationship between fish depth distribution, time of the day and temperature. The range of temperatures covered was 16-30°C, while the range of depth where fish concentrations were encountered was 5-120 m.

It was found that the three species mentioned above are concentrated, under normal temperature conditions (<23°C), at a mean depth of 15 m, slightly more than the anchoveta for which a value of 10 may be more appropriate (R. Vilchez, IMARPE, pers. comm.). From this information, we have derived an empirical equation relating the depth of main anchoveta biomass (DMB_i) to sea surface temperature, i.e.,

$$DMB_i = 15 + (107/(1 + e^{32.4-1.19T_i})) \qquad \ldots 7)$$

which provides estimates of DMB_i pertaining to the period from 6 a.m. to 10 p.m., i.e., during the main period of cormorant foraging activity (Jordan 1959).

The vertical overlapping index (V_i) for guano birds to anchoveta schools was calculated as dependent on the birds' maximum foraging depth (MFD) and DMB-values using the sigmoid function:

$$V_i = 1/(1+e^{p + q/MFD \cdot DMB_i}) \qquad \ldots 8)$$

For all three guano bird species, the same maximum foraging depth of 15 m has been used, ignoring the 2 m value reported for pelicans (Table 1) because one important foraging mode of pelican is piracy on the other two species (Duffy 1980) which enables pelicans to "extend" their low foraging depth by indirectly using the diving capacity of cormorants and boobies.

Using -18.5 for the constant "p" and 14.1 for "q" in equation (8), we obtained values of V_i close to 1 for a depth of 15 m and a rapid decline to zero for depths near and beyond 30 m.

The latter depth value was chosen because the average total extension (in the vertical plane) of pelagic schools is around 30 m, representing an approximately normal distribution with the density maximum in the center.

Thus, when the main concentration passes the 15 m threshold, a "tail" of around 15 m still remains within the birds' diving range, at least until the density maximum exceeds the 30 m depth.

With respect to temperature-related horizontal displacement (offshore and/or southward migration) and fish dispersion, a quantification is difficult because reliable data are not yet available.

In agreement with the literature cited above we assume that H_i and D_i of equation (6) decrease with increasing temperature. As a first attempt we set $H_i \times D_i = V_i$ resulting in:

$$Vul_{i,j} = V_{ij}^2 \qquad \ldots 9)$$

and using the same maximum foraging depth of 15 m for all the three seabird species:

$$Vul_i = V_i^2 \qquad \ldots 10)$$

Thus for example, an increase of surface temperature from 18 to 24°C causes a change of the preferred depth of anchoveta from 15 to 17.3 m which results in a decrease of V_i from 1 to 0.9 and, finally in a change of anchoveta vulnerability for guano birds from 1 to 0.8.

The use of mean monthly temperatures (see Table 2 in Pauly and Tsukayama, this vol.) is problematic because of the lack of information on within-month variability. This becomes important for the vulnerability estimates because a small change of 2 or 3 degrees centigrade causes drastic changes in the results.

Therefore, we have chosen to use two temperature values for each month, expressing the temperature range within month "i", for the vulnerability estimates.

Using an average within-month temperature deviation of + 15% we thus re-expressed, for example a mean value of 22°C as a range of 18.7-25.3°C and a mean of 21°C as a range of 17.9-24.2°C. Table 4 shows that vulnerability estimates differ considerably depending upon whether a single mean temperature or a temperature range is used.

All the vulnerability estimates cited have been calculated using the vulnerability means of the monthly temperature ranges.

Competition for anchoveta. Competition ($Comp_i$) is split into an intraspecific ($Icomp_i$) and a fishery-related component ($Fcomp_i$):

$$Comp_i = Icomp_i \cdot Fcomp_i \qquad \ldots 11)$$

Table 4. Relationships between sea surface temperature, depth of main anchoveta biomass (DMB), vertical overlap index between anchoveta and birds (V) and anchoveta vulnerability to the birds (Vul).[a]

	Temperature (°C)	Depth of anchoveta biomass (m)	Vertical overlap bird *vs* anchoveta (V)	Vulnerability of anchoveta (Vul)	Midrange of vulnerability estimates
Monthly mean	22.0	15.0	0.99	0.98	
% range	18.7	15.0	1.00	1.00	0.50
	25.3	24.8	0.01	0.00	
mean	21.0	15.0	1.00	1.00	
% range	17.9	15.0	1.00	1.00	0.76
	24.2	18.7	0.72	0.52	

[a] Note effect of using range instead of mean.

The product of both components varies between 1 (competition does not notably affect anchoveta consumption) and values close to zero (competition by fishery and/or the guano birds themselves drastically reduce anchoveta consumption per bird).

The simplest way to calculate "Fcomp" is to set it to zero when there is no anchoveta fishery (exploitation rate = 0) and to one respectively when the catch by the fishery is equal to the standing stock (exploitation rate = 1):

$$\text{Fcomp}_i = 1 - 0.011 \cdot \text{exploitation rate} \qquad \text{...12)}$$

We have used a multiplication factor of 0.011 instead of 0.010 resulting in Fcomp_i becoming close to zero when the exploitation rate by the fishery is less than 1. This takes into account the competition pressure of the other anchoveta predators which might become important when the anchoveta biomass is very low.

In view of our lack of knowledge of the mechanisms regulating seabird intraspecific competition, the concept applied here is a very crude one: we assume that competition between guano birds is high (Icomp = 0.7 in periods when seabird biomasses are high compared to that of anchoveta and becomes neligible (Icomp = 1) when the seabird biomass is very low compared to that of the anchoveta (Table 5).

Values of Icomp = 0.7 were thus used for the period between 1953 and 1956 when (i) the bird population sizes were highest and (ii) there was almost no fishery-induced disturbance and (iii) there were no temperature anomalies. During this period, the annual means of the ratio of the biomasses of the anchoveta and the birds (BA/BB) ranged between 340 and 550. The highest values occurred in 1965 (BA/BB = 3,200) and 1971 (BA/BB = 2,460).

Table 5. Assumed relationship between the ratio of anchoveta biomass to bird biomass (BA/BB) and the index of competition between individual guano birds (Icomp.); see text.

BA/BB	Icomp.
0- 499	0.70[a]
500- 999	0.75
1,000-1,499	0.80
1,500-1,999	0.85
2,000-2,499	0.90
2,500-∞	0.95-1

[a]This value corresponds to a bird population growth rate of about zero in undisturbed system.

A minimum value of Icomp = 0.7 was chosen because this corresponds to approximately zero population growth in an undisturbed system. Equation (2) gives the total consumption necessary for an approximately zero population growth. For the period 1954, 1955, 1956 the calculated annual means are: 2.5, 2.5 and 2.1 t x 10^6. For the same period (using: Icomp = 0.7) anchoveta consumption values of 2.1, 2.0 and 1.7 t x 10^6 were calculated. According to Jordan (1967) the non-anchoveta food in total seabird diet in 1955 ranged from 5 to 20%. Thus, adding a value of 20% to the annual anchoveta consumption we calculate for 1954, 1955, 1956 an annual total consumption of 2.5, 2.4 and 2.0 t x 10^6 and this is almost identical to the amounts needed for zero population growth.

Fig. 6 shows the flowchart of the computer program used for the anchoveta consumption estimates with emphasis on the dynamics of the variables controlling anchoveta consumption by guano birds between 1953 1982, notably relative anchoveta biomass, anchoveta exploitation rate, anchoveta biomass/bird biomass and the vulnerability and availabillity indices.

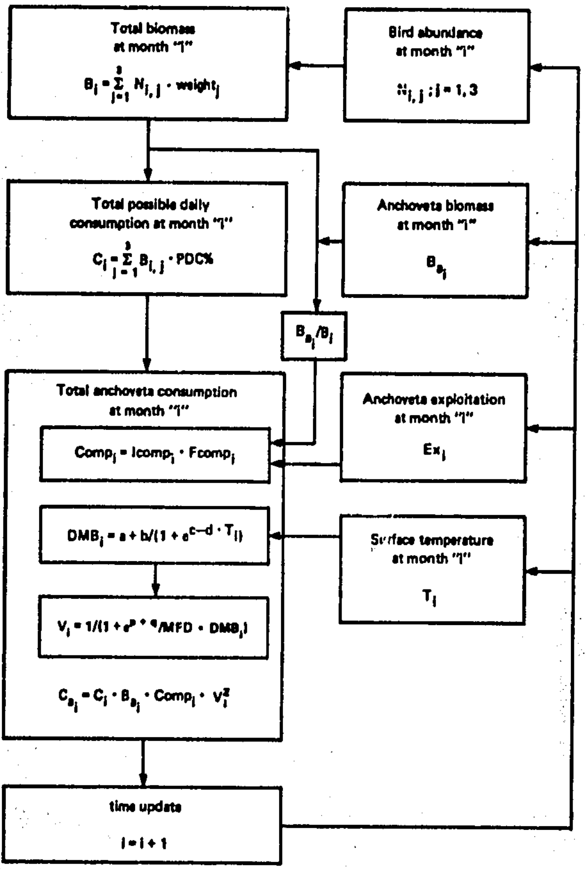

Fig. 6. Flowchart of the FORTRAN program used to estimate anchoveta consumption by cormorants, boobies and pelicans off Peru; month = i; bird species = j (see also text).

Results and Discussion

Monthly anchoveta consumption estimates are given in Tables 6, 7 and 8 for cormorants, boobies and pelicans respectively. Fig. 7 shows total annual anchoveta consumption for all three guano bird species, as well as their total annual possible consumption. Anchoveta consumption by guano birds was maximum between 1953 and 1956 (1.3-2.1 t x 10^6) and declined continuously to less than 20,000 t at the beginning of the 1970s.

Comparing annual anchoveta catch by the fishery with the relative anchoveta consumption by guano birds, we note that these values vary beween 1953 and 1982 by a factor of 50 (Fig. 8):

Table 6. Monthly anchoveta consumption by cormorants *(Phalacrocorax bougainvillii)* off Peru (4-14°S), 1953 to 1982 (in t x 10^3).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	86.4	100.2	.0	62.2	75.1	119.8	79.6	63.2	93.5	104.7	174.8	135.0
1954	86.8	113.9	106.0	163.9	202.3	231.3	163.5	128.7	149.2	147.5	205.2	102.9
1955	74.5	121.4	90.8	133.0	171.1	212.8	171.1	157.6	164.5	134.2	158.3	102.5
1956	63.2	84.0	111.6	166.4	149.3	179.7	150.7	106.2	112.2	129.1	121.2	83.2
1957	95.6	.5	4.1	22.3	1.0	56.0	30.2	15.9	50.8	104.8	124.3	61.0
1958	7.2	.6	6.2	51.7	65.9	48.3	6.5	42.5	53.5	66.1	55.4	37.6
1959	24.4	24.3	65.8	79.0	75.5	89.4	87.9	39.6	38.3	52.2	70.4	69.5
1960	63.9	51.1	62.4	60.0	58.9	75.8	58.2	32.3	38.4	27.9	65.6	61.0
1961	39.2	49.4	44.0	46.2	54.3	66.1	67.8	70.8	52.9	63.7	78.3	61.4
1962	26.6	36.7	43.2	50.6	62.2	36.2	62.6	51.6	49.2	41.9	48.4	42.6
1963	34.7	33.2	23.6	32.6	46.4	22.3	21.1	22.3	19.0	32.6	33.4	27.5
1964	19.3	15.4	22.9	16.8	37.3	28.5	21.2	17.7	19.7	22.4	18.4	15.4
1965	32.5	23.3	34.6	22.1	11.9	20.3	14.5	4.7	2.2	6.5	13.3	10.4
1966	12.4	10.6	7.7	11.6	6.0	8.2	8.3	12.1	14.0	7.8	5.3	5.9
1967	7.7	7.0	12.2	12.1	23.6	19.5	15.2	23.0	26.4	16.1	11.1	9.6
1968	6.3	6.3	4.8	6.2	7.1	7.5	6.8	7.9	6.1	4.0	4.4	3.9
1969	3.2	3.1	2.5	2.4	1.9	1.2	1.9	3.1	5.2	3.6	4.4	3.3
1970	.6	.6	.8	.7	.7	1.1	1.3	1.2	.8	.7	.5	.6
1971	1.2	1.2	1.2	1.9	1.9	2.5	2.3	2.2	1.5	1.7	1.1	.9
1972	1.3	1.6	.6	.2	.2	.1	.1	.0	.0	.3	.4	.1
1973	.0	.0	.9	1.1	1.5	1.7	1.5	.9	.8	.4	.6	.7
1974	.3	.5	.6	.5	.6	1.0	1.3	1.4	.6	.6	.6	.8
1975	.9	1.2	1.4	1.6	2.1	1.9	2.8	2.2	2.3	3.1	2.9	2.6
1976	1.1	1.0	1.6	1.6	1.3	1.2	1.1	1.1	1.1	.7	.6	.7
1977	1.4	1.1	.8	1.1	1.3	1.8	1.9	2.2	1.8	1.7	2.0	1.8
1978	1.0	.8	1.0	1.3	1.1	1.4	.9	1.2	.7	.9	.8	.8
1979	.7	1.4	.9	1.5	1.3	1.0	.9	.7	.6	.5	.4	.4
1980	.7	.6	.9	1.2	1.3	1.4	1.5	1.4	1.4	1.5	1.7	2.5
1981	.8	.8	.6	.5	.8	.5	.4	.4	.3	.5	.6	.7
1982	.5	.5	.4	.6	.4	.8	.7	.5	.5	.7	.1	.0

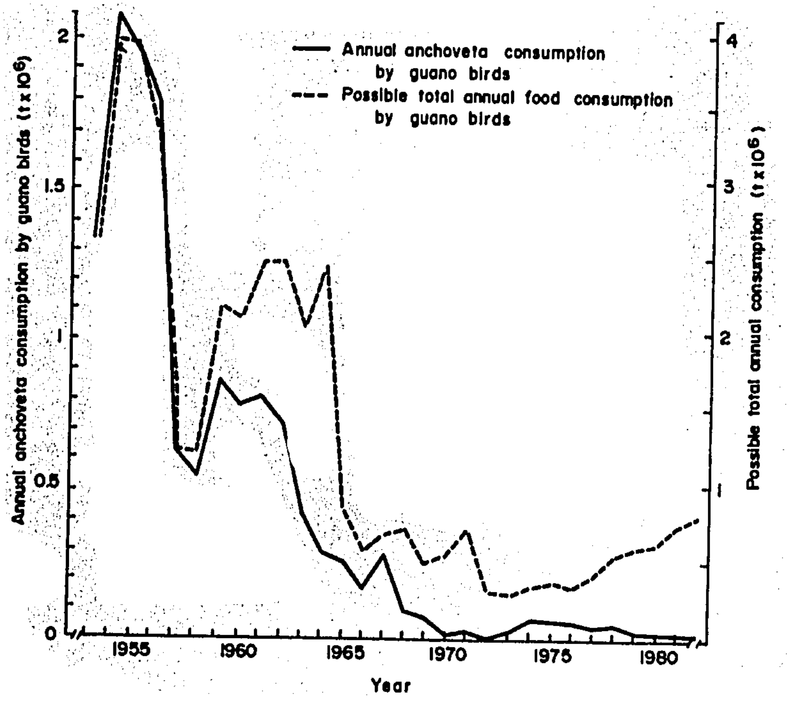

Fig. 7. Annual anchoveta and total possible food consumption by guano birds off Peru (4-14°S), 1953 to 1982. Note that anchoveta represented, in the mid-1950s about half of total possible consumption, a fraction much reduced in the following period.

Table 7. Monthly anchoveta consumption by boobies *(Sula variegata)* off Peru (4-14°S), 1953 to 1982 (in t x 10^3).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	14.1	15.3	.0	10.3	8.7	9.3	4.9	5.7	10.3	12.5	21.6	15.3
1954	10.1	12.4	12.0	13.3	12.6	16.6	11.1	8.6	11.5	16.1	19.8	20.4
1955	11.0	16.6	18.2	17.2	15.2	14.0	11.9	8.5	13.4	13.3	19.1	18.7
1956	13.7	14.7	15.9	14.7	9.9	12.7	12.4	6.9	10.4	17.9	31.9	21.4
1957	12.1	.1	.5	2.2	.0	.9	1.2	2.7	6.6	9.7	7.2	5.0
1958	1.3	.1	.9	7.1	14.3	6.9	2.8	3.5	4.3	9.1	10.5	8.8
1959	5.3	6.2	8.3	5.3	5.3	4.5	4.7	3.3	3.2	9.4	10.6	11.1
1960	8.9	6.0	4.7	6.7	5.4	7.3	5.2	6.6	6.7	5.6	8.9	9.5
1961	7.4	6.2	4.1	6.6	5.2	6.8	3.9	4.0	4.5	8.3	10.5	9.3
1962	5.0	6.6	5.3	5.1	6.3	5.0	3.3	3.4	5.9	10.1	9.1	11.5
1963	7.2	3.7	2.3	3.0	2.8	2.4	2.6	2.7	1.9	4.0	5.5	3.8
1964	2.7	3.2	2.1	2.2	1.8	2.0	2.4	1.3	2.5	2.9	3.9	3.4
1965	9.3	7.2	5.1	1.2	1.6	1.5	1.1	.8	2.2	3.5	3.6	8.1
1966	3.9	3.0	4.4	5.1	5.2	3.6	2.9	2.8	2.9	2.0	2.7	3.2
1967	3.9	4.2	3.9	5.0	2.8	4.1	6.5	6.1	3.7	3.2	4.4	6.5
1968	3.0	2.1	1.3	1.4	1.1	1.4	1.5	1.9	1.8	1.7	2.2	2.2
1969	2.3	2.0	2.2	1.4	1.4	1.2	1.7	1.1	.9	1.1	1.0	2.1
1970	.5	.5	.4	.3	.4	.4	.4	.3	.3	.4	.4	.4
1971	1.1	.6	.7	.6	.8	.8	.5	.6	.6	.5	.5	.5
1972	.9	.6	.1	.1	.1	.1	.1	.1	.1	.1	.2	.2
1973	.0	.0	.9	1.0	1.0	.9	.8	.9	1.0	1.2	1.4	1.4
1974	.9	1.0	.7	1.1	.7	.8	1.1	1.1	1.1	1.1	1.1	1.1
1975	2.6	2.2	2.3	1.9	1.5	2.3	1.3	1.3	2.0	2.6	2.8	4.1
1976	3.2	2.6	1.5	1.0	.8	1.2	1.0	1.0	1.0	1.1	.8	.9
1977	1.8	1.4	1.5	1.8	1.2	1.3	1.0	1.0	1.3	2.0	3.0	2.4
1978	1.7	1.9	2.1	1.6	2.1	1.5	1.4	1.5	1.4	1.7	1.5	1.2
1979	1.0	1.1	.8	.6	.6	.8	.5	.6	.6	.5	.5	.4
1980	.6	.7	.7	.8	.6	.8	.8	.8	.9	1.0	1.4	1.2
1981	.4	.4	.4	.5	.3	.3	.2	.2	.2	.3	.3	.3
1982	.3	.4	.3	.2	.3	.3	.2	.2	.1	.1	.1	0.0

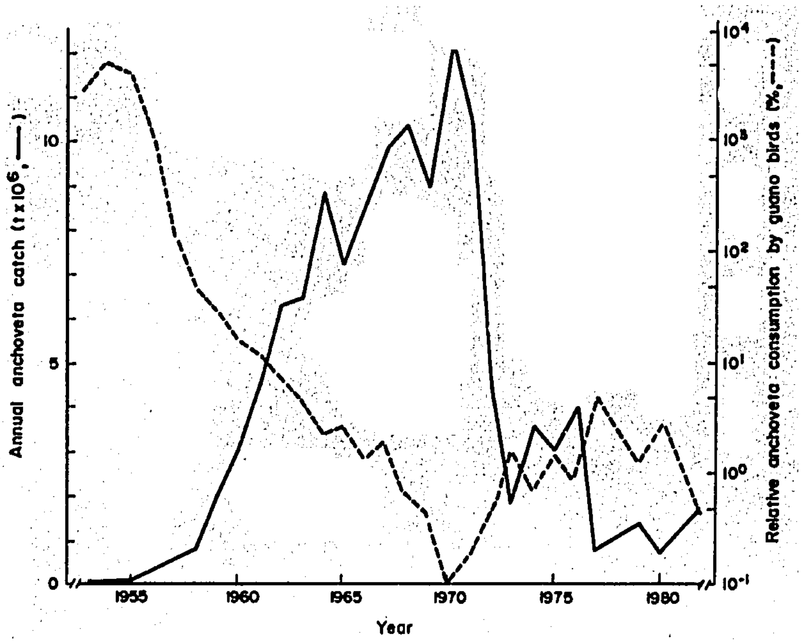

Fig. 8. Annual anchoveta catch by the fishery, compared with the relative anchoveta consumption by guano birds off Peru (4-14°S), 1953 to 1982. Note that the birds, which at first consumed approximately 5,000% of the fishery catch ended up consuming 0.1% at the end of 1969/early 1979, then reached an average of about 3% between 1970 and 1982.

Table 8. Monthly anchoveta consumption by pelicans *(Pelecanus thagus)* off Peru (4-14°S), 1953 to 1982 (in t x 10^3).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	4.1	8.1	.0	1.9	1.9	1.5	1.1	.7	.8	5.1	12.4	9.0
1954	5.7	9.1	8.3	6.1	5.7	4.6	3.0	2.5	2.0	3.8	6.2	7.1
1955	4.7	8.2	15.8	9.0	2.2	1.0	1.0	1.0	3.5	4.8	12.2	8.0
1956	7.1	14.3	8.2	3.5	6.7	4.4	1.2	.8	.6	1.5	5.0	5.0
1957	3.6	.0	.1	.1	.0	.9	.4	.2	1.4	1.9	2.8	2.6
1958	.5	.0	.2	3.2	3.3	3.0	2.0	1.3	3.2	2.8	3.2	2.4
1959	2.2	4.4	3.2	7.6	6.4	3.4	1.1	2.1	1.8	3.4	3.3	6.8
1960	4.4	2.8	1.0	3.0	3.1	3.3	4.1	2.9	2.6	1.8	3.3	2.2
1961	1.9	1.9	1.4	1.7	3.3	3.1	.7	.6	1.5	3.3	3.1	3.1
1962	2.1	2.1	1.7	1.1	1.4	.6	.5	.6	1.3	2.3	3.4	2.8
1963	1.8	2.1	2.0	3.2	1.8	.8	.6	.5	.3	.3	.3	.8
1964	.5	.8	1.0	.3	.6	.1	.3	.2	.3	.3	1.1	1.9
1965	5.0	2.6	3.4	3.5	3.6	1.5	.7	.5	.4	.8	1.5	1.5
1966	2.1	.7	1.1	1.1	1.6	1.1	.9	.8	1.5	2.0	1.2	1.9
1967	3.6	3.2	3.8	3.5	5.3	1.2	1.3	2.7	6.4	2.0	1.2	1.4
1968	2.0	1.4	1.6	.8	.9	.5	.6	.9	1.0	.7	.8	.9
1969	.6	.5	.6	.4	.2	.3	.2	.4	.3	.3	.5	.5
1970	.1	.1	.1	.2	.1	.1	.1	.1	.1	.2	.1	.1
1971	.1	.1	.1	.2	.2	.3	.7	.2	.1	.2	.1	.1
1972	.2	.2	.1	.1	.1	.1	.1	.1	.1	.1	.1	.1
1973	.0	.0	.4	1.0	.3	.3	.5	.3	.3	.5	.7	.5
1974	.4	.4	.5	.2	.3	.1	.1	.1	.4	.7	.5	.2
1975	.3	.7	.4	.4	.3	.1	.2	.1	.3	.2	.2	.4
1976	.2	.4	.4	.6	.2	.2	.1	.1	.1	.1	.2	.1
1977	.2	.3	.2	.2	.2	.1	.1	.3	.2	.3	.3	.8
1978	.5	.4	.9	.7	.5	.4	.2	.2	.3	.2	.3	.3
1979	.3	.4	.2	.2	.2	.2	.1	.2	.2	.2	.2	.1
1980	.1	.1	.2	.2	.3	.2	.1	.1	.2	.2	.3	.4
1981	.1	.1	.0	.1	.1	.1	.0	.0	.0	.1	.1	.1
1982	.1	.0	.0	.0	.1	.1	.0	.0	.0	.1	.0	.0

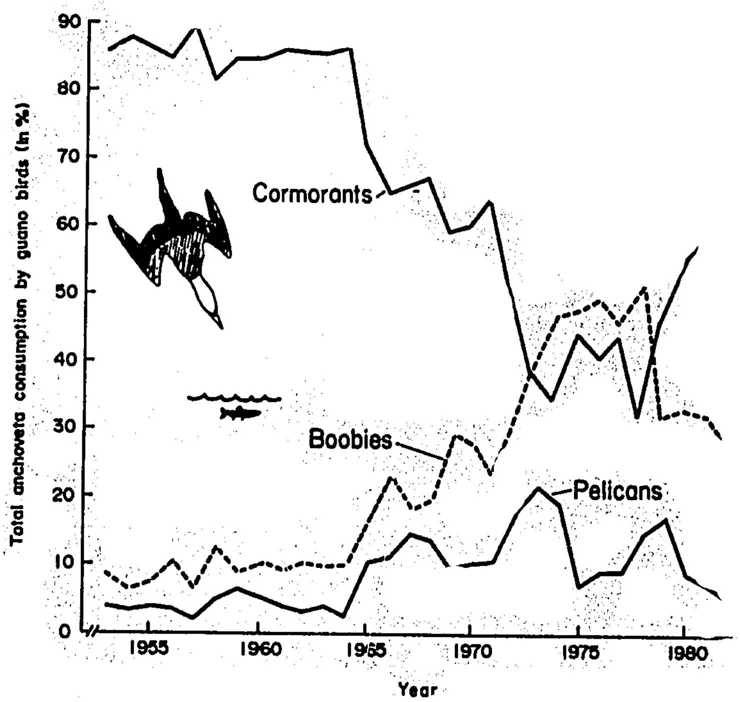

Fig. 9. Changes in the relative importance of anchoveta consumption by the three major bird species in the Peruvian upwelling ecosystem, 1953 to 1982.

before 1960 the annual guano consumption declined from 5,000% to 45% of the annual anchoveta catch. Between 1960 and 1970 the percentage dropped to 0.1% then reached an average of around 3% between 1970 and 1982 (Fig. 8).

The dynamics of seabird biomass between 1953 and 1964 correspond widely to the anchoveta availability curve (Fig. 5) and suggests a direct dependency.

The sudden population breakdown in 1957-1958 and the following recovery is accompanied by similar changes in anchoveta availability caused by extremely low anchoveta vulnerability during the 1956-1957 El Niño (Fig. 5), while between 1965 and 1967 and from 1977 to 1982 the trends of bird biomass and anchoveta availability were opposite.

Comparing species specific seabird consumption to total anchoveta consumption between 1953 and 1983 the following dynamics are established (Fig. 8): between 1953 and 1972 the dominant species are cormorants (*Phalacrocorax bougainvilli*), with between 50 and 90% of the total anchoveta consumption, while boobies (*Sula variegata*) consumed 10 to 40% and pelicans (*Pelecanus occidentalis*) 5 to 20%.

Between 1972 and 1979 a shift in dominance occurred from cormorants to boobies: during this period around half of the total anchoveta consumption was taken by boobies, around 40% by cormorants and around 10% by pelicans. As might be seen in Fig. 9, from 1979 on, the dominance pattern prevailing before 1972 was re-established, with cormorants taking 65%, boobies 30% and pelicans 5% of all anchoveta eaten by guano birds.

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Sea Lion and Fur Seal Predation on the Peruvian Anchoveta, 1953 to 1982*

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MUCK, P. and H. FUENTES. 1987. Sea lion and fur seal predation on the Peruvian anchoveta, 1953 to 1982, p. 234-247. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

The importance of the predation of the fur seal (*Arctocephalus australis*) and sea lion (*Otaria flavescens*) on fish, particularly on anchoveta (*Engraulis ringens* J.) from 1953-1982 for the area from 4 to 14°S along the Peruvian coast was examined.

Based on a population growth and consumption model, both pinniped species were estimated to have a maximum annual total consumption of fish of about 35,000-59,000 tonnes (t) in 1982. At its peak in 1967 annual pinniped anchoveta consumption was 10,000-17,000 t and only 3,000-5,000 t between 1968 and 1982. These values are negligible compared with the impact of the guano birds and of the fishery.

The population growth of Peruvian pinnipeds did not seem to have been affected by the breakdown of the anchoveta biomass in the early 1970s.

Introduction

A key element for understanding the fluctuations of resource species observed in the Peruvian upwelling system is the analysis of predation and its dynamics during the last decades.

In addition to fishes and guano birds, marine mammals especially pinnipeds, may be considered to have an impact on pelagic fish, particularly anchoveta, as suggested by Laevastu and Favorite (1980), who calculated that the herring consumption by mammals is about ten times the commercial catch in the Bering Sea.

The objective of this paper is to give an estimate of fish consumption by the Peruvian sea lion *(Otaria flavescens)* and fur seal *(Arctocephalus australis)* with special emphasis to their consumption of anchoveta (*Engraulis ringens*). Throughout this paper, it is assumed that the anchoveta consumed by seals off Peru have a size distribution roughly similar to those caught by the purse seine fishery (Fig. 1).

Materials and Methods

The Abundance Model

The sea lion and fur seal populations are estimated using a population model which calculates in monthly intervals the abundance of 5 age groups (0-1 year, 1-2 years, 2-3 years, 3-4 years, >4 years), and in which population growth is assumed to be influenced by El Niño events

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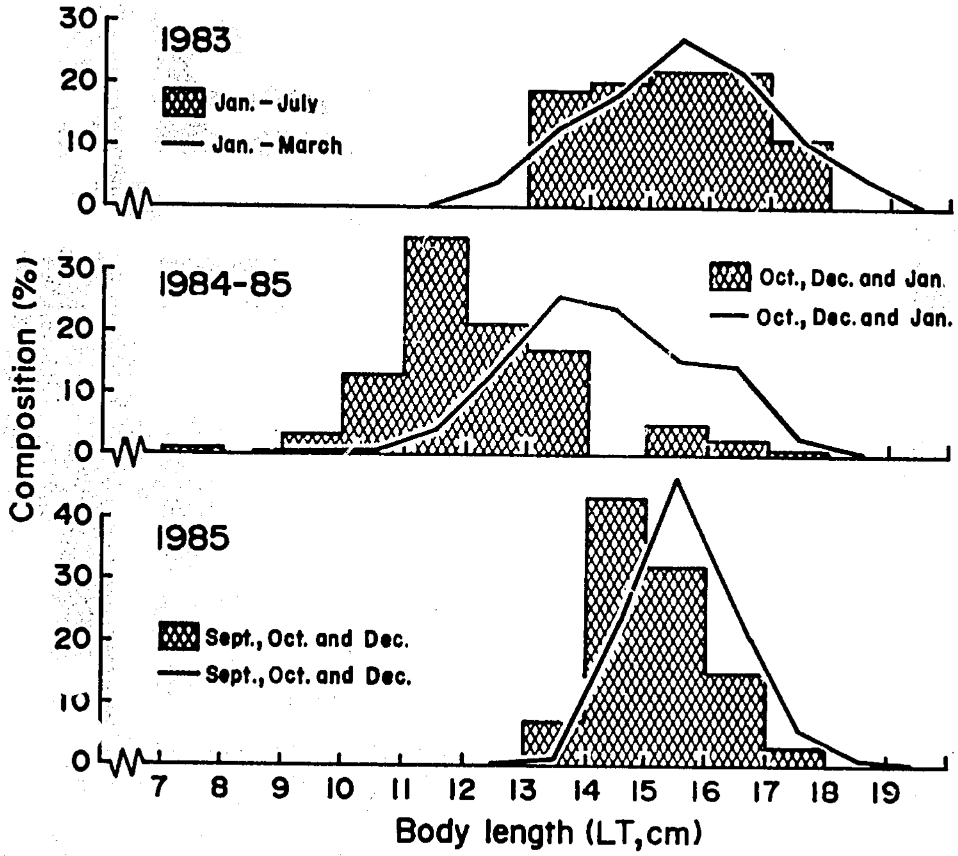


Fig. 1. Size-frequency distribution of anchoveta eaten by fur seal *(Actocephalus australis)* (shaded histograms) as reconstructed from otoliths recovered from scats (Majluf 1986 and pers. comm.), compared with the fishery catch size distribution in a comparable period (solid line, unpublished IMARPE data). Note rough correspondence in 1983 and late 1985 and shift toward smaller sizes in 1984, early 1985.

because these warm water periods seem to be critical for (i) the survival of the newborn, (ii) the mortality of juveniles and adults and (iii) the reproductive success of the adult females (Table 1, Fig. 2).

Majluf (1984, 1985) and Tovar and Fuentes (1984) registered extremely high pup mortality during the 1982-1983 El Niño with near zero survival of the generation born between October 1982 and March 1983 and with juvenile and adult mortalities higher than in normal years. Studies of fur seal behavior (Majluf 1985) have shown that the high mortality of the suckling pups is probably caused by starvation because the females are longer absent (searching for food), during El Niño events, than under normal environmental conditions and/or produce less milk.

P. Majluf (pers. comm.) suggests that under such conditions, the average number of births per female fur seal is less than one per year and that this lack of reproductive success is probably related to the low level of food available to the adult females.

This agrees with results of Tovar and Fuentes (1984) suggesting depressed reproduction of fur seal in the season immediately succeeding the 1982-1983 El Niño.

Census data collected before and after the 1982-1983 El Niño suggest strong differences in the reproduction of sea lion and fur seals to El Niño events (Table 2).

However, it is probably the combined effect of (i) low food availability, (ii) long foraging trips and (iii) metabolic stress because of abnormal, high environmental temperatures which affects pinniped mortality and reproduction during El Niño periods.

Food availability to the seal and thus duration of their foraging trips are dependent on sea temperature because rises in water temperature (El Niño) result in the dispersion of their pelagic fish food (Furness 1982), in their southward migration (Vogt 1942) and/or their migration to deeper, cooler water (Schweigger 1940; Fiedler et al. 1943; Jordan and Fuentes 1966; Valdivia 1978, 1980; Johanneson and Vilchez 1980).

Table 1. Initial data set and constants used in pinniped population and anchoveta consumption model.

Characteristic		Fur seal	Sea lion
Initial population size (Jan. 1953)	0-0.9 year	45	876
	1-1.9 year	273	1,153
	2-2.9 year	213	902
	3-3.9 year	166	702
	>4 year	510	2,156
Natural monthly mortality rate (M_B)		0.0115	0.0170
Sex ratio (SR)		0.80	0.82
Constants for the calculation of reproductice success (RS) and temperature related mortality (M_T):	a	0.95	0.20
	b	33.0	33.0
	c	1.3	1.3
Anchovy availability index (IA):	d	-18.2	-18.2
	f	14.1	14.1
Weighting factor for monthly reproduction intensity (W_i)			
month:	I	0.45	0.05
	II	0.45	0.00
	III	0.05	0.00
	IV-IX	0.00	0.00
	X	0.00	0.05
	XI	0.00	0.45
	XII	0.05	0.45

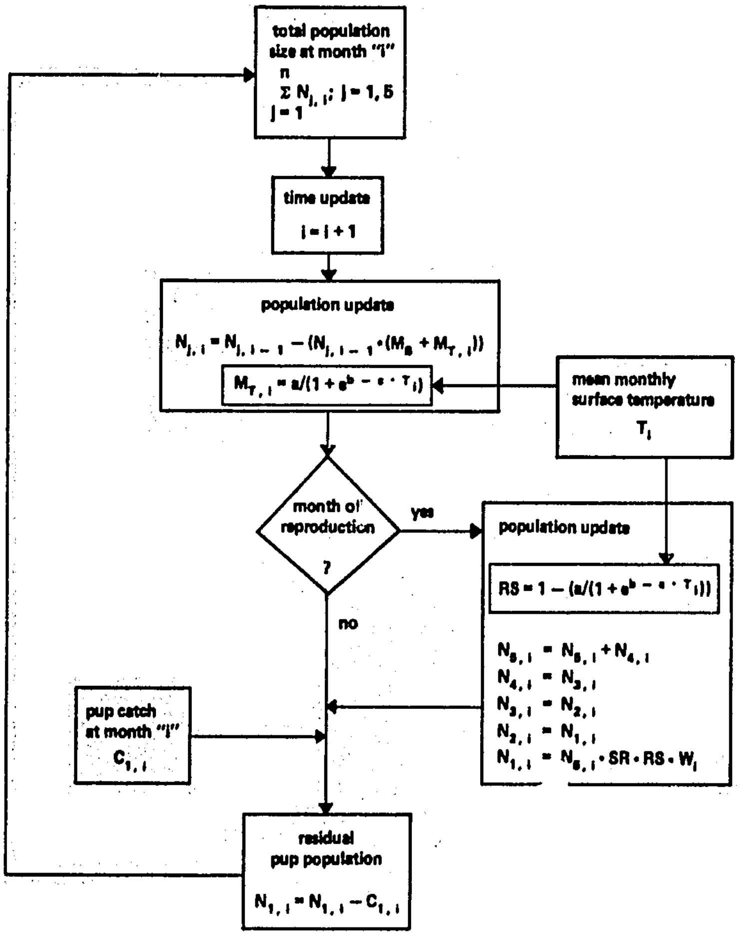


Fig. 2. Flowchart of model used to estimate population sizes of fur seals and sea lions off Peru (see also Table 1 and text).

Table 2. Differences in the impact of the 1982-1983 El Niño on fur seal and sea lion populations.

Census data	Population estimate Fur seal	 Sea lion
April-May 1979	20,455	25,055
March 1984	15,369	33,861
difference	-25%	+ 35%

Although the use of sea temperature seems to be an adequate concept for the modification of biological rates by El Niño conditions, its application to the population growth of Peruvian fur seals and sea lions is difficult because of the complex character of temperature-mediated mechanisms.

Modelling was done as follows:

Mortality and reproductive success are described empirically as functions of surface temperature. Thus mortality has been split into a basic term (M_B) and a temperature related one (M_T), i.e.,

$$M = M_B + M_T \qquad \ldots 1)$$

Similarly, annual reproductive success (RS) is set to 1 under normal conditions and becomes reduced by a temperature related term (X_T):

$$RS = 1 - X_T \qquad \ldots 2)$$

M_T and X_T are zero for temperatures less than $20^{o}C$ (= mean maximum sea surface temperature in March, 30-year average. For the mathematical description of M_T and X_T, we have used a sigmoid function, in agreement with the general theory of biological response curves:

$$M_T, X_T = a/(1+e^{b-cT}) \qquad \ldots 3)$$

The constants a, b and c were estimated empirically by fitting the calculated results of population growth to field data (see below). The temperature related mortality effect on pups was assumed to be three times higher than on juveniles and adults.

The number of newborn pups for the month "i" is calculated by:

$$N_{pup,i} = N_{4+,i} \cdot SR \cdot RS \cdot W_i \qquad \ldots 4)$$

where "$N_{4+,i}$" is the total number of adults (i.e., animals of 4 years and more (Piazza 1959)) for month "i", "SR" the sex ratio, "RS" the annual reproductive success and "W_i" is a weighting factor for the reproduction intensity in the month "i". W_i is set at zero for all months without reproduction and reaches a cumulative value of 1 between December and March in sea lion and October and December in fur seal (see Table 1).

Fig. 2 shows the flowchart of the program used for the monthly calculation of the five fur seal and sea lion age groups. Table 1 gives the constants and initial values used for the computation and Fig. 3 shows a comparison between field and model data.

The field data are based on census conducted between 1961 and 1984 by different private and state organizations authorized by the Peruvian Government. Most of the census were done during the reproductive season when the main part of the population is terrestrial. The fraction of juveniles and adults in the sea was estimated visually by seaborn teams.

The authors participated in the last two of these population census which, while not being well standardized, tend to reflect the trend of pinniped populations off Peru.

There are no direct estimates of population size before 1961. Piazza (1959) mentioned that one single company killed 36,500 individuals (88% pups) between December 1941 and March

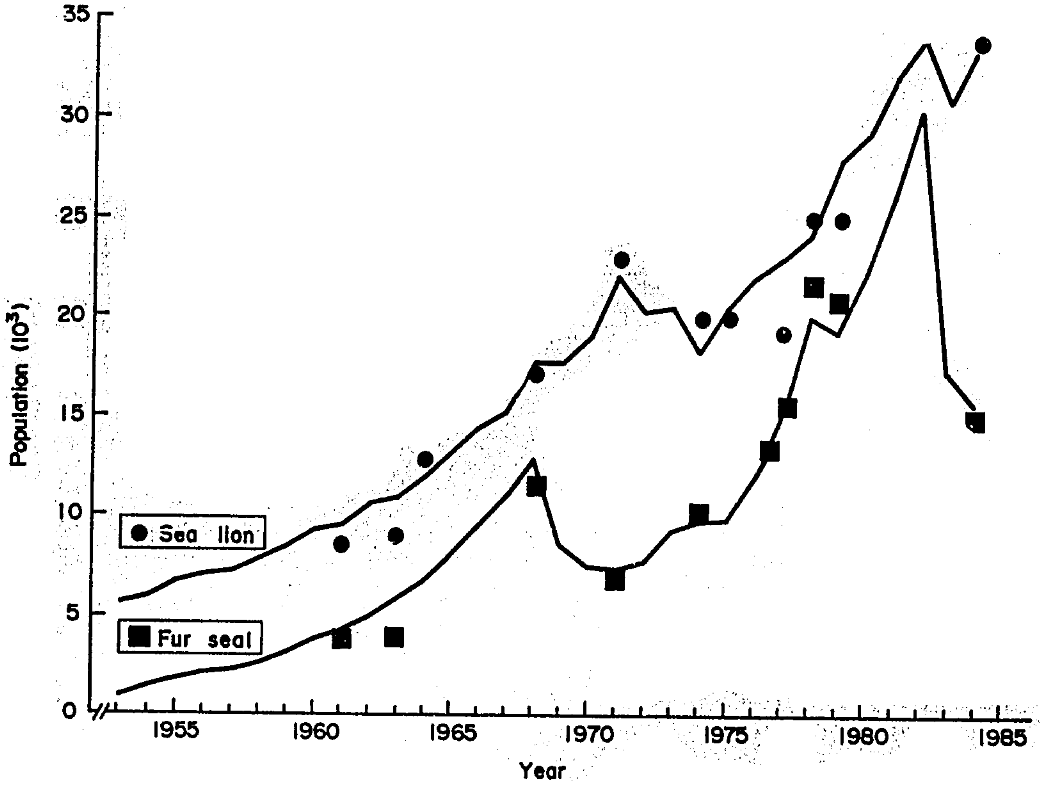


Fig. 3. Population changes of fur seal and sea lion off Peru (4-14°S); dots and squares are census estimates, used to calibrate parameters of population growth model (see Table 1).

1942, and Walker (1975) gives annual values of total catches of up to 75,000 individuals for the years before 1942.

Majluf (1980) assumes a total population size of both species of between 400,000 and 500,000 individuals for 1940. When compared with the 12,500 individuals estimated in 1961 or the 49,200 estimated in the 1984 census, these figures, however crude, nevertheless give vivid impression of the extent of the population collapse due to overexploitation during the first half of this century. In 1946 the Peruvian Government initiated first preventive measures by restricting the harvest season to 4 months per year and since 1950 (fur seal) and 1956 (sea lion), except for the period 1971-1975, harvesting is totally prohibited.

For the present calculations we assume that both species had their lowest population size during the first half of the 1950s.

We do not believe in zero catches during the years with harvest prohibition, because there is information that even the persons responsible for the protection of the fur seal and sea lion colonies traded in pelts, mainly those of pups. For our model, we assumed that an average of 10% of each pup generation dies of unnatural causes.

The causes of the decrease (-40%) in population size of fur seals between the census of March 1968 (11,800 individuals) and May 1971 (7,250) are difficult to identify. A possible reason could be the combined effect of (i) increasing mortality due to food shortage (intensified by abnormal sea temperatures) and (ii) high pup mortality by harvest: positive temperature anomalies occurred in 1969 (May: +2.5°C). The harvest prohibition for pups was suspended in 1971, and the anchoveta biomass as an important food resource for pinnipeds was reduced from 21 t x 10^6 in 1967 to only 12 t x 10^6 in 1971 (annual means, see Table 3 in Muck and Pauly, this vol.).

Assuming that population growth is regulated mainly by survival of the newborns, we have adjusted the population curve to the field results of this period by gradually increasing the monthly pup mortality rate of fur seals between April 1968 and February 1971.

Table 3. Mean length, mean weight and mean daily ration of sea lion and fur seal age groups (see text for sources).

Age (years)	Sea lion Males length (cm)	Weight (kg)	Daily ration (% body weight)	Females length (cm)	Weight (kg)	Daily ration (% body weight)	Fur seal Males & length (cm)	Females weight (kg)	Daily ration (% body weight)
0-0.9	110	31	11	102	26	11	102	21	12
1-1.9	146	68	9	127	45	10	127	39	10
2-2.9	168	100	8	142	60	9	142	54	9
3-3.9	184	129	7	152	72	9	152	65	9
4 +	219	208	7	176	104	8	176	100	8

To convert sea lion abundance into biomass the following equations based on length *vs.* age data in Vaz-Ferreira (1982), have been used:

males : length = $68.18 \times \text{age}^{0.27}$ ...5)
females : length = $70.43 \times \text{age}^{0.21}$ ...6)
males : weight = $0.000079 \times \text{length}^{2.74}$ ...7)
females : weight = $0.000209 \times \text{length}^{2.54}$ ...8)

where the weight is given in kg, the total body length in cm and the age in months. For fur seals, the length/weight equation given in Ximenez et al. (1984) was used. Since these authors did not find any difference between males and females, a common equation has been applied to both. For the length/age relationship, we have used the same equation as for sea lion females because no data for fur seal were available:

males & females:length = $70.43 \cdot \text{age}^{0.21}$ ... 9)
males & females:weight = $0.000034 \cdot \text{length}^{2.88}$ ...10)

The Consumption Model

This model follows the approach described in Muck and Pauly (this vol.) for the consumption of anchoveta by guano birds. Monthly total possible consumption (C_i) is defined by:

$$C_i = B_i \cdot PMC\% \qquad ...11)$$

where "B_i" is the predator biomass for the month "i" and "PMC%" the possible monthly consumption in percent of body weight. For the estimation of "PMC%" we have used the formula given in Perez and Mooney (1984) calculated from data reported by Bigg et al. (1978) on feeding rates of captive adult fur seal females:

$$MJ = 1.571 \cdot W^{0.75} \qquad ...12)$$

where "MJ" is the daily energy consumption in megajoules and "W" the seal's body weight in kg (Table 3). To convert energy consumption in % of body weight, the estimates given in Antonelis and Perez (1984) for the relationship mj/kg of northern fur seal diet (75% fish, 25% squid) have been used. The average of 28 monthly samples is 1 kg = 6.31 mj, s.d. = 0.85.

Therefore the total possible monthly consumption in % of body weight is given by:

$$PMC\% = 747.0 \cdot W^{-0.25} \qquad ...13)$$

The monthly anchoveta consumption (C_{ai}) can be described as:

$$C_{ai} = C_i \cdot A_i \qquad ...14)$$

where "A_i" is the relative anchoveta availability to pinnipeds at month "i" (>0, <1) equivalent to the product of relative anchoveta biomass (B_{ai}, >0, <1), anchoveta vulnerability (Vul_i, >0, <1) and an element ($Comp_i$) expressing competition for anchoveta by other predators, i.e.:

$$A_i = B_{ai} \cdot Vul_i \cdot Comp_i \qquad \text{...15)}$$

The relative anchoveta biomass at month "i" has been calculated using the preliminary anchovy biomass values in Muck and Pauly (this vol.) divided by the highest annual mean (20.8 t x 10^6 in 1967). Anchoveta vulnerability has been treated as a distribution problem between predator and prey which is most probably controlled by the temperature-related migratory behavior of pelagic fish schools. Thus, vulnerability can be split into a spatial overlapping index with a vertical (V_i) and a horizontal (H_i) component, and a dispersion index (D_i):

$$Vul_i = V_i \cdot H_i \cdot D_i \qquad \text{...16)}$$

The diving capacity of pinnipeds is much higher than that of seabirds (Kooyman et al. 1981, 1982). Majluf (1985) reports a mean foraging depth of 20-40 m and maximum values of around 100 m for fur seals.

Thus, using an average of 50 m as a first approximation for the "critical depth" for both species, equation (8) in Muck and Pauly (this vol.), can be used to calculate the vertical overlapping index "V_i" for predator (pinniped) and prey (anchoveta):

$$V_i = 1/(1 + e^{-18.5 + 14.1/50\ DMB_i}) \qquad \text{...17)}$$

where "DMB_i" gives the (temperature-dependent) mean depth at which the main anchoveta biomass is concentrated.

Horizontal displacements (offshore and/or southward migrations) and fish dispersion, in addition to sea temperature-related changes in vertical overlapping between predator and prey, will also reduce anchoveta vulnerability for pinnipeds (Majluf 1985). We use as a first approximation H_i x $D_i = V_i$, resulting in:

$$Vul_i = V_i^2 \qquad \text{...18)}$$

Table 4 gives calculated estimates of V and Vul for different DMB-values.

With respect to the temperature used for the computation of DMB, the same technique as described in Muck and Pauly (this vol.) has been used: a mean DMB-value for month "i" was calculated using the minimum and the maximum temperature values which result from expressing the monthly mean temperatures as a +/- 15% range (see Table 4 in Muck and Pauly, this vol.); an application example of this approach is given here as Table 5.

Between 1959 and 1982, anchoveta exploitation by the fishery was probably the dominant component of "competition" affecting the anchoveta availability for all anchoveta-feeding species.

Thus, as a first attempt to estimate the influence of competition on anchoveta availability for Peruvian pinnipeds we use the anchoveta exploitation rate by the fishery ($Expl_i$) as defined in Muck and Pauly (this vol.):

$$Comp_i = 1 - 0.011 \cdot Expl_i \qquad \text{...19)}$$

No attempt was made to model intraspecific competition as described for guano birds (Muck and Pauly, this vol.) because, in contrast to the guano birds, the pinnipeds, between 1953 and 1982, had very low biomasses in relation to those of the anchoveta, and less erratic population fluctuations.

The biomass and consumption estimates calculated by the model refer to the whole of the Peruvian littoral (3-18.5°S) but in agreement with the reference area used in this volume for biological and physical parameters, we give corrected estimates for this smaller area (4-14°S), using the mean fraction of population within the restricted range, as derived in Table 6.

Table 4. Estimates of vertical overlap between anchoveta and seals (V) and anchoveta vulnerability to seals (Vul) as a function of the depth of main anchoveta biomass (DMB) (see text for details).

DMB (m)	V	Vul
50	0.98	0.96
60	0.78	0.61
70	0.18	0.03

Table 5. Example of the estimated relationships between mean sea surface temperature in month (i), depth of main anchoveta biomass (DMB_i) and vulnerability of anchoveta to seals (Vul_i).

Month (i)	Mean temp. (°C)	DMB_i (m)	Vul_i
1	24.9	60	0.6
2	25.2	63	0.4
3	25.5	65	0.3
4	25.5	65	0.3
5	26.3	67	0.1
6	26.1	66	0.2
7	21.1	15	1.0
8	18.1	15	1.0

Table 6. Estimation of mean fraction of Peruvian pinniped occurring between 4 and 14°S.

Year	Fraction of total population occurring within 4-14°S Fur seal	Sea lion	Source
1969-1979	–	0.52	Majluf and Trillmich (1981)
1971-1979	0.20	–	Majluf and Trillmich (1981)
1978	0.15	0.60	Tovar (1979); Tovar and Fuentes (1984)
1982	0.29	0.64	Tovar (1979); Tovar and Fuentes (1984)
Means	0.21	0.59	Used in this study

Results

Tables 7 and 8 give monthly data for biomass and anchoveta consumption for sea lion and fur seal, respectively between 1953 and 1982 for the area 4-14°S.

Fig. 4 shows the dynamics of total annual consumption and annual anchoveta consumption between 1953 and 1982. Total consumption increases continuously from around 10,000 t in 1953 to 60,000 t in 1982, directly reflecting the population growth of both pinniped species. Anchoveta consumption had its maximum of approximately 11,000 t in 1965-1967 and an average of approximately 3,700 t (s.d. = 2,000 t) between 1968 and 1982.

The mean anchoveta fraction in total pinniped diet is 40% and varies from 81% in 1953 to 2% in 1982. Because of their dominant biomass in the area considered here (4-14°S), sea lions account for about 88% of total pinniped consumption while anchoveta consumption by fur seals accounts for only around 12%.

The population growth of sea lions does not seem to be affected by the continuous decline of anchoveta availability (Fig. 5), which decreased from 0.8 to less than 0.1 between 1953 and 1982 while the sea lion biomass increased from approximately 300 t in 1953 to 1,800 t in 1982. A similar relationship was found for fur seals although there is a short period (1968-1971) for which anchoveta availability and fur seal biomass show the same declining trend.

Discussion

The consumption estimates presented were derived to obtain an idea on the importance of pinniped predation for the pelagic ecosystem off Peru with particular reference to anchoveta (*Engraulis ringens* J.).

Table 7. Monthly biomass (in brackets) and anchoveta consumption estimates of sea lion off Peru, 4-14°S (all weights in t).

Year	Jan		Feb		Mar		Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec	
1953	(328)	499	(333)	673	(328)	646	(322)	693	(617)	642	(311)	631	(306)	477	(301)	383	(296)	443	(291)	566	(286)	730	(344)	675
1954	(352)	519	(356)	704	(352)	677	(346)	724	(340)	673	(334)	662	(328)	525	(323)	400	(317)	464	(312)	590	(307)	762	(368)	708
1955	(377)	547	(382)	741	(377)	712	(371)	762	(364)	708	(358)	676	(352)	550	(346)	420	(340)	489	(334)	624	(329)	802	(395)	745
1956	(404)	575	(409)	777	(404)	746	(397)	779	(390)	742	(384)	730	(377)	578	(371)	440	(364)	510	(358)	653	(352)	843	(423)	854
1957	(433)	744	(438)	796	(432)	767	(425)	819	(417)	759	(410)	746	(403)	591	(396)	450	(389)	524	(383)	667	(376)	863	(452)	788
1958	(462)	599	(468)	808	(462)	779	(454)	833	(446)	771	(439)	758	(431)	603	(424)	461	(417)	534	(410)	682	(403)	876	(484)	816
1959	(495)	567	(501)	582	(495)	723	(486)	678	(478)	638	(470)	601	(462)	617	(454)	371	(446)	365	(439)	738	(431)	887	(518)	1,034
1960	(530)	815	(537)	836	(530)	638	(521)	684	(513)	668	(504)	682	(495)	570	(487)	416	(479)	433	(470)	331	(462)	673	(555)	785
1961	(568)	670	(576)	666	(568)	542	(559)	703	(549)	590	(540)	626	(531)	351	(522)	256	(513)	423	(504)	624	(495)	698	(595)	764
1962	(609)	439	(617)	556	(609)	635	(599)	646	(589)	614	(577)	564	(569)	454	(559)	446	(550)	496	(540)	527	(531)	628	(638)	774
1963	(653)	573	(662)	471	(653)	408	(642)	417	(631)	368	(620)	361	(610)	365	(599)	368	(589)	365	(579)	416	(569)	444	(684)	525
1964	(700)	319	(709)	323	(700)	302	(688)	276	(677)	250	(665)	262	(654)	252	(643)	237	(632)	231	(621)	252	(610)	282	(734)	320
1965	(750)	670	(760)	650	(751)	702	(738)	734	(725)	744	(713)	752	(701)	697	(689)	715	(677)	719	(665)	719	(654)	750	(786)	966
1966	(804)	797	(815)	790	(804)	729	(790)	678	(777)	617	(764)	554	(751)	534	(738)	514	(726)	598	(713)	553	(701)	498	(842)	649
1967	(862)	761	(873)	813	(862)	1,076	(847)	1,057	(833)	1,030	(819)	986	(805)	961	(791)	944	(778)	920	(765)	879	(752)	815	(903)	846
1968	(924)	483	(936)	465	(924)	433	(908)	415	(893)	400	(878)	368	(863)	369	(848)	363	(834)	357	(820)	308	(806)	322	(968)	375
1969	(990)	342	(1,004)	333	(991)	339	(974)	278	(957)	286	(941)	273	(925)	288	(909)	288	(893)	301	(878)	278	(863)	332	(1,037)	413
1970	(1,061)	87	(1,075)	83	(1,061)	84	(1,043)	80	(1,026)	73	(1,008)	82	(991)	80	(974)	77	(958)	75	(941)	73	(925)	71	(1,112)	81
1971	(1,138)	152	(1,153)	155	(1,138)	151	(1,118)	147	1,099)	144	(1,081)	140	(1,062)	136	(1,044)	132	(1,027)	128	(1,009)	105	(992)	91	(1,192)	102
1972	(1,219)	165	(1,210)	152	(1,194)	141	(1,174)	125	(1,153)	117	(1,134)	106	(1,114)	89	(1,075)	84	(1,076)	72	(1,058)	81	(1,040)	84	(1,232)	102
1973	(1,259)	475	(1,248)	464	(1,232)	449	(1,211)	442	(1,190)	426	(1,170)	410	(1,150)	394	(1,131)	379	(1,112)	373	(1,093)	367	(1,074)	368	(1,265)	431
1974	(1,298)	241	(1,252)	235	(1,236)	237	(1,215)	242	(1,194)	242	(1,174)	243	(1,154)	243	(1,135)	247	(1,115)	243	(1,096)	263	(1,078)	274	(1,240)	321
1975	(1,278)	541	(1,255)	517	(1,240)	497	(1,219)	481	(1,198)	466	(1,178)	451	(1,158)	437	(1,138)	416	(1,119)	475	(1,100)	532	(1,081)	624	(1,237)	758
1976	(1,275)	504	(1,298)	484	(1,282)	452	(1,260)	414	(1,239)	381	(1,218)	350	(1,197)	319	(1,177)	290	(1,157)	256	(1,137)	229	(1,118)	215	(1,320)	217
1977	(1,357)	427	(1,380)	345	(1,362)	365	(1,339)	382	(1,316)	387	(1,294)	414	(1,272)	429	(1,250)	443	(1,229)	446	(1,208)	460	(1,188)	472	(1,402)	557
1978	(1,433)	407	(1,451)	398	(1,432)	384	(1,408)	340	(1,384)	326	(1,360)	302	(1,337)	288	(1,315)	266	(1,292)	245	(1,270)	257	(1,249)	261	(1,498)	314
1979	(1,528)	241	(1,545)	254	(1,525)	236	(1,479)	218	(1,473)	200	(1,448)	189	(1,424)	165	(1,399)	156	(1,376)	140	(1,352)	131	(1,329)	109	(1,612)	121
1980	(1,648)	214	(1,670)	219	(1,648)	229	(1,620)	238	(1,593)	246	(1,566)	242	(1,539)	238	(1,513)	234	(1,487)	241	(1,462)	271	(1,437)	311	(1,731)	389
1981	(1,773)	142	(1,797)	135	(1,774)	117	(1,744)	105	(1,715)	87	(1,685)	76	(1,657)	60	(1,629)	59	(1,601)	58	(1,574)	71	(1,547)	79	(1,855)	108
1982	(1,898)	113	(1,924)	104	(1,900)	91	(1,867)	84	(1,836)	77	(1,804)	70	(1,774)	64	(1,743)	52	(1,714)	62	(1,685)	76	(1,655)	90	(1,772)	115

Table 8. Monthly biomass (in brackets) and anchoveta consumption estimates of fur seal off Peru, 4-14°S (all weights in t).

Year	Jan		Feb		Mar		Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec	
1953	(18)	30	(18)	39	(17)	37	(17)	40	(17)	37	(17)	37	(17)	29	(16)	23	(16)	26	(19)	38	(19)	53	(20)	45
1954	(20)	33	(20)	43	(19)	41	(19)	44	(19)	41	(19)	41	(19)	33	(18)	25	(18)	29	(21)	44	(22)	61	(23)	51
1955	(23)	38	(23)	50	(23)	48	(22)	51	(22)	48	(22)	47	(21)	38	(21)	29	(21)	34	(25)	51	(26)	71	(27)	60
1956	(27)	44	(27)	57	(26)	55	(26)	59	(26)	55	(26)	55	(25)	44	(25)	33	(25)	39	(29)	58	(30)	80	(31)	72
1957	(30)	60	(30)	61	(29)	59	(29)	63	(29)	59	(28)	58	(28)	46	(28)	35	(27)	41	(33)	63	(34)	87	(35)	71
1958	(35)	52	(34)	67	(34)	64	(34)	69	(33)	64	(33)	64	(32)	51	(32)	39	(32)	46	(38)	69	(40)	95	(41)	80
1959	(41)	53	(40)	52	(40)	65	(39)	61	(39)	58	(38)	55	(38)	57	(37)	34	(37)	34	(45)	82	(46)	106	(48)	111
1960	(48)	84	(47)	83	(47)	63	(46)	68	(46)	67	(45)	69	(44)	58	(44)	42	(43)	44	(52)	40	(54)	87	(56)	91
1961	(55)	74	(55)	71	(54)	58	(53)	76	(53)	64	(52)	68	(52)	38	(51)	28	(50)	47	(61)	82	(63)	98	(65)	96
1962	(64)	53	(63)	65	(63)	74	(62)	75	(61)	72	(61)	67	(60)	54	(59)	53	(59)	59	(71)	75	(73)	96	(75)	106
1963	(75)	75	(74)	59	(73)	51	(72)	53	(72)	47	(71)	46	(70)	47	(69)	48	(68)	48	(83)	65	(86)	74	(88)	78
1964	(88)	46	(87)	45	(86)	42	(85)	38	(84)	35	(83)	37	(82)	36	(81)	34	(80)	33	(77)	43	(100)	51	(103)	52
1965	(102)	104	(101)	77	(100)	105	(99)	110	(97)	112	(96)	114	(95)	107	(94)	110	(93)	111	(112)	132	(116)	147	(120)	170
1966	(119)	134	(117)	128	(116)	118	(115)	111	(113)	101	(112)	92	(111)	89	(109)	86	(108)	100	(131)	110	(135)	106	(139)	124
1967	(138)	139	(137)	144	(135)	190	(134)	188	(132)	184	(131)	177	(129)	173	(128)	171	(126)	168	(153)	191	(158)	189	(163)	177
1968	(162)	97	(160)	89	(158)	83	(147)	74	(142)	69	(139)	64	(137)	64	(135)	63	(134)	62	(153)	61	(159)	68	(160)	69
1969	(152)	57	(147)	52	(144)	52	(142)	43	(140)	44	(139)	43	(137)	45	(136)	45	(134)	48	(149)	49	(156)	63	(157)	69
1970	(148)	13	(143)	12	(140)	11	(138)	11	(136)	10	(135)	11	(133)	11	(132)	11	(130)	10	(142)	11	(151)	12	(152)	12
1971	(143)	20	(141)	20	(139)	19	(138)	19	(136)	18	(134)	18	(133)	18	(108)	0	(107)	13	(108)	11	(110)	10	(115)	11
1972	(115)	17	(114)	15	(112)	14	(111)	13	(109)	12	(108)	11	(107)	9	(105)	9	(104)	8	(114)	9	(118)	10	(122)	12
1973	(120)	51	(117)	50	(117)	48	(116)	48	(115)	46	(113)	45	(112)	43	(111)	42	(109)	41	(126)	47	(124)	47	(128)	51
1974	(127)	27	(126)	27	(125)	27	(123)	28	(122)	28	(120)	28	(119)	29	(118)	29	(116)	29	(132)	32	(130)	35	(134)	39
1975	(133)	64	(131)	64	(130)	61	(128)	59	(127)	57	(125)	56	(124)	54	(123)	53	(121)	51	(145)	68	(151)	82	(156)	103
1976	(155)	76	(153)	69	(152)	64	(150)	59	(148)	55	(146)	51	(145)	47	(143)	43	(141)	39	(171)	41	(178)	40	(185)	40
1977	(184)	73	(182)	65	(179)	50	(177)	53	(175)	56	(173)	57	(171)	61	(169)	64	(167)	66	(199)	79	(206)	87	(212)	95
1978	(211)	73	(209)	67	(206)	64	(204)	61	(201)	55	(199)	53	(197)	49	(195)	47	(192)	44	(229)	47	(235)	53	(242)	57
1979	(240)	43	(237)	43	(235)	44	(232)	41	(229)	38	(227)	35	(224)	35	(221)	29	(219)	27	(267)	30	(275)	29	(284)	26
1980	(282)	39	(278)	41	(275)	41	(272)	43	(269)	44	(266)	46	(263)	46	(260)	45	(257)	45	(312)	55	(323)	66	(333)	81
1981	(331)	34	(327)	30	(323)	27	(320)	24	(316)	21	(312)	18	(309)	16	(305)	12	(302)	12	(365)	14	(378)	19	(390)	22
1982	(387)	26	(383)	26	(378)	23	(374)	20	(370)	19	(365)	17	(361)	16	(357)	14	(353)	12	(425)	17	(438)	22	(442)	27

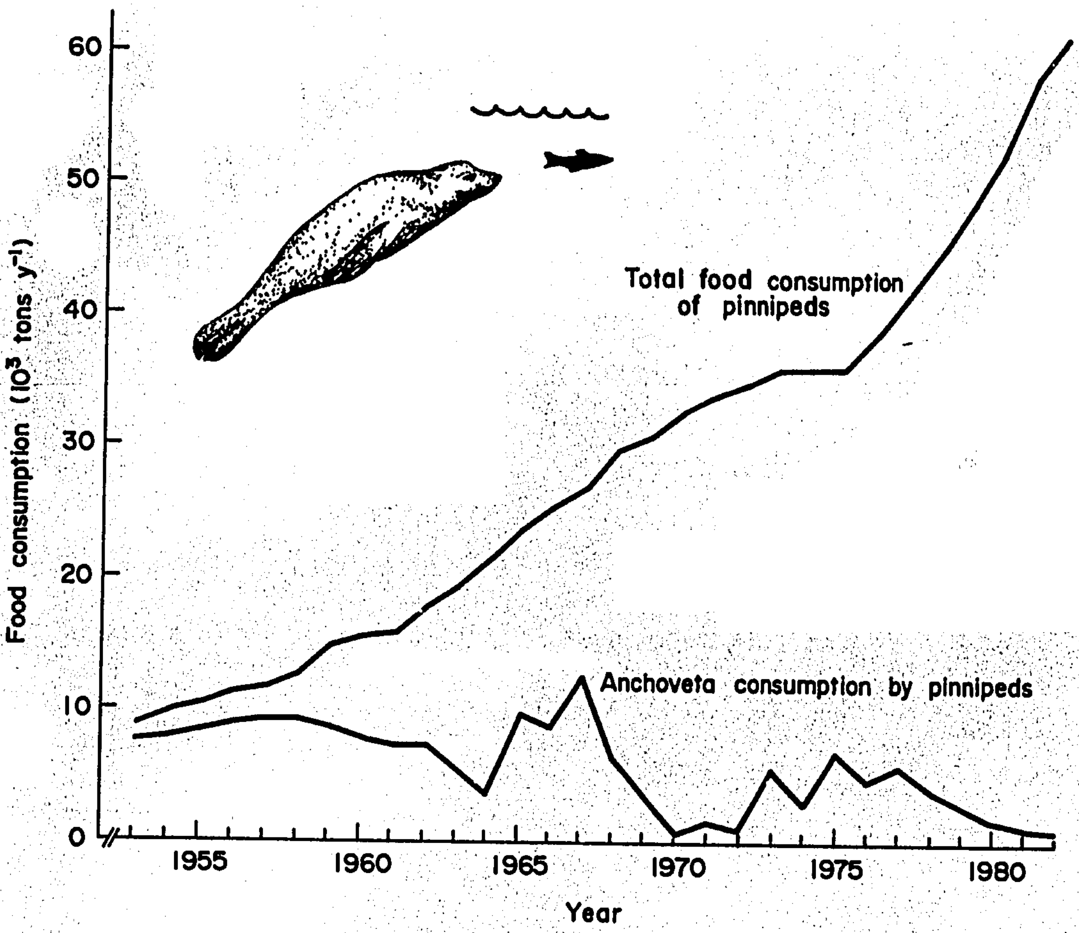
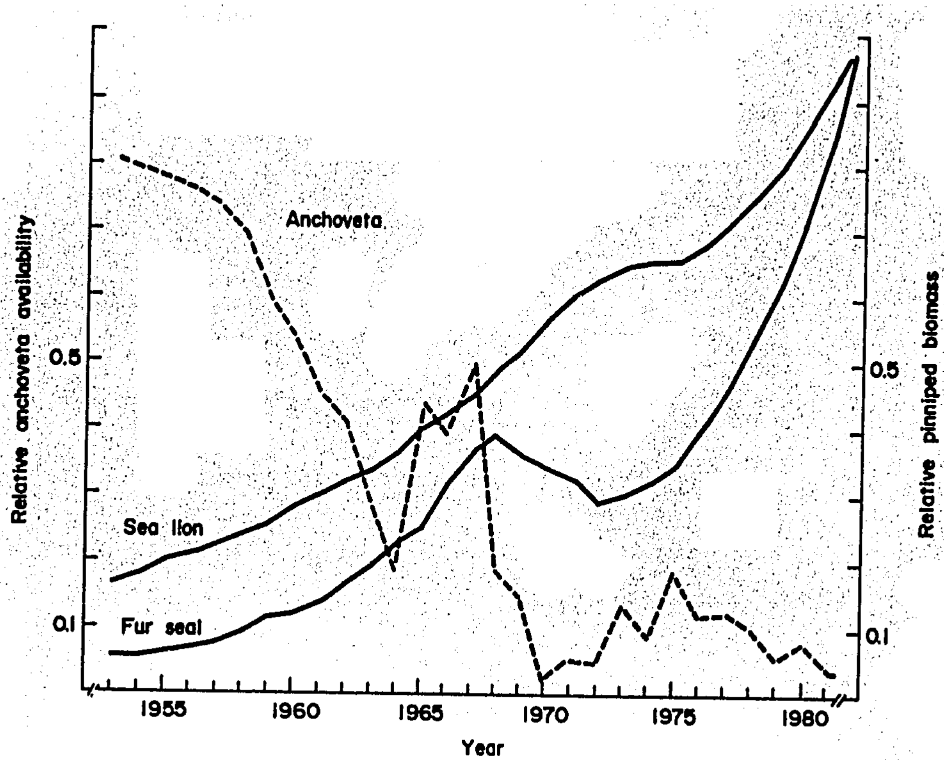


Fig. 4. Estimated food consumption and anchoveta consumption by pinnipeds (sea lion and fur seal) off Peru (4-14°S), 1953 to 1982.



ig. 5. Time series of two factors affecting anchoveta consumption by pinnipeds of Peru: ancho-
ta relative avaiablity and relative pinniped biomass (see text for details).

Because the time series of census results are incomplete the monthly pinniped abundance between 1953 and 1982 was calculated using an analytical population growth model. The mean deviation between calculated abundance and census results is 10% (n = 10, s.d. = 8%) for fur seal (*Arctocephalus australis*) and 8% (n = 11, s.d. = 6%) for sea lion (*Otaria flavescens*).

Considering the many assumptions which were necessary and the indirect character of the abundance data, the consumption estimates should be considered a rough approximation, with a probable precision of +/- 25%. Thus the calculated maximum annual total consumption is about 107,000 to 179,000 t in 1982 for the total Peruvian coast and 47,000 to 78,000 t for the area between 4 and 14°S, respectively. As fish consumption is around 75% of total consumption (Antonelis and Perez 1984), maximum fish consumption has been estimated as 80,000 to 134,000 t in 1982 (entire coast) and as 35,000 to 59,000 t for the area between 4 and 14°S.

Parrish and Shearer (1977) give 100,000 to 120,000 t as total annual fish consumption of grey seals in the North Sea; 100,000 to 250,000 t are estimated by Bailey and Ainley (1981/1982) as annual hake consumption of the 80,000 to 125,000 t Californian sea lion (*Zolophus californianus*)

Maximum anchoveta consumption (4-14°S) was estimated in 1967 as 10,000 to 17,000 t with an average of 3,000 to 5,000 t/year between 1968 and 1982. However, compared with the Peruvian pelagic fishery or with the fish consumption of the guano birds, even the total annual fish consumption by pinnipeds is negligible (see Table 9 and Pauly, this vol.).

Table 9. Estimated fish consumption by Peruvian pinnipeds compared with commercial catch of pelagic species.

Year	Fish consumption ($t \cdot 10^3$)	% of anchoveta catch[a]	% of catch of other pelagics[a,b]
1965	37	0.5	49
1966	41	0.5	48
1967	45	0.5	55
1968	48	0.5	72
1969	49	0.6	68
1970	51	0.4	72
1971	52	0.5	53
1972	53	1.2	54
1973	55	3.6	20
1974	55	1.5	20
1975	56	1.8	43
1976	61	1.6	22
1977	67	8.5	5
1978	73	6.1	4
1979	79	5.8	4
1980	88	12.0	5
1981	98	8.0	8
1982	107	6.0	7

[a] Based on IMARPE, unpublished data and Tsukayama and Palomares, this vol.

[b] Sardine, horse mackerel, mackerel and others.

The estimated anchoveta fraction in pinniped diet varies from 81 to 2% and reflects the dynamics of anchoveta availability between 1953 and 1982. Antonelis and Perez (1984) calculated that the percentage of northern anchovy (*Engraulis mordax*) in the diet of northern fur seal changed from 43% off California to only 11% off the Washington-Oregon coast, depending on the relative availability of anchovy.

This corresponds to the findings of Antonelis and Ficus (1980), Bonner (1982), Kajimura (1982) and Perez and Bigg (1981) who suggested that pinnipeds are not specialized predators but opportunistic ones, feeding on a wide range of seasonally abundant prey species. Changes in availability might result from a variety of factors such as depletion of resource by commercial fishery, interspecific competition and climatic changes (MacCall 1983; Moyle and Cech 1982).

The consumption model presented here suggests that anchoveta availability for pinnipeds is principally controlled by changes in anchoveta biomass and by competition of the anchoveta fishery. In contrast to the Peruvian sea birds (Muck and Pauly, this vol.) the influence of El Niño periods on anchoveta vulnerability and therefore anchoveta consumption seems to be of little importance before 1983. The situation becomes different for the 1982-1983 El Niño which was probably the strongest in this century. Table 5 gives vulnerability estimates (Vul_i) and estimates of the mean depth were the main anchoveta biomass is concentrated (DMB_i) related to the (surface) temperature regime during the first 8 months of 1983.

Total consumption by pinnipeds was calculated using feeding rates of captive fur seal females (Perez and Mooney 1984) which most probably are equal or at least close to the possible upper limits of food consumption when food is abundant. These rates were used for the entire 1953-1982 period because the steady increase of pinniped biomass from around 600 t in 1953 to approximately 50,000 t in 1982 suggests no limitations by food resource. The period 1968 to 1971 is an exception in the case of fur seals, when the census results show a 40% decrease in population size. Comparing anchoveta availability for the same period a similar tendency has been calculated (Fig. 5): as a consequence of (i) the anchoveta fishery as competitor to pinniped anchoveta predation and (ii) reduced total anchoveta biomass, anchoveta availability dropped from 0.19 in 1968 to 0.05 in 1971. Therefore we cannot exclude the possibility that a shortage of anchoveta between 1968 and 1972 affected fur seal population growth. However, in general, population growth of Peruvian pinnipeds seems to be independent of anchoveta availability and biomass, as confirmed by the fact that both seal populations had highest growth rates when the anchoveta stock was much reduced (1978-1982).

This suggests a change of food by the predator and agrees with results of Majluf (1985) for the Peruvian fur seals. Analyzing the otoliths from fur seal scats, she found a shift from almost 100% anchoveta to a diet of sardine and horse mackerel in times of low anchoveta abundance. Therefore it is doubtful whether pinnipeds still feed on anchoveta when its availability drops below a threshold value. Ecological models, e.g., that of Murdoch et al. (1975) and field data on pinnipeds (Bailey and Ainley 1981/1982) suggest a "switch" in feeding behavior to alternative prey when the traditional resource becomes scarce. In this case the calculated anchoveta consumption for periods with very low anchoveta availability (1969 to 1982) could be overestimated.

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Population Dynamics and Estimated Anchoveta Consumption of Bonito (*Sarda chiliensis*) off Peru, 1953 to 1982*

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Abstract

The population dynamics of bonito *(Sarda chiliensis)* off Peru is reviewed, with emphasis on its growth, mortality and biomass. A food consumption model is derived, based on actual data on *S. chiliensis* and other scombrids. Daily rations in % body weight were estimated as ranging from 2.23 (at 14°C) to 7.04 (at 24°C), and used, along with food composition data, to estimate monthly anchoveta (*Engraulis ringens*) consumption by bonito off Peru, between 4 and 14°S, from 1953 to 1982. These estimates ranged from a maximum of 86,000 tonnes (t) in May 1953 to 400 t, first reached in June 1975. Overall, bonito appears to have a modest impact on the anchoveta stock.

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Introduction

This account is an attempt to estimate, on a monthly basis, the consumption of anchoveta (*Engraulis ringens*) by bonitos (*Sarda chiliensis chiliensis*) off Peru (4 to 14°S) from 1953 to 1982.

Peruvian data on the biology and fishery of bonitos are available which make such an estimate possible, given that one dares to fill in gaps through inferences from comparable stocks and/or related species. The assumptions made here to estimate the anchoveta consumption of bonitos are justified by the fact that any account of the population dynamics of the Peruvian anchoveta will be incomplete if it ignores the role of bonitos as highly specialized predators of anchoveta. The value of the present exercise, however, may not be solely in the fact that it provides estimates of anchoveta consumption. Rather, it is also meant to illustrate how far historic data collected on a given fish stock - off Peru or elsewhere - can be "stretched" when one includes in an analysis as much as possible the relevant information on a given species and allied forms.

This exercise, therefore may be seen as a complement to Yoshida's (1980) excellent synopsis of data on the genus *Sarda*, emphasis being given here to the Peruvian stock of *Sarda chiliensis chiliensis*, and to the numerous Peruvian contribution on bonitos (most in manuscript form) not incorporated in said synopsis.

This contribution may also be seen, finally as an attempt to refine two previous "educated guesses" of the annual consumption of anchoveta by bonito. The first of these educated guesses was by Saetersdal et al. (1965) who wrote that

> the estimated annual consumption of anchoveta by guano birds is of about 3 t x 10^6. If we assume that bonitos (with an estimated biomass of 300,000 t) and other fishes consume the same quantity (i.e., 1.6 t x 10^6) of anchoveta, then...

Boerema et al. (1965) wrote, on the other hand that

> ...Another predator of the anchovy is the bonito. Nearly 100,000 t of this species are caught annually in Peruvian waters. It it is assumed that these fish have needed for their growth about 10 times their weight in food, and that this food mainly consists of anchovy, this adds another million tons to the figure of predation.

The Catch and the Species Caught, 1953 to 1982

Although there have been uncertainties concerning the taxonomic status of the Peruvian bonitos, it is now agreed that all bonitos occurring in the eastern Pacific can be attributed to two species, *Sarda orientalis* and *S. chiliensis*. The latter has an anti-equatorial distribution (Randall 1981) and is separated in two units now given subspecies rank - *S. chiliensis lineolata* north and *S. chiliensis chiliensis* south of the equator while the distribution of *S. orientalis* straddles the zero latitude line (Collette and Chao 1975; Yoshida 1980; and see Fig. 1).

Because of its narrow distribution - barely touching the north coast of Peru and rarely overlapping with the distribution of anchoveta (Vildoso, pers. obs.) - *S. orientalis* usually contributes negligible amounts to the Peruvian catch of bonito, for which reason this catch will be treated below as if consisting only of *S. chiliensis chiliensis*. This might introduce an error in periods where El Niño events, by warming up the surface waters off Peru, necessarily extend southward the distribution of *S. orientalis*. However, this occasional (and partial) replacement of one bonito species by another shall be treated here as if it had no impact on fishermen or anchoveta consumption.

We should note here that three different, size-dependent names are given to specimens of *S. chiliensis chiliensis* in Peru, namely *chauchilla* for fish up to 30 cm, *cerrajon* for fish between 30

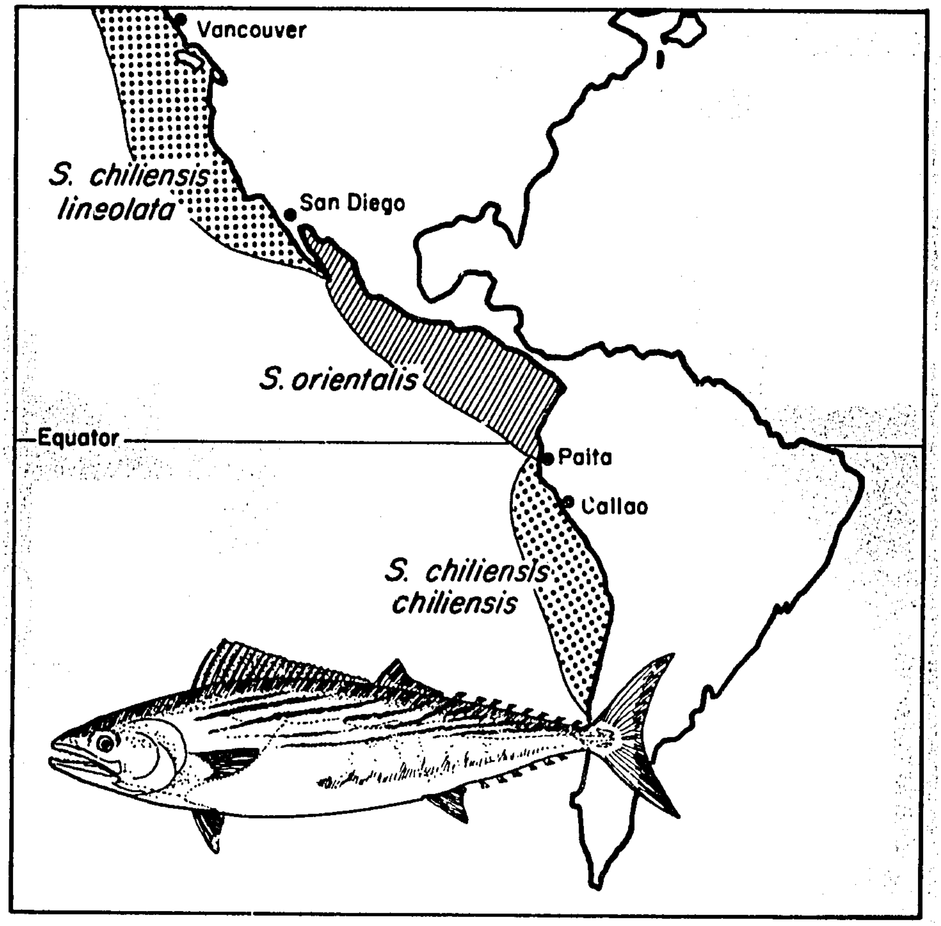

Fig. 1. Distribution of *Sarda orientalis*, *S. chiliensis chiliensis* and *S. chiliensis lineolata* in the Eastern Pacific. Note that *S. orientalis* also occurs in other parts of the Pacific and the Indian Ocean, while *S. chiliensis* occurs only in the Eastern Pacific. Note also that occasional specimens of *S. chiliensis lineolata* have been reported from Alaska (adapted from Yoshida 1982).

and 50 cm, and *bonito* (*sensu stricto*) for fish above 50 cm (Vildoso 1961); the latter group shall be called "large bonitos" in the rest of this contribution.

Table 1 gives estimates of the annual bonito catch off Peru from 1951 to 1983. This catch, which had gradually increased, from near zero in 1940 to 50.8 thousand t in 1951, peaked in the early 1960s with a maximum of over 100,000 t in the early 1960s, declined to negligible values in the late 1970s then increased again in the 1980s.

At this peak, from the mid-1950s to the mid-1960s, the Peruvian bonito fishery represented a very significant part of the overall fishery sector, both in terms of supplies to the Peruvian (fresh and frozen bonitos) as well as the export (i.e. US and western Europe) markets. For example, the value of canned bonitos exported in 1958-1959 amounted to 25% of the value of Peru's fishmeal exports for the same period (computed from data in Anon. 1960).

The bonito fishery for various reasons, however, never attracted an amount of attention proportional to its value, and hence the impact of bonitos on the anchoveta stock remained unappreciated.

Growth and Natural Mortality of *Sarda chiliensis chiliensis*

Several models presented further below require a concise description of the growth parameters of *S. chiliensis*. This applies particularly to our attempt to estimate biomasses through catch data and fishing mortality estimates. However, the growth curves and growth parameter

Table 1. Annual catch, fishing effort, fishing mortality and estimated biomass of large bonitos off Peru, 1951 to 1983.

Year	Annual catch whole of Peru (x 10^3 t)[a]	Standardized catch per effort of chimbote fleet[b]	Standardized fishing effort[c]	Estimated fishing mortality	0.9 catch/ fishing mortality[e]	Biomass of large bonitos (4-14°S, x 10^3 t)[f]
1951	50.8	–	(8.0)	0.718	63.7	63.7
1952	50.1	–	(7.9)	0.709	63.6	64.6
1953	43.7	–	(6.6)	0.592	66.4	64.4
1954	52.3	–	(8.3)	0.744	63.2	61.1
1955	71.2	–	(13.3)	1.193	53.7	52.2
1956	83.4	–	(21.1)	1.893	39.7	51.2
1957	57.7	–	(9.6)	0.861	60.3	55.6
1958	65.8	–	(11.6)	1.041	56.9	52.6
1959	82.3	–	(20.4)	1.830	40.5	47.8
1960	96.9[g]	–	(21.1)	1.893	46.1	45.6
1961	105.3[g]	–	(21.1)	1.893	50.1	46.2
1962	90.3[g]	4.24	21.3	1.911	42.5	50.3
1963	90.7[g]	5.80	15.6	1.399	58.3	45.8
1964	76.4	3.66	20.9	1.875	36.7	48.7
1965	62.3	5.12	12.2	1.094	51.2	44.0
1966	71.4	4.40	16.2	1.453	44.2	39.9
1967	63.6	2.41	26.4	2.368	24.2	28.7
1968	54.3	1.76	30.9	2.772	17.6	19.5
1969	59.3	1.68	35.3	3.166	16.7	16.9
1970	57.4	1.64	35.0	3.140	16.5	19.7
1971	72.9	–	(28.2)	2.530	25.9	21.1
1972	64.2	–	(31.0)	2.781	20.8	18.7
1973	34.8	–	(37.1)	3.328	9.4	10.7
1974	7.4	–	(41.2)	3.696	1.8	4.1
1975	4.9	–	(41.5)	3.723	1.2	1.3
1976	4.1	–	(41.6)	3.732	1.0	1.2
1977	5.7	–	(41.4)	3.714	1.4	1.2
1978	4.7	–	(41.5)	3.723	1.1	1.3
1979	5.3	–	(41.5)	3.723	1.3	1.4
1980	6.8	–	(41.3)	3.705	1.7	1.7
1981	9.0	–	(41.0)	3.678	2.2	2.7
1982	16.4	–	(39.9)	3.579	4.1	3.5
1983	17.2	–	(39.8)	3.570	4.2	4.2

[a] Various IMARPE documents.
[b] From Mejia (1967) and IMARPE (1971). Units are tonnes of bonitos caught per trip.
[c] See text and Fig. 4.
[d] Obtained by multiplication of standardized fishing effort by q = 0.0897 (see text and Fig. 6).
[e] Correction by 0.9 to account for catches outside of 4 to 14°S.
[f] Obtained by smoothing (through running average over 3 years) the biomass estimates obtained in (e).
[g] Catch values in excess of "MSY" were assumed to have been obtained by an effort to equal to f_{opt}.

estimates available in the literature are contradictory and confusing. Kuo (1970), based on otolith readings in *S. chiliensis lineolata* and *S. chiliensis chiliensis*, presented growth "curves" that are almost linear over the interesting span of ages (1 to 6 years), and which have values of L_∞ much larger than the maximum sizes recorded in bonitos (Fig. 2) while the growth parameters reported by Campbell and Collins (1975), based on analysis of otoliths and length-frequency data, appear also to be questionable (Table 2).

The maximum length reported for *S. chiliensis lineolata* is about 102 cm (Yoshida 1980). The southern subspecies, on the other hand, tends to remain smaller, with a definitive record of 79 cm (De Buen 1958). Mann (1954) and Vildoso (1961) state that Chilean bonitos may exceed 80 cm and reach 90 cm, respectively. Vildoso (1955) reported never to have encountered a bonito in excess of 75 cm in Peruvian waters from which however, one exceptionally large specimen of 93 cm and 94 kg has been reported (Anon. 1958).

Length-frequency data from the early phase of the fishery are available (see Table 3) which allow estimation of asymptotic length (L_∞) in Peruvian bonito using the method of Wetherall

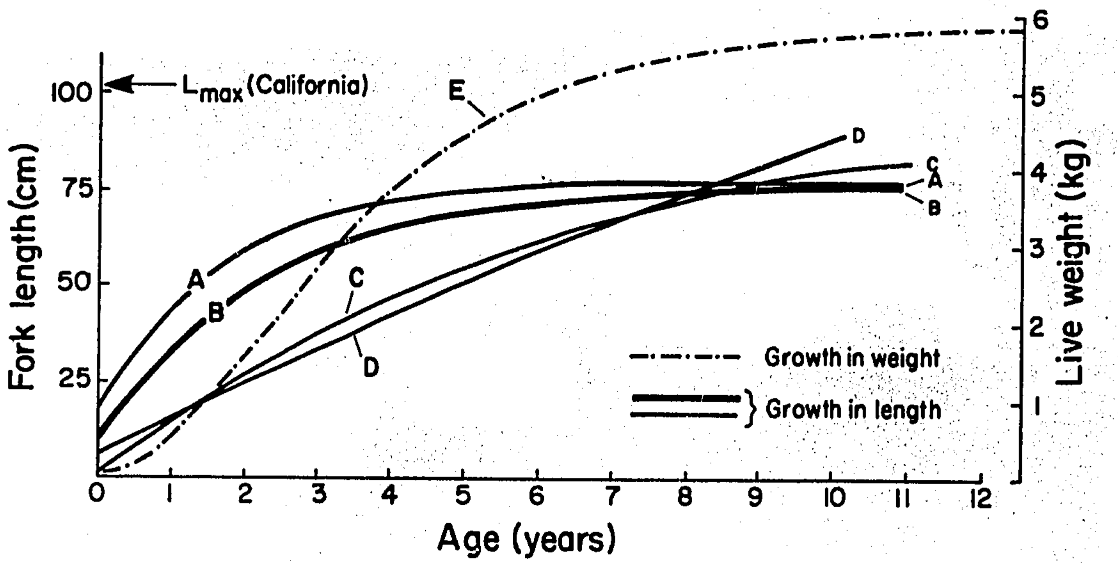

Fig. 2. Available growth curves for *Sarda chiliensis*: A. Campbell and Collins (1975), for *S. chiliensis lineolata*; B. This study, for *S. chiliensis chiliensis* off Peru (see also Fig. 3); C. Kuo (1970) for *S. chiliensis lineolata*; D. Kuo (1970) for *S. chiliensis chiliensis* and E. This study, growth in weight of *S. chiliensis* off Peru (see also Table 4).

(1986), in which a length-frequency sample representative of the steady-state population is used in conjunction with a regression of the form

$$\overline{L_i} = a + b\,L'_i \qquad \text{...1)}$$

(where $\overline{L_i}$ is mean length above L'_i, the lower limit of length class (i)) to estimate L_∞ through

$$L_\infty = a/(1-b) \qquad \text{...2)}$$

Fig. 3 illustrates this method, which also allows estimation of the ratio Z/K (see below) via

$$Z/K = b/(1-b) \qquad \text{...3)}$$

The value of L_∞ = 76 cm, estimated using equations (1) and (2) and length-frequency data for the period 1951-1953 (Fig. 3) corresponds rather well to the maximum lengths discussed above, and shall be used here as best estimate of asymptotic length in Peruvian bonito.

Pauly and Munro (1984) suggested that the parameters ϕ' could be used to express the average growth performance in a given taxon when growth can be described in the von Bertalanffy Growth Function (VBGF) of the form

$$L_t = L_\infty\ (1-e^{-K(t-t_0)}) \qquad \text{...4)}$$

where L_t is the length at age t, and K and t_0 are the constants which, besides L_∞, must be estimated empirically. In such case, ϕ' is defined by

$$\phi' = \log_{10}K + 2\log_{10}L_\infty \qquad \text{...5)}$$

(See Pauly 1979 for derivation of this equation). As might be seen in Table 4, the three sets of L_∞ and K values available on *S. chiliensis* lead to a mean value of ϕ' = 3.40, very close to the value of ϕ' = 3.43 estimated for *Sarda sarda*.

We have used here equation (5), the overall mean value of ϕ' = 3.42 (see Table 4) and L_∞ = 76 cm to estimate K = 0.455 for Peruvian bonito.

Table 2. Length-at-age data in Fig. 1 of Bartoo and Parker (1983) based on Campbell and Collins (1975). Note bimodal distribution in age groups I and II, possibly due to erroneous age reading. L = fork length.

L (cm)	Age I	L (cm)	Age II	L (cm)	Age III	L (cm)	Age IV	L (cm)	Age V
45	2	57	1	67	2	68	1	71	1
46	3	58	3	68	2	69	2	72	5
47	13	59	15	69	6	70	4	73	3
48	37	60	25	70	6	71	12	74	5
49	74	61	41	71	8	72	20	75	2
50	77	62	38	72	8	73	14	76	2
51	71	63	15	73	11	74	11	77	3
52	48	64	9	74	9	75	8		
53	44	65	3	75	1	76	5		
54	26	66	3			77	2		
55	13	67	1			78	1		
56	1	68	1						
57	0	69	2						
58	1	70	1						
59	2								
60	8								
61	1								
62	3								

Table 3. % length composition data on bonito *(Sarda chiliensis chiliensis)* caught off Peru, 1951-1976.[a]

Location:		Callao[c]	Callao	Callao	Paita	Callao	Callao	Callao	Callao	Paita	Callao	Callao	Paita	Callao	Paita	Callao	Paita	Callao
Year :		1951-52	1952-53	1962	1962	1964	1965	1966	1967	1967	1968	1969	1969	1970	1970	1971	1971	1976
Number :		807	800	14,090	86	9,795	675	869	2,486	701	1,865	2,067	5,148	3,838	12,826	30,452	10,807	
FL (cm)[b]	Mean weight, g																	
35.5	603														1.10			
36.5	656														2.10			
37.5	711														1.60		2.40	
38.5	770														1.10		2.40	1.00
39.5	831												0.48		1.60		3.00	0.50
40.5	896												0.48		2.60		4.20	1.00
41.5	964												1.80		3.70	1.10	6.00	2.00
42.5	1,035												2.70	1.10	5.80	2.20	7.20	0.50
43.5	1,110											1.50	4.60	2.70	5.30	3.20	8.50	3.00
44.5	1,188								1.00	1.00		3.00	5.90	3.20	5.80	4.90	8.50	7.00
45.5	1,270			0.24					2.40	2.00		4.00	9.10	3.20	6.40	7.00	7.80	5.00
46.5	1,356			0.24					3.40	2.50	0.50	4.00	11.40	4.30	6.40	9.70	8.50	6.00
47.5	1,445			0.48					4.40	3.00	0.50	6.60	12.70	5.40	6.40	10.80	(8.50)	13.00
48.5	1,538			0.50			1.10		5.40	4.00	1.00	8.60	13.50	7.60	6.80	(10.90)	7.20	11.00
49.5	1,635	0.20		0.70		1.00	6.90		4.90	6.00	2.50	8.60	(10.90)	9.20	6.90	9.70	6.00	5.00
50.5	1,737	0.20		1.40	1.00	2.60	3.70	2.00	3.90	10.00	4.50	10.70	5.90	10.90	6.90	9.70	5.40	12.00
51.5	1,842	1.00		2.80	1.00	4.10	2.60	1.50	2.40	11.00	6.50	(9.60)	3.60	(9.80)	6.40	8.10	4.80	(12.00)
52.5	1,951	0.80		4.80	2.00	5.70	2.60	0.80	2.90	(8.00)	6.50	8.60	2.70	8.10	(5.30)	6.50	4.20	10.00
53.5	2,065	1.70		6.20	2.40	6.70	3.70	2.00	4.40	7.50	8.50	7.60	2.30	7.00	4.20	5.40	3.00	3.00
54.5	2,183	2.50	1.60	7.60	1.00	8.20	7.90	7.00	3.40	6.00	10.10	6.60	2.30	4.90	3.20	4.30	2.40	1.00
55.5	2,305	3.40	1.70	8.60	5.30	10.30	5.80	9.00	4.40	6.50	11.60	5.60	2.30	4.30	2.60	3.20		1.00
56.5	2,432	5.50	2.30	9.50	8.20	11.90	7.40	11.10	5.80	5.00	(11.10)	5.00	1.80	3.20	2.10	2.20		2.00
57.5	2,563	5.00	4.10	9.90	10.70	12.90	10.00	16.20	7.80	5.50	10.60	4.00	1.40	3.20	1.60	1.10		1.00
58.5	2,699	5.30	7.80	9.50	14.50	(11.90)	14.40	18.20	8.80	6.00	9.10	3.00	0.90	2.70	1.10			2.00
59.5	2,840	8.40	10.70	9.00	15.40	9.80	(12.80)	(13.60)	11.20	5.50	6.00	2.00	0.70	2.70	0.50			0.00
60.5	2,986	15.30	15.30	8.00	6.30	7.20	10.00	6.60	(9.30)	4.00	4.50	1.00	0.48	2.70	0.50			1.00
61.5	3,136	(12.60)	(11.90)	(6.20)	7.80	4.10	4.20	4.00	5.40	2.00	3.00		0.48	2.20	0.50			
62.5	3,292	8.60	13.30	4.80	(12.10)	2.60	4.80	3.00	3.90	1.00	2.00		0.48	1.10	0.25			
63.5	3,452	8.40	9.20	3.30	5.80	1.00	2.10	1.00	2.40	0.50	1.00		0.48	0.50	0.25			
64.5	3,618	6.30	7.20	2.40	3.50			1.50	1.50	0.50	0.50		0.48		0.25			
65.5	3,789	5.90	6.60	1.40	2.00			1.00	1.00	0.50			0.23		0.25			
66.5	3,965	3.60	4.30	1.00	1.00			0.50		0.50					0.25			
67.5	4,146	1.70	3.30	0.48				0.50		0.50					0.25			
68.5	4,333	1.30	2.30	0.48				0.50		0.25								
69.5	4,526	0.60	1.00	0.48						0.25								
70.5	4,724	0.40	0.40							0.25								
71.5	4,928	0.20	0.20							0.25								
72.5	5,138		0.40															
Mean wt (in g)		3,081	3,240	2,638	2,844	2,486	2,524	2,652	2,397	2,179	2,363	1,878	1,598	1,915	1,558	1,635	1,350	1,635
Z[d]		1.96	1.76	2.37	3.99	3.81	4.05	3.14	3.51	1.74	2.98[e]	2.76	2.65	2.25	2.56	3.21	3.72	4.33

[a] Data for 1951-1953: Vildoso (1955); data for 1962-1971: IMARPE (1971); data for 1976: Mayo (1976).

[b] Class midrange

[c] Values in brackets indicate first % frequency used for computation of $\bar{L}$; lower class limit of this class thus represents L'.

[d] Z values computed using equation (10), with L_∞ = 76 and K = 0.455.

[e] Note added in proofs: all computations were (erroneously) performed with Z = 3.89 instead of the correct value of 2.98. This does not affect results noticeably, due to the simultaneous use of all 17 values of Z in estimating M and q.

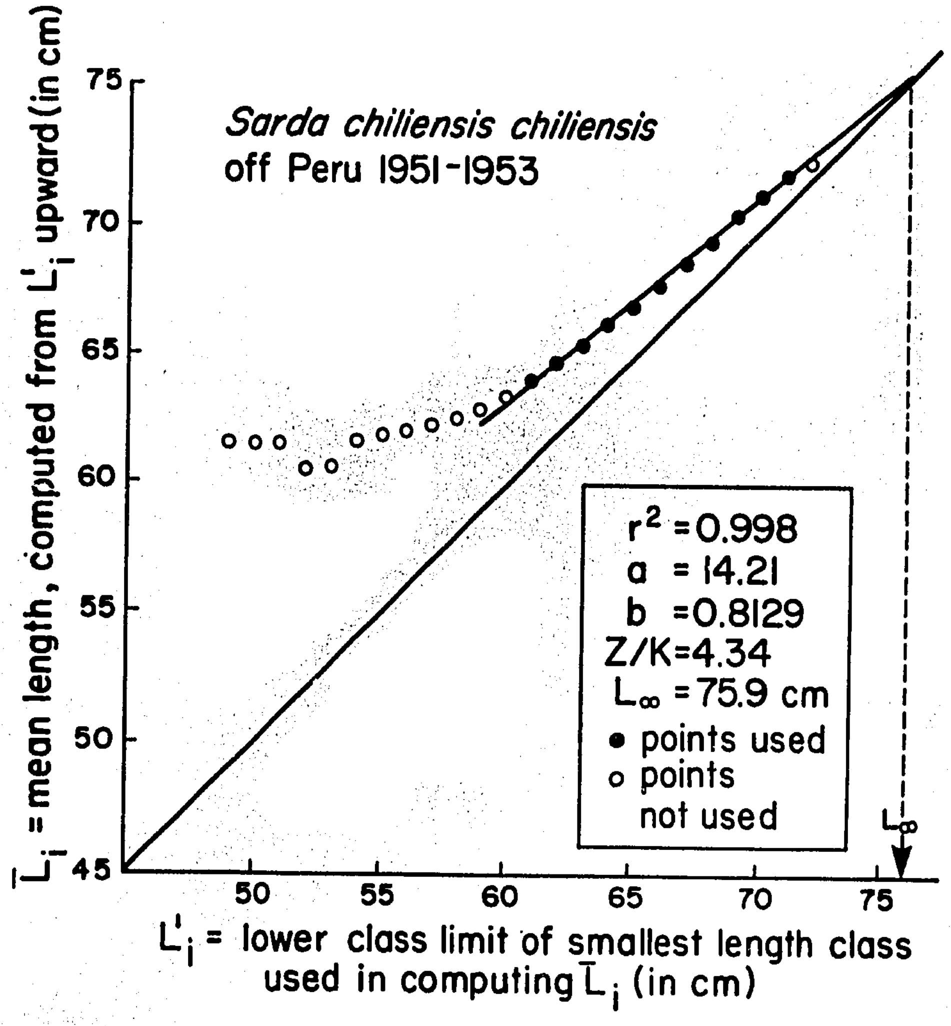

Fig. 3. Estimation of L_∞ and Z/K using the method of Wetherall (1986); based on length-frequency data in Table 5 (average of two samples) and equations (1) to (3).

Table 4. Available growth parameter estimates in *Sarda* species.[a]

Species	FL_∞ (cm)	K (y^{-1})	ϕ'	Mean
Sarda sarda	81.5	0.525	3.54	3.43
Sarda sarda	67.8	0.795	3.56	
Sarda sarda	103	0.132	3.15	
Sarda sarda	95.6	0.237	3.34	
Sarda sarda	64	0.860	3.55	
Sarda chiliensis	266	0.038	3.43	3.40
Sarda chiliensis	101	0.154	3.20	
Sarda chiliensis	77	0.622	3.57	

[a] Growth parameters for *S. sarda* from Pauly (1978); growth parameters for *S. chiliensis* from Yoshida (1980).

The value of the parameter t_o is estimated finally from an empirical equation of Pauly (1979), i.e.

$$\log 10\,(-t_o) = -0.3922 - 0.2752 \log 10 L_\infty - 1.038 \log 10 K \qquad \ldots 6)$$

which, given L_∞ (in cm) and K (1/year) values, provides crude estimates of t_o when these cannot be obtained by any other method. Thus, we have to describe the growth in length of Peruvian bonitos,

$$L_t = 76\,(1 - e^{-0.455(t+0.28)}) \qquad \ldots 7)$$

where L_t (fork length, in cm) is the length at age t (in years) (Fig. 2).

A number of allometric length-weight relationship have been estimated for Peruvian bonitos by various authors (Table 5). We shall use here, however, a simple isometric length-weight relationship of the form

$$W = (c.f./100) \cdot L^3 \qquad \ldots 8)$$

Table 5. Length-weight relationships in Peruvian bonito *(Sarda chiliensis chiliensis)*.

Case No.	L-W relationships		Range (in cm)	n	Computed weight at 60 cm	Source and/or remarks
	"a"	"b"				
1	0.006311	3.19	20-71	513	2,968	Vildoso (1962),
2	0.006491	3.19	22-71	565	3,052	Vildoso (1962),
3	0.01169	3.03	30-71	930	2,855	Canal (1974)
4	0.02011	2.89	30-58	204	2,769	Mayo (1976)
5	0.01348	3	(60)	–	2,911[a]	used in this study

[a] Mean of cases No. 1-4, as used to estimate,based on b = 3, a value of a = 0.01348, corresponding to c.f. = 1.348.

with a mean c.f. (condition factor) estimated from the data in Table 4 of 1.348, and leading to weights in g when (fork) length is expressed in cm. Thus we shall express the growth in weight of Peruvian bonito as

$$W_t = 5917\,(1 - e^{-0.455\,(t+0.28)})^3 \qquad \ldots 9)$$

which is reasonable in view of the fact that none of us ever observed a Peruvian bonito exceeding 5 kg (see also Vildoso 1955).

Catch per Effort and Effort in the Peruvian Bonito Fishery, 1953 to 1982

Effort and catch-per-effort data are not available which cover the whole period considered here. In fact, the only previous contributions dealing in some detail with the bonito fishery off Peru is the unpublished thesis of Mejia (1967) and an IMARPE internal report (1971), in which standardized effort and catch-per-effort of the Chimbote fleet of purse seiners for the period 1967 to 1970 were derived and analyzed.

Since Chimbote was the main base of the Peruvian bonito fishery (Mejia 1967) we have divided the catch per effort of the Chimbote fleet for this period into the total Peruvian catch to obtain estimates of total Peruvian effort (see Table 1). Then, we have fitted a simple parabolic surplus yield model to the total catch and overall effort data (Fig. 4). The yield curve was then used to generate, from the catch data prior to 1962 and beyond 1970, estimates of effort, based on the assumption that the low yields of the earlier period were associated with effort levels below f_{opt} (the effort level associated with MSY), and that the low yields of the recent period were associated with effort levels beyond f_{opt}. We believe these two assumptions to be reasonable given what is presently known of the early development of the Peruvian fishing fleet in general, and of the bonito stock and fishery in particular (see below and other contributions in this volume).

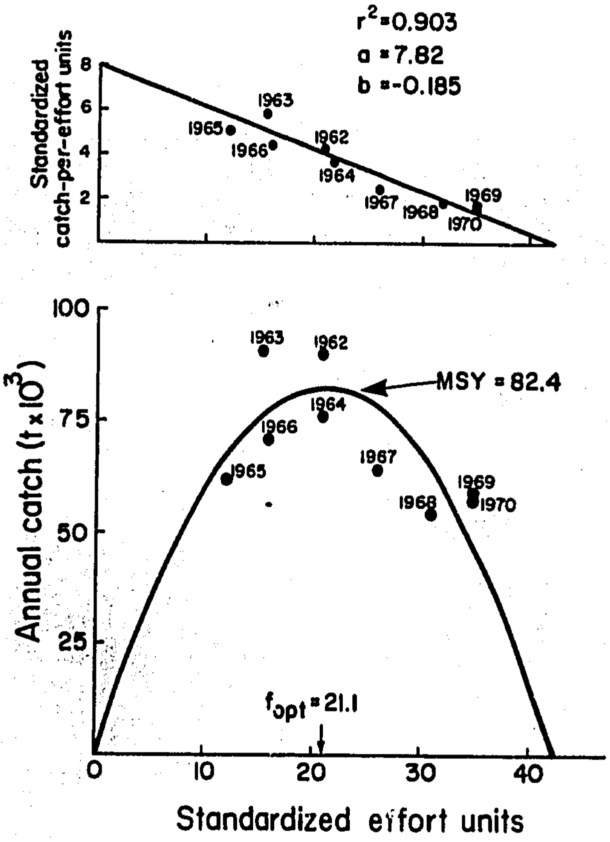

Fig. 4. "Schaefer" model of the Peruvian bonito fishery, based on data for the period 1962 to 1970 (Table 1) and used to estimate fishing effort from available catch data for the periods 1951 to 1961 and 1971 to 1983 (see also Table 1 and text).

Total, Natural and Fishing Mortality of Bonito

Size-frequency distributions of fish caught by the Peruvian bonito fishery off Callao and Paita are available for the years 1951-1953, 1962, 1964 to 1971 and 1976 (Table 3). From these, total mortality (Z) was estimated using the equation

$$Z = K \cdot (L_\infty - \bar{L})/(\bar{L} - L') \qquad ...10)$$

where $\bar{L}$ is the mean length in the catch, computed from the first length (L') fully represented in samples (Beverton and Holt 1956). The estimate of Z obtained in this fashion are given in Table 3.

A first estimate of natural mortality was obtained through the model of Csirke and Caddy (1983), in which annual catch is plotted against total mortality, and in which the Z-intercept of the fitted parabola provides an estimate of M (see Fig. 5). The estimate of M = 0.878 obtained in this fashion corresponds well with the value of M obtained through the empirical equation of Pauly (1980) in which

$$\log_{10} M = -0.0066 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} K + 0.4634 \log_{10} T \qquad ...11)$$

and which leads for a mean water temperature off Peru (4 to 14°S, 1953-1982) of T = 18°C and the values of L_∞ and K obtained above, to an estimate of M = 0.675.

Averaging these two relatively independent estimates of M yields a mean value of M = 0.775 which will be used for all further computations.

The estimates of effort and of Z derived above were then combined with the estimate of M to estimate a mean catchability coefficient (q), defined as

$$F = q \cdot f \qquad \text{...12)}$$

where f is fishing effort and F is fishing mortality, defined for any given year (i) by

$$F_i = Z_i - M \qquad \text{...13)}$$

The value of q estimated from the data at hand (see Fig. 6) is q = 0.0897, which was used to compute, using equation (12), values of F given the corresponding values of effort for 1951 to 1983 (see Table 1).

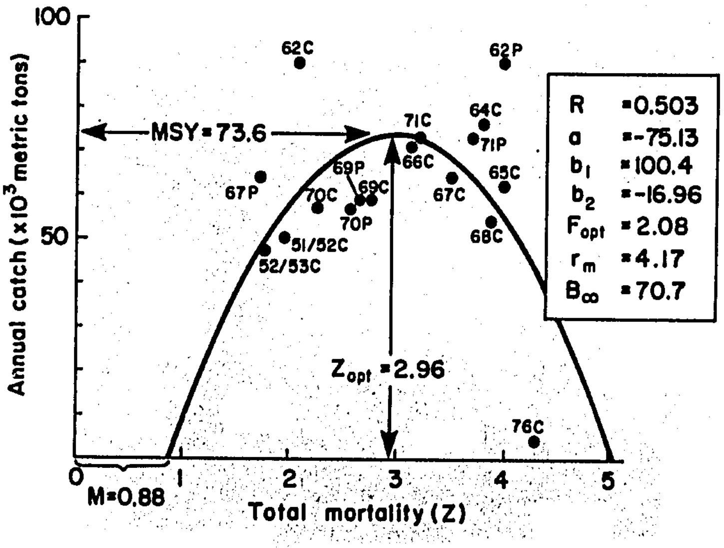

Fig. 5. "Csirke and Caddy" model of the Peruvian bonito fishery, based on data for the period 1951 to 1976 and used to obtain preliminary estimate of natural mortality. Note that estimated MSY corresponds well with value estimated using Schaefer model (see Fig. 4). (P refers to Paita, C to Callao; see Table 3).

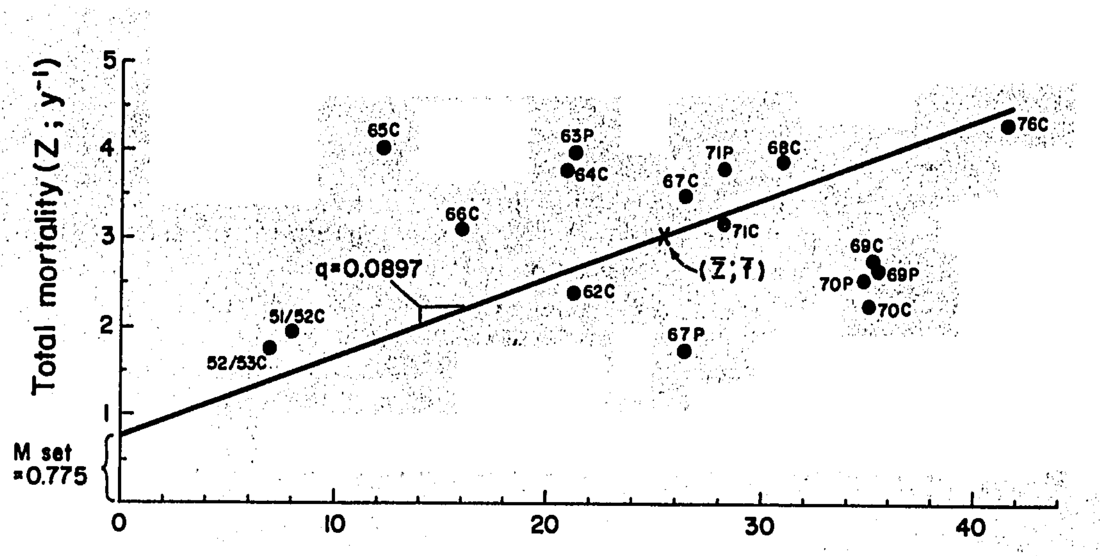

Fig. 6. Estimation of a mean catchability coefficient (q) for the Peruvian bonito fishery, 1951 to 1983. Note that the line is not a linear regression used to estimate q and M, but rather was forced through an assumed value of M (see text) and the mean of the available f and Z values (P refers to Paita, C to Callao; see Table 3).

Mean Annual and Monthly Biomass of Large Bonitos, 1953 to 1982

Mean annual biomasses (B_i), for 1953 to 1982 were estimated from

$$B_i = Y_i/F_i \qquad ...14)$$

where Y_i is the catch of a given year, and F_i the fishing mortality for that year.

It will be noted that equation (14), being used with catch figures referring to "large bonitos", will generate biomass estimates for only the "large bonito" fraction of the stock of *Sarda chiliensis chiliensis* off Peru. We accept this here, since it is only the large bonitos which prey upon anchoveta of roughly the same size as those caught by the anchoveta fishery itself (see text below and Fig. 7).

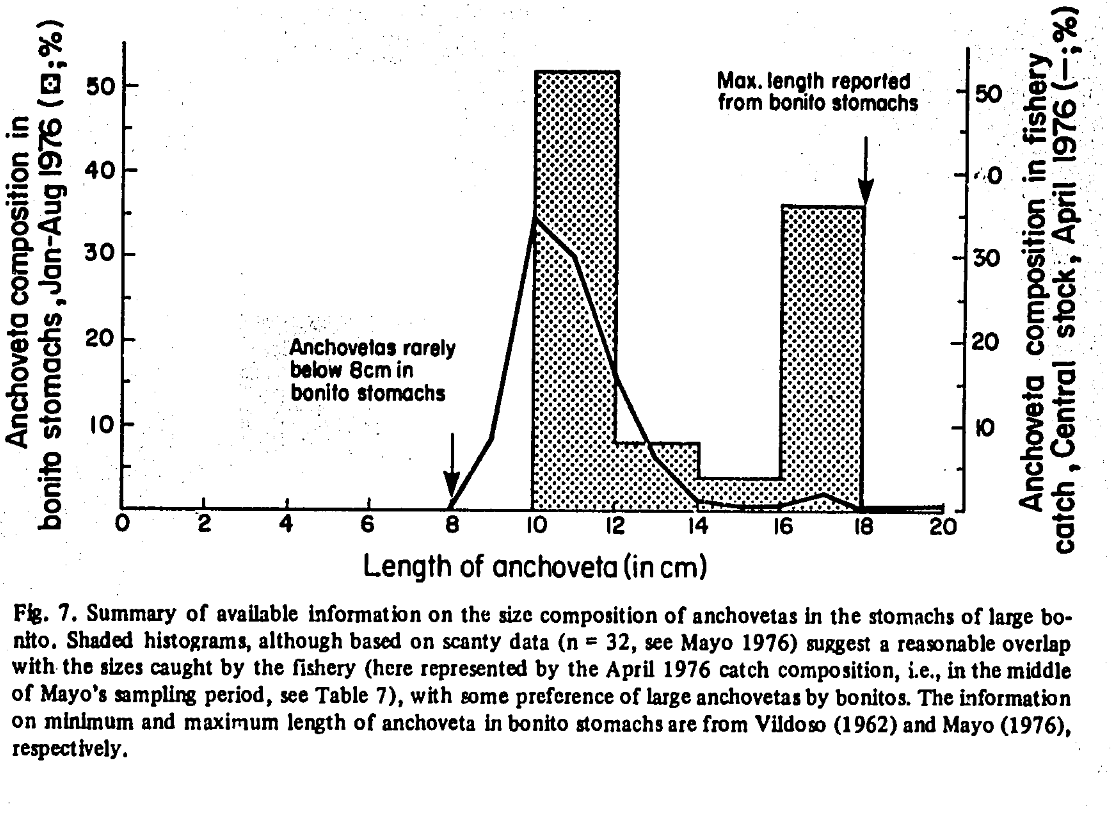

Fig. 7. Summary of available information on the size composition of anchovetas in the stomachs of large bonito. Shaded histograms, although based on scanty data (n = 32, see Mayo 1976) suggest a reasonable overlap with the sizes caught by the fishery (here represented by the April 1976 catch composition, i.e., in the middle of Mayo's sampling period, see Table 7), with some preference of large anchovetas by bonitos. The information on minimum and maximum length of anchoveta in bonito stomachs are from Vildoso (1962) and Mayo (1976), respectively.

Although the stretch of the Peruvian coast (4 to 14°S) considered here includes only 60% of the whole Peruvian coast (approximately 3 to 18°S), we have multiplied the estimates obtained through equation (14) by a factor of 0.9, to account for the fact that about 90% of the Peruvian catch of bonito actually stems from the coastal area between 4 and 14°S (Ancieta 1964, Table 4).

The values of "$Y_i 0.9/F_i$" obtained for each year from 1951 to 1983 were then smoothed (using a 3-year running mean) to account for the fact that the real biomass of large bonitos off Peru probably fluctuated less rapidly than suggested by the rapid fluctuation of fishing effort (see Table 1).

To obtain a smooth transition of the between-year estimates of biomass, the values obtained by the method outlined above were assumed to apply to the months of June and July of a given year; transitory values were derived by linear interpolation between the July estimate of a given year and the June estimate of the following one. The monthly biomass estimates obtained in this fashion are given in Table 6. This approach assumes that within-year variations of biomass are small compared with the between-year variations, which is probably true in view of the enormous fluctuation of catch experienced by the fishery in the last forty years.

Table 6. Estimated monthly biomass of large bonitos off Peru (4 to 14°S), 1953 to 1983 (in t x 10^3) derived by linear interpolation of the smoothed annual biomass estimate in Table 1, last column).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	64.50	64.50	64.50	64.40	64.40	64.40	64.40	64.10	63.80	63.50	63.20	62.90
1954	62.60	62.30	62.00	61.70	61.40	61.10	61.10	60.30	59.50	58.70	57.90	57.10
1955	56.20	55.40	54.60	53.80	53.00	52.20	52.20	52.10	52.00	51.90	51.80	51.70
1956	51.70	51.60	51.50	51.40	51.30	51.20	51.20	51.60	52.00	52.40	52.80	53.20
1957	53.60	54.00	54.40	54.80	55.40	55.60	55.60	55.30	55.10	54.80	54.50	54.20
1958	54.00	53.70	53.40	53.10	52.90	52.60	52.60	52.20	51.70	51.30	51.90	50.40
1959	50.00	49.50	49.10	48.70	48.20	47.80	47.80	47.60	47.40	47.20	47.00	46.80
1960	46.60	46.40	46.20	46.00	45.80	45.60	45.60	45.70	45.70	45.80	45.80	45.90
1961	45.90	46.00	46.00	46.10	46.10	46.20	46.20	46.60	46.90	47.30	47.70	48.10
1962	48.40	48.80	49.20	49.60	49.90	50.30	50.30	49.90	49.50	49.10	48.70	48.30
1963	47.80	47.40	47.00	46.60	46.20	45.80	45.80	46.10	46.30	46.60	46.90	47,10
1964	47.40	47.60	47.90	48.20	48.40	48.70	48.70	48.30	47.80	47.40	47.00	46.60
1965	46.10	45.70	45.30	44.90	44.40	44.00	44.00	43.60	43.30	42.90	42.50	42.10
1966	41.80	41.40	41.00	40.60	40.30	39.90	39.90	38.90	37.90	36.80	35.80	34.80
1967	33.80	32.80	31.80	30.70	29.70	28.70	28.70	27.90	27.00	26.20	25.40	24.50
1968	23.70	22.80	22.00	21.20	20.30	19.50	19.50	19.30	19.00	18.80	18.60	18.30
1969	18.10	17.80	17.60	17.40	17.10	16.90	16.90	17.20	17.40	17.70	17.90	18.20
1970	18.40	18.70	18.90	19.20	19.40	19.70	19.70	19.80	20.00	20.10	20.20	20.30
1971	20.50	20.60	20.70	20.80	21.00	21.10	21.10	20.90	20.70	20.40	20.20	20.00
1972	19.80	19.60	19.40	19.10	18.90	18.70	18.70	18.00	17.20	16.50	15.80	15.10
1973	14.30	13.60	12.90	12.20	11.40	10.70	10.70	10.10	9.50	8.90	8.30	7.70
1974	7.10	6.50	5.90	5.30	4.70	4.10	4.10	3.80	3.60	3.30	3.10	2.80
1975	2.60	2.30	2.10	1.80	1.60	1.30	1.30	1.30	1.30	1.30	1.30	1.20
1976	1.20	1.20	1.20	1.20	1.20	1.20	1.20	1.20	1.20	1.20	1.20	1.20
1977	1.20	1.20	1.20	1.20	1.20	1.20	1.20	1.20	1.20	1.20	1.20	1.20
1978	1.30	1.30	1.30	1.30	1.30	1.30	1.30	1.30	1.30	1.30	1.30	1.30
1979	1.40	1.40	1.40	1.40	1.40	1.40	1.40	1.40	1.50	1.50	1.50	1.50
1980	1.60	1.60	1.60	1.60	1.70	1.70	1.70	1.80	1.90	2.00	2.10	2.20
1981	2.20	2.30	2.50	2.50	2.60	2.70	2.70	2.80	2.80	2.90	3.00	3.10
1982	3.10	3.20	3.40	3.40	3.40	3.50	3.50	3.60	3.60	3.70	3.80	3.80

Food, Feeding Habits and Food Consumption of Bonitos

Several studies on the food habits of bonitos have been conducted in Peru (Table 7). All of them emphasize the importance of anchoveta in the diet of this predator. Fig. 7 summarizes the available data on the size distribution of anchoveta found in bonito stomachs which resembles that of anchoveta in the commercial catch (see also Tsukayama and Palomares, this vol.). Thus, the estimates of anchoveta consumption obtained below can be straightforwardly added to the commercial catch.

Several authors have presented anecdotal information on the weight of stomach contents in Peruvian bonito (Table 7), but only the data of Canal (1974) were presented in a fashion which allowed further analysis (see Table 8). Table 9 suggests that, on the average, only about half of the bonito of a given stock have food in their stomach at any given time, as is commonly reported from scombrids.

Data on stomach evacuation rate, from which food consumption estimates could be obtained using the model of Elliott and Persson (1978), are not available for any *Sarda* species, although aquarium observations on the feeding behavior of *S. chiliensis lineolata* are available (Magnuson and Prescott 1966). We shall therefore use here data obtained by Magnuson (1969) from captive skipjack (*Katsuwonus pelamis*). This approach appears justified in that bonito and skipjack - once account is taken of differences in internal and external temperature - are quite similar, particularly with regard to the shape and length of their guts (Godsil 1954; Collette 1983). Another justification for our use of data obtained from an experiment with skipjack is that these were fed small pelagic fish, the main food of Peruvian bonito, and that food type has in experiments, along with temperature, a stronger effect than the taxonomic affinities of the investigated fish (Durbin et al. 1983).

Table 7. Summary of information on major diet components of Peruvian bonito *(Sarda chiliensis chiliensis)*.

No. of bonitos examined	Major food items	% in total food	Details on stomach contents	Source and/or remarks
(?)	a) *Engraulis ringens* b) Crustaceans *(Munida cokeri)*	58.6 –	–	del Solar (1942)
345	a) *Engraulis ringens*		anchoveta occurring in 60.6% of stomachs; remaining stomachs were empty	Ancieta (1945, 1964), based on data collected from November 1944 to January 1945
191	a) *Engraulis ringens*	–	anchoveta occurring in all stomachs examined	De Buen (1958); data collected off northern Chile
192	a) *Engraulis ringens* b) Crustaceans (mainly *Munida cokeri*) c) Unidentified items	76 1 23	usually 5-6 anchoveta (60-80 g, max. of 330 g)	Some other pelagic fishes, notably *Sardinops sagax*, *Austramenida regia* and *Prinotus quiescens* also reported from bonito stomachs by earlier authors (Vildoso 1955)[a]
2,640	a) *Engraulis ringens* (plus some other fishes)	77-85	size of anchoveta 12-14 cm, max. of 28 cm, max. weight of stomach content is 404 g	Canal (1974)[b]
206	a) *Engraulis ringens* b) Miscellaneous fishes and invertebrates	>27 <73	see Fig. 7 for size distribution of anchoveta	Mayo (1976)[c] based on data collected from January to August 1976

[a] These results are reported again in Vildoso (1962), along with the remarks that *(i)* the mean stomach contents of bonitos are usually proportional to their weight, although there is much variability; *(ii)* females of a given length have smaller stomach contents than males of the same length; *(iii)* stomach content weights of more than 50 g always consist of anchoveta; *(iv)* the size of anchoveta in bonito stomach is rarely less than 8 cm and that *(v)* the highest stomach content observed was 500 g, and the bulk of it consisted of 52 identifiable anchoveta.

[b] See Table 8 for more detail on this study, notably for stomach contents expressed in % of body weight. Also note that field data were collected from April 1967 to September 1972 (without samples in 1970).

[c] Note that the miscellaneous fishes reported by Mayo (1976) from bonito stomachs all tended to be larger than anchoveta, and ranged between 13 and 31 cm.

Durbin et al. (1983), based on Fig. 2 in Magnuson (1969), estimated a value of 8.5 (per day) for the instantaneous rate of stomach evacuation (R) in *K. pelamis*, held at a temperature of about 25°C. They also estimated from data on a number of fish species a mean value of b = 0.115 for the exponent of a generalized relationship linking, in fishes, stomach evacuation rate (R) and temperature (T) of the form

$$R = a \cdot e^{bT} \qquad \text{...15)}$$

Solving for the value of R = 8.5 gives a = 0.48. Magnuson (1969) used fish between 39 and 50 cm, with a mean weight of 1.6 kg. We shall assume that the relationship between R and body weight is, as most other physiological processes controlled by metabolic level, i.e., by the relationship between body weight and gill surface area (Pauly 1981). This relationship in skipjack is

$$\text{Gill surface area} \propto W^{0.85} \qquad \text{...16)}$$

Table 8. Relationship between body weight and mean stomach content weight in *Sarda chiliensis chiliensis*.[a]

No	Body weight[b] (in g)	Mean stomach content (in g)	n	Stomach content (as % of body weight)
1	421	9.0	18	2.14
2	625	14.5	20	2.32
3	827	23.1	28	2.79
4	1,028	18.0	13	1.75
5	1,228	18.1	26	1.47
6	1,429	16.6	38	1.16
7	1,629	12.4	49	0.76
8	1,830	21.2	64	1.16
9	2,030	21.3	106	1.05
10	2,230	41.0	134	1.84
11	2,430	37.7	132	1.55
12	2,631	4.5	89	1.77
13	2,831	56.0	74	1.98
14	3,031	59.0	47	1.95
15	3,231	48.5	8	1.50
16	3,431	9.4	7	0.27
17	3,631	213.5	2	5.88
18	3,831	46.5	1	1.21
19	4,031	315.0	1	7.81
20	4,944	209.0	1	4.23
			858	1.6045[c]

[a] Adapted from Table VII in Canal (1974); note that fish with stomachs considered "empty" are not included here.

[b] Original data were grouped in weight classes; presented here are the geometric means of the lower and upper class limit (except No. 20, which is the actual weight).

[c] Weighted mean content of stomachs that were not empty. Note that this value refers to anchoveta plus a number of other organisms, notably the fishes *Odontestes (= Austramenidia) regia*, *Trachurus murphyi*, *Normanichthys crokeri* and *Prionotus (quiescens?)*. Other organisms identified were *Loligo* sp. (but probably not *L. opalescens*, as reported), Octopus sp., *Munida cokeri* and unidentified euphausids.

The value of m (mean stomach content, in % BWD) in the text considers the stomachs reported to be empty (see Table 9, footnote b) and is thus m = 1.6045 (1 – 0.514) = 0.78 i.e., m = 0.8%.

(Muir 1969; Muir and Hughes 1969) which would lead to a decline of R with weight such that

$$R \propto W^{-0.15} \qquad ...17)$$

Gooding et al. (1981) report a positive exponent for the respiration-weight relationship of skipjack, but also note that their "weight coefficient is opposite in sign from that typical of fishes (and of organisms, generally)" for which reason their results will not be considered further.

Combining equation (17) with equation (15), and solving for the mean fish weight in Magnuson's experiments leads to

$$R = 1.45\, W^{-0.15} \cdot e^{0.115T} \qquad ...18)$$

as generalized equation relating evacuation rate, body weight and temperature in skipjack and, by inference, also in bonito.

Table 9. Percentage of empty stomachs reported from studies on the food and feeding habits of bonito in the Pacific[a] *(Sarda orientalis* and *Sarda chiliensis).*

Species	Area	% of empty stomachs	No. of fish sampled	Source
Sarda orientalis	Southern Kyushu Coast (Japan)	83.3	18	Yabe et al. (1953); not seen, as cited in Silas 1964)
Sarda orientalis	Southern Kyushu Coast (Japan)	50	24	Yokota et al. (1961); not seen, as cited in Silas (1964, Table X)
Sarda chiliensis lineolata	Southern California	55.2	1,498	Oliphant (1971)
Sarda chiliensis chiliensis	off Callao (Peru)	49.4	345	Ancieta (1945, as cited in Ancieta 1964)
Sarda chiliensis chiliensis	off Callao (Peru)	77	992	Vildoso (1955)
Sarda chiliensis chiliensis	off Callao (Peru)	42.4	2,640	Canal (1974)
Sarda chiliensis chiliensis	Peruvian Coast	46.6	206	Mayo (1976)
Sarda chiliensis chiliensis	Peruvian Coast	51.4	4,813	this study[b]

[a] None of these studies provides data on seasonal changes of the % of empty stomachs.

[b] Estimated by taking the mean % (weighted by sample size) of the four values reported from Peru.

Elliott and Persson (1978) derived a model in which food consumption (Q) is computed as the product of mean stomach content (m) and instantaneous stomach evacuation rate (R), or

$$Q = R \cdot m \qquad ...19)$$

which applies to a given fish size (age). To estimate food consumption per unit biomass (Q/B) of an age-structured fish population, equation (19) can be extended to a model of the form

$$\frac{Q}{B} = \frac{\int_{t_r}^{t_{max}} (R_t \cdot m_t \cdot N_t)dt}{\int_{t_r}^{t_{max}} (W_t \cdot N_t)dt}$$

where R_t is the stomach evacuation rate expressed as a function of age (obtained by insertion of equation (15) into equation (9)), W_t the age at age t, see equation (9), t_r and t_{max} are the age at recruitment and the maximum age reached by bonitos respectively, m_t the mean stomach content expressed as a function of age (obtained by multiplying W_t by the mean stomach content expressed as a fraction of body weight, here 0.008 (see Table 8), and N_t is the number of fishes in the population.

The simplest fashion by which N_t can be modelled realistically is by using

$$N_t = e^{-Z(t-t_r)} \qquad ...21)$$

with $N = 1$ when $t = t_r$.

Age at "recruitment" will be set here at $t_r = 2$, nearly corresponding to the age at which *cerrajon* (i.e., middle-sized bonito) reach 50 cm, and hence recruit into the stock of "large bonitos".

All terms of equation (20) are available as continuous functions of t, and can be numerically integrated. The integrations were performed using a BASIC program (available from the first author) on a monthly basis, i.e., using the temperature value for the month in question and monthly estimates of "F", the latter values being computed, as defined in equation (14) from the monthly biomass of a given year in Table 6, and the annual catch for the same year in Table 1. (Note that the monthly values of F so obtained are not necessarily proportional to *monthly* fishing effort).

The estimates of Q/B obtained through equation (20) (see Table 10) are well within the range of rations estimated for tunas (Table 11), while being, as should be expected, above values typical of less active fishes (see Durbin et al. 1983).

Table 10. Estimated values of Q/B (daily ration in % of body weight) for large bonito off Peru (4 to 14°S). See text for variables and constants used.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	3.97	4.80	5.73	5.05	4.06	3.38	3.30	3.01	3.08	2.95	3.02	3.23
1954	3.66	3.88	3.62	3.12	2.85	2.57	2.72	2.35	2.46	2.49	2.71	3.57
1955	5.03	4.38	3.57	3.84	3.27	3.20	3.13	2.89	3.03	2.83	2.96	3.21
1956	3.95	4.64	4.86	4.14	3.87	3.69	3.61	3.36	3.21	3.06	3.13	3.05
1957	3.48	5.84	5.70	5.50	5.75	5.12	4.62	3.84	3.43	3.51	3.51	4.79
1958	5.61	5.87	5.74	4.62	3.98	3.72	3.63	3.24	3.25	3.29	3.45	3.26
1959	4.25	5.47	5.12	4.57	4.12	3.72	3.36	3.24	3.32	3.48	3.65	4.10
1960	4.40	4.67	4.51	3.93	3.59	3.55	3.35	3.43	3.39	3.35	3.35	3.76
1961	4.47	5.38	4.63	4.32	4.08	3.68	3.43	3.39	3.30	3.30	3.30	3.45
1962	4.33	4.37	3.89	3.59	3.67	3.42	3.26	3.19	3.27	3.06	3.20	3.25
1963	3.61	4.24	4.56	3.98	4.07	3.85	3.76	3.63	3.59	3.46	3.46	3.88
1964	4.23	4.48	4.32	3.68	3.06	2.85	2.75	2.89	2.92	3.00	3.07	3.07
1965	3.51	4.42	4.86	5.39	4.98	4.40	4.15	3.88	3.54	3.50	3.68	3.99
1966	4.74	5.02	4.38	3.87	3.61	3.34	3.19	3.13	2.93	3.16	3.28	3.41
1967	4.04	4.66	4.43	3.74	3.47	3.22	3.19	2.95	2.97	2.85	2.90	3.39
1968	3.81	3.83	4.27	3.46	3.40	3.09	3.20	3.28	3.44	3.33	3.54	3.76
1969	4.60	4.77	5.62	5.70	6.06	5.11	4.01	3.95	3.90	3.93	3.92	4.14
1970	4.82	5.15	5.26	4.73	4.46	4.06	3.62	3.65	3.65	3.82	3.68	3.77
1971	4.41	4.89	5.17	5.28	4.65	4.28	4.28	4.29	4.01	3.76	3.90	3.95
1972	4.56	5.72	6.58	6.30	6.03	6.33	6.11	5.43	4.83	4.93	5.16	6.64
1973	7.32	7.22	5.99	4.33	3.91	3.60	3.36	3.21	3.33	3.58	4.04	3.80
1974	3.16	3.67	3.89	4.10	4.02	4.35	3.66	3.38	3.15	3.08	3.38	3.36
1975	3.33	3.98	5.71	5.04	4.49	3.85	3.76	3.51	3.47	3.43	3.31	3.70
1976	3.90	6.04	6.25	5.14	5.26	5.32	5.02	4.85	4.08	4.28	4.48	5.51
1977	6.11	6.18	6.25	6.25	5.26	4.74	4.43	4.13	3.95	3.95	4.23	4.53
1978	4.33	5.44	5.38	4.91	4.13	3.64	3.68	3.40	3.52	3.68	3.90	3.99
1979	4.63	4.63	5.02	4.90	4.52	4.03	4.08	4.08	3.84	3.92	4.02	4.46
1980	4.81	4.92	5.28	5.10	4.58	4.42	4.18	3.80	3.67	3.64	3.73	4.01
1981	4.15	4.82	4.62	4.47	4.54	4.06	3.71	3.68	3.43	3.74	3.68	3.68
1982	4.59	5.21	5.34	5.17	5.41	4.95	4.84	4.37	4.32	5.28	7.06	8.69

Monthly Anchoveta Consumption by Bonito, 1953 to 1982

There are two basic approaches by which the anchoveta consumption by bonitos in the Peruvian upwelling system could be computed for the period 1953 to 1982, using the information presented above.

One, rather straightforward, could consist of multiplying, for each month, the biomasses in Table 6 by the Q/B estimates in Table 10, then multiplying these estimates of absolute food consumption by some constant factor expressing the average proportion of anchoveta in the diet of bonito.

Table 11. Estimates of daily ration in four scombrid species.

Species	Area (temperature)	Daily ration[a]	Size/age groups	Source/remarks
Scomber scombrus	Georges Bank (8°C)	0.93-1.42	1-9 yrs	Grosslein et al. (1980, Table 21)
Thunnus albacares	Eastern Pacific (24°)	6.60	30-54 cm (age I)	Computed from Fig. 4 and Table 1 in Olson (1981) and a length-weight relationship of $W = 0.02L^3$, (FL in cm, W in g.)
"	"	3.20	55-85 (age II)	
"	"	2.10	86-121 (age III)	
"	"	2.60	122-160 (age IV)	
"	"	3.9	23.6-45.1 cm	food dynamics Olson and Boggs (1986)
"	"	5.2	n.a.	bioenergetics
"	"	6.2	age 1 and 2	caesium dynamics
Katsuwonus pelamis	Bioenergetic model (24°C)	5.90	1 kg	maintenance ration Kitchell et al. 1978
"	"	7.30-19.0	1 kg	growing fish
"	"	30.00	1 kg	maximum intake
Sarda chiliensis	off Peru (14°C)	2.23	ages 2-12 years (length 50-75 cm and W = 1.6 to 5.5 kg age-structured population (with F = 1 and M = 0.775)	this study
"	" (16°C)	2.80		
"	" (18°C)	3.53		
"	" (20°C)	4.44		
"	" (22°C)	5.59		
"	" (24°C)	7.04		

[a] % of body weight

Table 12. Values of the proportion of anchoveta in the diet of large bonitos, used for estimating their consumption of *E. ringens* for the years 1953 to 1982.

Period	Assumed proportion of anchoveta in the diet of large bonito	Rationale
January 1953 to December 1971	0.75	During this period of high anchoveta abundance about 0.75 of the food consumed by large bonitos consisted of *E. ringens* (see Table 7)
January 1972 to December 1973	Proportion declining linearly from 0.75 to 0.25	1972 and 1973 are the years when the anchoveta stock collapsed (see other contributions in this vol.)
January 1973 to December 1982	0.25	The only available estimate for the period of low anchoveta abundance suggests about 0.25 of the food of large bonito consists of *E. ringens* (see Table 7)

The other, more elaborate alternative, could consist of deriving a density-dependent model of anchoveta predation by bonito similar to the ones developed for the mammals and the birds of the Peruvian upwelling ecosystem (see Muck and Fuentes, and Muck and Pauly, respectively, this vol.).

We have opted for an intermediate approach which acknowledges the feature that bonito, as opposed to air-breathing birds and mammals can pursue their prey into any depth and location along the coast, and hence are able to maintain a relatively constant proportion of anchoveta in their diet, yet takes into account the major reduction of anchoveta biomass which occurred in 1972/1973 (see Table 12). The results are presented in Table 13.

Table 13. Estimated anchoveta consumption in t x 10^3 by large bonitos off Peru (4 to 14°S), 1953 to 1983 (based on Tables 6, 10 and 12 and on constants presented in the text).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Annual sum
1953	59.50	68.50	85.90	73.20	60.80	50.00	47.80	44.90	44.20	43.40	42.90	47.20	668.30
1954	53.30	57.80	52.20	43.30	40.70	35.30	38.60	32.90	32.90	34.00	35.30	47.40	503.70
1955	65.70	52.80	45.30	46.50	40.30	37.60	38.00	35.00	35.50	34.10	34.50	38.60	503.90
1956	47.50	50.30	58.20	47.90	46.20	42.50	43.00	40.30	37.60	37.30	37.20	37.70	525.50
1957	43.40	68.60	72.10	67.80	73.80	64.10	59.70	49.40	42.50	44.70	43.00	60.40	689.50
1958	70.40	68.60	71.30	55.20	49.00	44.00	44.40	39.30	37.80	39.20	39.50	38.20	596.90
1959	49.40	58.90	58.40	50.10	46.20	40.00	37.30	35.90	35.40	38.20	38.60	44.60	533.00
1960	47.70	45.50	48.40	40.70	38.20	36.40	35.50	36.40	34.90	35.70	34.50	40.10	474.10
1961	47.70	53.80	49.50	44.80	43.70	38.30	36.80	36.70	34.80	36.30	35.40	38.60	496.50
1962	48.70	46.40	44.50	40.10	42.60	38.70	38.10	37.00	36.40	34.90	35.10	36.50	479.00
1963	40.10	43.70	49.80	41.70	43.70	39.70	40.00	38.90	37.40	37.50	36.50	42.50	491.60
1964	46.60	44.80	48.10	39.90	34.40	31.20	31.10	32.50	31.40	33.30	32.50	33.30	439.10
1965	37.60	43.90	51.20	54.50	51.40	43.60	42.50	39.30	34.50	34.90	35.20	39.10	507.60
1966	46.10	45.20	41.80	35.40	33.80	30.00	29.60	28.30	25.00	27.00	26.40	27.60	396.10
1967	31.70	33.20	32.80	25.80	24.00	20.80	21.30	19.10	18.00	17.40	16.60	19.30	280.00
1968	21.00	18.30	21.80	16.50	16.00	13.60	14.50	14.70	14.70	14.60	14.80	16.00	196.60
1969	19.40	18.50	23.00	22.30	24.10	19.40	15.80	15.80	15.30	16.20	15.80	17.50	223.00
1970	20.60	20.90	23.10	20.40	20.10	18.00	16.60	16.80	16.40	17.90	16.70	17.80	225.40
1971	21.00	21.90	24.90	24.70	22.70	20.30	21.00	20.80	18.70	17.80	17.70	18.40	250.00
1972	17.70	17.10	16.40	15.70	15.10	14.40	13.70	13.10	12.40	11.70	11.10	10.40	168.80
1973	9.70	9.00	8.40	7.70	7.00	6.40	5.70	5.00	4.40	3.70	3.00	2.40	72.40
1974	1.70	1.70	1.80	1.60	1.50	1.30	1.30	1.00	0.90	0.80	0.80	0.70	15.00
1975	0.70	0.70	0.90	0.70	0.60	0.40	0.40	0.40	0.30	0.30	0.30	0.30	6.00
1976	0.40	0.50	0.60	0.50	0.50	0.50	0.50	0.50	0.40	0.40	0.40	0.50	5.50
1977	0.60	0.50	0.60	0.60	0.50	0.40	0.40	0.40	0.40	0.40	0.40	0.40	5.50
1978	0.40	0.50	0.50	0.50	0.40	0.40	0.40	0.30	0.30	0.40	0.40	0.40	5.00
1979	0.50	0.50	0.50	0.50	0.50	0.40	0.40	0.40	0.40	0.50	0.50	0.50	5.60
1980	0.60	0.60	0.70	0.60	0.60	0.60	0.60	0.50	0.50	0.60	0.60	0.70	7.00
1981	0.70	0.80	0.90	0.80	0.90	0.80	0.80	0.80	0.70	0.80	0.80	0.90	9.80
1982	1.10	1.20	1.40	1.30	1.40	1.30	1.30	1.20	1.20	1.50	2.00	2.60	17.50

Discussion

Although the data available for this investigation are somewhat spotty, they provided results that are comparable with those obtained elsewhere with comparable fishes and which match what might have been expected, given the previous knowledge on the Peruvian bonito and its fishery.

Growth parameters were obtained which match those in other *Sarda* stocks, while similar estimates of natural mortality were derived, using two widely different methods.

Also, two similar estimates of MSY (82.4 x 10^3 and 73.6 x 10^3 t/year) were obtained, along with corresponding estimates of optimum fishing mortality, both surplus production models suggesting that the bonito stock off Peru became seriously overfished in the 1960s, and virtually, collapsed in the 1970s.

This decline through overfishing is consistent with the observed decline of mean size (length and weight) occurring during the period considered here (Table 1). A similar decline, in fact seems to have also occurred in the Chilean bonito fishery (Serra et al. 1980). Thus, we see no reason to agree with earlier statements to the effect that the reduction of the mean size of bonito was caused by the decline of the anchoveta, their favorite prey.

It can be expected, obviously, that the availability of anchoveta has had an effect on the abundance of bonito. However, such effect might be indirect, e.g., through the production of eggs by the bonito spawning stock and the survival of juveniles (on which absolutely no quantitative data are available).

The estimates of food consumption per unit biomass (Q/B) appear reasonable when compared with Q/B estimates in other scombrids. These estimates, when multiplied with the estimated biomass of large bonito indicate that, at their peak, the large bonitos off Peru devoured approximately 500,000-700,000 t/year of anchoveta. These values make bonito an anchoveta predator whose impact is between that of the fish-eating birds and that of the seals (see Muck and Pauly this vol. and Muck and Fuentes, this vol.).

Interestingly, it also turns out that the "educated guesses" of anchoveta consumption by bonito, cited in the introduction, were of the right order of magnitude, even though they were based on rather tenuous assumptions.

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Abundance of Sardine, Mackerel and Horse Mackerel Eggs and Larvae and Their Relationship to Temperature, Turbulence and Anchoveta Biomass off Peru*

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Abstract

Data from 81 egg and larval surveys conducted from 1964 to 1986 off Peru were analyzed with emphasis on the interrelationships between sardine eggs, larvae of mackerel and horse mackerel, sea surface temperature (SST) and SST anomaly, turbulence and anchoveta biomass. A significant negative correlation was found between anchoveta biomass and sardine eggs, while a significant positive correlation was found to occur between SST and the abundance of mackerel and horse mackerel larvae. Some biological implications of these findings are provided.

Introduction

Sardine (*Sardinops sagax*), mackerel (*Scomber japonicus*) and horse mackerel (*Trachurus murphyi*) are important predators of Peruvian anchoveta (*Engraulis ringens*). Sardine has been shown to prey on anchoveta eggs (Santander et al. 1983) while the two other species have been found to ingest anchoveta of all sizes (see Muck and Sanchez, this vol.).

Information on the biomass of sardine, mackerel and horse mackerel off Peru are available only since 1977 (see Muck and Sanchez, this vol.). Annual catch statistics are available for earlier years but complementary information (such, e.g., as detailed effort data) are missing which, after calibration, could be used to turn these earlier catch figures into absolute biomass estimates for each of these three species. On the other hand, egg and larval surveys have been conducted since 1964 whose results could be used to infer the relative abundance of sardine, mackerel and horse mackerel off Peru.

The present contribution presents a preliminary analysis of data obtained from the surveys, with emphasis on two questions:

i) Were earlier abundances (1964-1976) in these three species markedly different from more recent ones (1977-1986)?

ii) If so, what are the possible reasons for the change?

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*PROCOPA Contribution No. 54.

Materials and Methods

The data used here stem from 81 egg and larval surveys conducted off Peru from 1964 to 1986 (Table 1). Sampling was performed as described, for anchoveta eggs, by Santander and Castillo (1969) and Santander (this vol.), who also describes the sampling gear. The surveys ranged from 10 nautical miles (nm) to 220 nm offshore (mean 90 nm), and, on the average, from 5 to 17°S (see Table 1). Because of the wide differences in the areas covered by the various surveys, the eggs and larvae sampled were not related to the survey area and expressed as absolute numbers (as was done for anchoveta eggs; see Santander, this vol.). Rather, eggs or larvae have been related to the sampling area through

$$\text{eggs/m}^2 = \text{total eggs sampled/(no. of hauls} \cdot 0.3) \quad ...1)$$

for sardine, and

$$\text{larvae/m}^2 = \text{total larvae sampled/(no. of hauls} \cdot 0.3) \quad ...2)$$

for mackerel and horse mackerel.

Results and Discussion

Table 1 summarizes the key results of the 81 egg and larval surveys which form the basis of this contribution.

Sardine eggs were found in 71% of the surveys. Mackerel larvae occurred more frequently (56%) than horse mackerel larvae (34%), and a similar relationship is obtained when one campares their mean larvae densities, of 1.07 *vs.* 0.31 larvae/m^2, respectively, for the period 1964-1986. For the period 1977-1986, the apparent dominance of mackerel over horse mackerel is even stronger, the ratio between their respective values of 0.85 and 0.06 larvae/m^2 being 14:1.

However, this ratio, suggesting a dominance of mackerel over horse mackerel does not match what is known on the relative biomasses and catches of these two species. Thus, in each of the nine acoustic surveys conducted between 1977 and 1986, horse mackerel was found to have higher biomass than mackerel. The mean ratio between these biomasses (3.2:1) is indeed very similar to the mean ratio of their catches during the same period (3.1:1), see Muck and Sanchez, this vol.).

The main spawning area of horse mackerel off Peru appears to be off the shelf edge, 200 nm offshore, about 16°S (Rojas and Mujica 1981; Santander and Flores 1983; Zuzunaga 1986). Given the limits of the surveys in Table 1, it is obvious that only a small fraction of the horse mackerel larvae occurring off Peru have been sampled. We shall, therefore, abstain from performing detailed analyses of the data on horse mackerel larvae given in Table 1.

Table 2 shows that both sardine and mackerel have two spawning peaks per year, the sardine in January and September and the mackerel in March and July-September. Horse mackerel larvae were found from August to April with a peak in September, but, as mentioned above, the data for this species are too scanty for a clear seasonal pattern to emerge. It will also be noted that direct relationships between the seasonality of spawning and SST occur in none of the three species (Table 2).

Table 1 shows that sardine were virtually absent from ichthyoplankton samples before 1972. This feature is emphasized in Table 3, and contrasted with the abundance of mackerel and horse mackerel larvae, which did not markedly change during the two periods distinguished here. In this preliminary analysis, we have examined three factors likely to impact on ichthyoplankton survival and hence, its relative abundance: (i) SST, (ii) turbulence and (iii) anchoveta biomass.

The temperature time series used here to compute means and anomalies for 1964 to 1982 stem from Table 2 in Pauly and Tsukayama (this vol.), with updates to July 1986, as given in Table 4. The wind-based turbulence data (in m^3/s^3) for 1964 to 1985 are from Mendo et al. (this vol.; Tables 4 and 5) and pertain to Trujillo and Callao, respectively. The anchoveta biomass used here are the preliminary estimates documented in Table 3 of Muck and Pauly (this vol.).

Table 1. Egg and larvae abundance of sardine, mackerel and horse mackerel recorded off Peru, during surveys conducted from 1964 to 1986.

									Number of eggs or larvae								
			Sampling area				Sardine			Mackerel			Horse mackerel			Temperature	Temperature anomaly
Survey no.	Year	Month	from (°S. min.)	to	Miles offshore	No. samples	Positive samples	No. eggs	Egg/m^2	Positive samples	No. larvae	Larvae/m^2	Positive samples	No. larvae	Larvae/m^2	(°C)	(°C)
1	1964	2	4.07	15.19	80	135	0	0	0.00	10	106	2.62	0	0	0.00	19.5	−0.50
2		5	4.00	19.05	90	166	0	0	0.00	0	0	0.00	0	0	0.00	16.2	−2.47
3		8	3.08	19.02	90	206	0	0	0.00	0	0	0.00	7	7	0.11	15.7	−1.23
4		11	4.15	19.59	80	212	0	0	0.00	0	0	0.00	0	0	0.00	16.2	−0.95
5	1966	2	3.57	19.00	140	95	0	0	0.00	3	308	10.81	1	1	0.04	20.4	0.40
6		5	3.58	18.55	120	125	0	0	0.00	0	0	0.00	0	0	0.00	17.5	−1.17
7		8	4.00	18.43	100	157	0	0	0.00	0	0	0.00	2	3	0.06	16.2	−0.73
8		11	3.57	19.01	120	129	0	0	0.00	0	0	0.00	1	1	0.03	16.5	0.65
9	1967	2	4.15	20.18	120	156	1	2	0.04	4	4	0.09	0	0	0.00	19.6	−0.40
10		5	4.15	19.04	120	87	0	0	0.00	0	0	0.00	0	0	0.00	16.9	−1.77
11		9	4.15	20.49	100	191	1	12	0.21	3	4	0.07	12	33	0.56	15.4	−1.32
12		11	4.00	19.05	120	141	1	1	0.02	3	4	0.09	23	345	8.15	15.1	−2.05
13	1968	2	7.42	20.52	120	121	2	18	0.50	0	0	0.00	1	3	0.08	17.6	−2.40
14		9	4.04	19.19	150	83	0	0	0.00	0	0	0.00	3	5	0.20	16.4	−0.32
15		11	4.15	18.58	80	87	0	0	0.00	0	0	0.00	0	0	0.00	16.6	−0.55
16	1969	1[a]	3.25	11.53	60	35	2	871	82.95	0	0	0.00	0	0	0.00	18.7	−0.27
17		6	12.31	18.20	100	39	0	0	0.00	0	0	0.00	0	0	0.00	19.5	1.51
18		7	3.30	12.30	100	28	0	0	0.00	0	0	0.00	0	0	0.00	17.4	−0.03
19		8	6.56	14.18	60	107	8	342	10.65	0	0	0.00	1	1	0.03	17.3	0.37
20	1970	5	3.18	11.56	60	30	1	36	4.00	0	0	0.00	0	0	0.00	18.6	−0.07
21		9	4.15	18.15	80	63	1	31	1.64	0	0	0.00	0	0	0.00	16.9	0.18
22		10	5.15	13.50	60	35	0	0	0.00	0	0	0.00	0	0	0.00	17.3	0.50
23		11	3.35	18.18	90	79	0	0	0.00	3	4	0.17	1	1	0.04	17.0	−0.15
24	1971	5	3.29	17.31	120	46	0	0	0.00	0	0	0.00	0	0	0.00	18.7	0.03
25		8	4.00	17.40	100	43	2	5	0.39	0	0	0.00	0	0	0.00	18.0	1.07
26		11	3.33	17.31	100	74	0	0	0.00	1	10	0.45	0	0	0.00	17.1	−0.05
27	1972	3	3.16	18.13	120	102	5	78	2.55	21	239	7.81	0	0	0.00	21.8	1.73
28		7	6.50	18.22	80	74	10	1,470	66.22	14	127	5.72	0	0	0.00	21.1	3.67
29		8	4.30	18.20	80	200	22	1,768	29.47	15	83	1.38	0	0	0.00	20.0	3.07
30		9	5.10	18.25	100	269	3	231	2.86	48	185	2.29	29	177	2.19	18.9	2.18
31		10	4.25	18.25	100	400	14	80	0.67	76	175	1.46	6	6	0.05	19.0	2.20
32		12	3.00	12.30	100	109	0	0	0.00	8	14	0.43	2	7	0.20	21.4	3.56
33	1973	1	5.05	18.12	100	364	15	1,510	13.83	58	709	6.49	0	0	0.00	23.2	4.23
34		3	3.35	17.35	100	84	4	15	0.60	11	95	3.77	0	0	0.00	21.3	1.23
35		8	7.12	14.00	80	168	12	437	8.67	0	0	0.00	0	0	0.00	15.5	−1.43
36		9	6.02	18.36	100	313	7	80	0.85	9	39	0.42	17	57	0.61	15.7	−1.02
37		11	5.15	18.20	90	300	8	35	0.39	5	11	0.12	13	898	9.97	17.1	−0.05
38	1974	2	4.05	13.55	80	298	23	1,035	11.58	41	283	3.17	0	0	0.00	18.2	−1.80
39		5	5.05	18.28	80	402	13	1,596	13.23	0	0	0.00	0	0	0.00	18.6	−0.07
40		8	6.00	18.20	90	344	61	13,394	129.79	6	8	0.08	0	0	0.00	16.8	−0.13
41		9	5.45	18.25	100	337	91	3,221	31.86	3	36	0.36	0	0	0.00	16.1	−0.62
42		11	4.30	18.15	40	179	8	28	0.52	0	0	0.00	0	0	0.00	16.5	−0.65

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[a] Data for this cruise not used for further analysis because of narrow range of latitude covered.

Continued

Table 1. Continued

Survey no.	Year	Month	Sampling area from (°S. min.)	Sampling area to (°S. min.)	Miles offshore	No. samples	Number of eggs or larvae: Sardine Positive samples	Sardine No. eggs	Sardine Egg/m²	Mackerel Positive samples	Mackerel No. larvae	Mackerel Larvae/m²	Horse mackerel Positive samples	Horse mackerel No. larvae	Horse mackerel Larvae/m²	Temperature (°C)	Temperature anomaly (°C)
43	1975	2	6.05	18.20	80	248	21	446	5.99	41	550	7.39	2	2	0.03	18.1	−1.90
44		6	5.20	18.25	100	282	43	4,171	49.30	23	77	0.91	4	4	0.05	16.1	−0.83
45		9	4.25	18.33	80	351	32	3,744	35.56	0	0	0.00	0	0	0.00	16.0	−0.72
46		11	4.00	12.00	70	67	0	0	0.00	1	3	0.15	0	0	0.00	15.6	−1.55
47	1976	1	5.20	18.20	70	303	26	24,609	270.73	31	80	0.88	12	24	0.26	17.2	−1.77
48		7	3.46	18.20	100	125	25	2,383	63.55	5	44	1.17	0	0	0.00	19.4	1.97
49		8	5.00	18.12	60	331	127	14,346	144.47	23	78	0.79	7	33	0.33	19.1	2.17
50		10	3.30	18.18	60	173	49	5,284	101.81	16	48	0.92	1	1	0.02	18.0	1.20
51	1977	3	4.00	18.00	70	345	63	15,441	149.19	73	460	4.44	0	0	0.00	20.6	0.53
52		4	5.15	13.55	20	26	7	608	77.95	1	7	0.90	0	0	0.00	20.6	1.31
53		7	6.20	13.80	70	307	56	15,177	164.79	0	0	0.00	0	0	0.00	17.6	0.17
54		8	12.20	18.00	30	117	67	16,404	467.35	3	3	0.09	0	0	0.00	17.0	0.07
55		10	5.30	18.30	100	338	46	4,327	42.67	6	11	0.11	6	7	0.06	16.6	−0.20
56	1978	3	5.50	18.17	30	193	10	470	8.12	24	53	0.92	0	0	0.00	19.9	−0.17
57		7	5.00	18.20	80	251	75	20,054	266.32	0	0	0.00	0	0	0.00	16.6	−0.83
58		10	4.55	13.40	20	90	10	6,421	237.81	1	1	0.04	0	0	0.00	16.5	−0.20
59		12	4.00	18.00	40	195	27	14,453	247.06	1	1	0.02	0	0	0.00	17.3	−0.54
60	1979	2	3.30	18.17	80	259	54	9,160	117.89	36	138	1.78	1	2	0.03	18.5	−1.50
61		9	3.30	18.17	100	346	222	89,177	859.12	17	205	1.97	2	3	0.03	17.0	0.28
62		11	3.45	18.21	60	87	13	489	18.74	5	14	0.54	0	0	0.00	17.4	0.25
63	1980	2	4.30	18.70	80	285	108	18,218	213.08	35	222	2.60	1	1	0.01	18.8	−1.20
64		9	3.00	18.20	100	267	119	3,583	44.73	0	0	0.00	10	12	0.15	16.6	−0.12
65	1981	4	6.00	18.20	100	151	33	2,207	48.72	5	23	0.51	1	1	0.02	18.3	−0.99
66		8	6.14	14.00	90	925	265	51,173	184.41	0	0	0.00	1	1	0.01	16.8	−0.13
67		10	4.50	18.20	100	208	64	11,759	188.45	0	0	0.00	1	1	0.01	17.0	0.20
68	1982	2	3.40	18.10	100	285	87	9,474	110.81	14	97	1.13	15	53	0.62	18.8	−1.20
69		9	3.30	18.20	100	293	85	29,407	334.55	23	51	0.58	19	23	0.26	17.5	0.78
70		11	6.10	18.20	130	80	12	1,103	45.96	4	28	1.17	0	0	0.00	21.9	4.75
71	1983	2	3.30	12.08	240	151	0	0	0.00	38	261	5.76	0	0	0.00	25.2	5.20
72		4	6.38	18.19	110	180	4	37	0.69	20	41	0.76	0	0	0.00	25.5	6.21
73		8	8.12	14.27	50	103	71	6,000	194.17	22	85	2.75	0	0	0.00	18.6	1.67
74		10	8.03	18.18	120	142	7	108	2.54	7	9	0.21	5	11	0.26	17.4	0.60
75	1984	8	4.00	14.00	140	103	24	357	11.55	2	3	0.10	0	0	0.00	16.8	−0.13
76		12	3.27	8.58	60	119	20	1,928	54.01	1	1	0.03	4	15	0.42	18.2	0.36
77	1985	2	3.54	13.43	90	1,065	93	25,813	80.79	4	6	0.02	0	0	0.00	19.5	−0.30
78		7	4.58	18.00	220	73	11	807	36.85	1	1	0.05	0	0	0.00	16.5	−0.93
79		8	3.35	14.02	136	1,192	83	5,620	25.72	1	1	0.00	0	0	0.00	16.5	−0.43
80	1986	4	3.30	12.59	100	110	15	169	5.12	0	0	0.00	2	2	0.06	18.6	−0.69
81		11	9.00	18.20	70	117	21	239	6.81	0	0	0.00	0	0	0.00	–	–

Table 2. Seasonality of spawning[a] by sardine and mackerel (1964-1986) and of SST[b] off Peru (1953-1985).

	Sardine egg/m^2	%	Mackerel larvae/m^2	%	Mean SST (°C)
Jan	123	16.4	2.5	18.8	18.97
Feb	54	7.2	3.2	24.1	20.00
Mar	40	5.3	4.2	31.6	20.07
Apr	30	4.0	0.6	4.5	19.29
May	3	0.4	0	0	18.67
Jun	0	0	0	0	17.99
Jul	100	13.3	1.2	9.0	17.43
Aug	89	11.8	0.4	3.0	16.93
Sep	130	17.3	0.6	4.5	16.72
Oct	72	9.5	0.3	2.3	16.80
Nov	11	1.5	0.2	1.5	17.15
Dec	100	13.3	0.1	0.8	17.84

[a] From data in Table 1.

[b] From Table 2 in Pauly and Tsukayama (this vol.) and from Table 4.

Table 3. Mean abundance of sardine, mackerel and horse mackerel larvae during two phases of anchoveta abundance.[a]

Years	Sardine Summer	Sardine Winter	Mackerel Summer	Horse mackerel Summer and winter
1964-1971	0.1	1.6	3.4	0.93
1972-1986	145	76	3.5	0.68

[a] Based on data in Table 1.

Table 4. Mean monthly sea surface temperature off Peru, 1983-1986. (Source: IMARPE, unpublished data).

Month	Year 1983	1984	1985	1986
J	24.9	19.8	19.0	19.5
F	25.2	20.4	19.5	20.7
M	25.5	20.5	20.1	19.5
A	25.5	20.1	18.3	18.6
M	26.3	18.7	17.2	18.0
J	26.1	17.3	17.4	17.2
J	21.3	16.9	16.5	17.2
A	18.6	16.8	16.5	–
S	17.7	17.0	16.7	–
O	17.4	17.3	17.3	–
N	18.4	17.5	17.4	–
D	18.8	18.2	18.0	–

Table 5. Correlations between sardine egg or mackerel larval abundance and some environmental factors likely to affect ichthyoplankton off Peru.[a]

Species	Spawning peak[b]	Anchoveta biomass (t x 10^6)[c]	SST (°C)[d]	SST anomaly (°C)[d]	Turbulence (m^3/s^3)[e] Callao	Turbulence (m^3/s^3)[e] Trujillo
Sardine	Summer and winter	−0.403* (38)	−0.095 (46)	−0.029 (46)	−0.000 (46)	−0.217 (46)
Sardine	Summer	−0.349 (13)	−0.388 (16)	−0.281 (16)	0.151 (16)	0.057 (16)
Sardine	Winter	−0.449* (23)	0.021 (28)	0.020 (28)	0.098 (28)	−0.321 (28)
Mackerel	Summer and winter	−0.024 (38)	−0.696* (46)	0.346* (46)	0.415*[g] (46)	−0.037 (46)
Mackerel	Summer	−0.014 (13)	0.526* (16)	0.465[f] (16)	−0.111 (16)	0.042 (16)
Mackerel	Winter	−0.288 (23)	0.715* (28)	0.719* (28)	0.614*[g] (28)	0.105 (28)

[a] Product moment correlation coefficients, marked with an asterisk (*) if significant ($P < 0.05$) for the available degrees of freedom (in brackets).

[b] Summer peak = January, February and March only; winter peak = July, August and September only; see Table 1.

[c] Taken for the appropriate months from Table 3 in Muck and Pauly (this vol.).

[d] From Table 1.

[e] From Tables 4 and 5 in Mendo et al. (this vol.).

[f] Critical value for significance is here 0.468.

[g] But see Table 7 and text.

Analysis of these data yielded the correlation matrix in Table 6, which indicate significant relationship between:

- sardine eggs and anchoveta (negative correlation)
- mackerel larvae and temperature (positive correlation)
- mackerel larvae and temperature anomaly (positive correlation)
- mackerel larvae and turbulence (positive correlation).

Table 6 shows (first-order) partial correlations (Sachs 1978) derived from the correlation matrix in Table 5. As might be seen, this analysis suggested that turbulence *per se* has no effect on mackerel larvae, the (zero order) correlation in Table 5 being due to the fact that turbulence itself correlates with temperature.

The regression expressing the relationship between sardine egg abundance (summer and winter) and anchoveta biomass (B_a; t x 10^6; Fig. 1A) is

$$\text{sardine eggs/m}^2 = 183 - 11.9 \cdot B_a \qquad ...3)$$

The regression expressing the relationship between mackerel larvae (summer and winter) and SST (Fig. 1B) is:

$$\text{mackerel larvae/m}^2 = -13.6 + 0.84 \cdot \text{SST} \qquad ...4)$$

These results strongly suggest that sardine have, in the past, been kept at low biomass level through predation on their eggs by the large anchoveta biomass, as earlier suggested by Ursin (1980) and Santander and Tsukayama (1984).

A rough estimate of sardine biomass (B_s) in the 1960s, when anchoveta had high biomasses, may be obtained from the following:

i) mean sardine biomass from 1978 to 1981 was 3.3 x 10^6 t (Santander and Tsukayama 1984);

ii) mean sardine egg abundance for the same period was 220 eggs/m^2 (summer and winter data; see Table 1);

Table 6. Partial correlations between the abundance of mackerel larvae, temperature and turbulence off Callao.[a]

Correlation between:	Spawning season	With turbulence partialed out	With temperature partialed out
Larval abundance and temperature	Summer and winter	0.615*	–
	Winter	0.545*	–
	Summer	0.516*	–
Larval abundance and turbulence	Summer and winter	–	0.044
	Winter	–	0.255
	Summer	–	–0.199

[a]Significant correlations ($P < 0.05$) are marked with an asterisk.

iii) combining the information in (i) and (ii) with Equation (3), we obtain

$$B_s = 3.3 \cdot (183 - 11.9 \cdot B_a)/220 \qquad ...5)$$

Thus, when $B_a > 12.6 \times 10^6$ t, $B_s < 0.5 \times 10^6$ t, i.e., the high anchoveta biomass occurring in the 1960s probably kept sardine biomass below half a million tonnes.

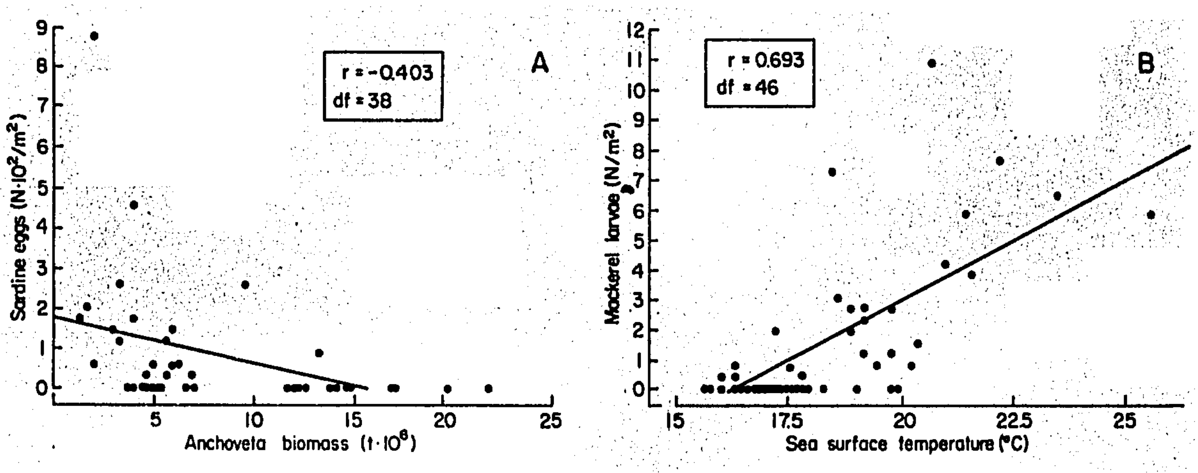

Fig. 1. A: Relationship between sardine eggs and anchoveta biomass off Peru, 1964-1982; B: Relationship between mackerel larvae and sea surface temperature off Peru, 1964-1986.

The situation is different with mackerel and probably with horse mackerel as well. There, no relationship between larval abundance and anchoveta biomass was detected, temperature (and/or temperature anomaly) apparently providing, instead, the key regulating factor. There are two likely explanations for the absence of mackerel larvae when SST < 16.5°C during the peak spawning season:

- adults occur in the area with SST < 16.5°C, but do not spawn; and
- mature adults stay outside the area when SST < 16.5°C.

Evidence is available which tends to support the second hypothesis:

i) Zuta et al. (1983) give 16-25°C and 17-25°C as temperature limits for mackerels and horse mackerels, respectively;

ii) catch statistics for mackerel and horse mackerel indicate that catches decline (probably due to offshore migration by the fish) during the cold season (Muck and Sanchez, this vol.); this is also confirmed by the temperature-dependent offshore-onshore migrations of mackerels reported by Tsukayama (1983), Zuzunaga and Niquen (1985) and Zuzunaga (1986); and

iii) comparing mackerel and horse mackerel biomasses within 100 nm off the Peruvian coast from different periods with different temperature regimes yielded strong evidence for a temperature effect (see Table 7).

Table 7. Relationship between mackerel and horse mackerel biomass and the temperature anomaly within 100 nm off the Peruvian coast.[a]

Period	Anomaly (°C)	Biomass (t x 10^6)	
		Mackerel	Horse mackerel
March-May 1983	+6.4	1.8	8.9
June-September 1984	−0.2	0.8	5.2
March-May 1985	−1.0	0.5	0.2

[a] Adapted from data in Muck and Sanchez (this vol.).

All of this support the hypothesis of Muck and Sanchez (this vol.) that water temperature controls the migration patterns of mackerel and hence the distribution of their biomass along the Peruvian coast. This expresses itself - as far as spawning products are concerned - in high abundances near the coast when temperature is abnormally high, i.e., during El Niño years (see Table 1, 1972-1973, 1976, 1982-1983).

On the other hand, when the coastal temperatures are too low, spawning of mackerel and horse mackerel takes place in warm oceanic waters along the outer edge of the continental shelf, from 200 to 900 nm offshore (Rojas and Mujica 1981).

It is obvious that under such condition, the survival of mackerel and horse mackerel eggs and larvae will be largely independent of the biomass of the highly coastal anchoveta. There is therefore no reason to assume that the biomass of the two former fishes should, in the past, have been very different from their present values.

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The Importance of Mackerel and Horse Mackerel Predation for the Peruvian Anchoveta Stock (A Population and Feeding Model)*

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Abstract

Mackerel *(Scomber japonicus)* and horse mackerel *(Trachurus murphyi)* predation on the Peruvian anchoveta *(Engraulis ringens)* was estimated, on a monthly basis, for the period 1953-1982. A key element of the model used to derive the estimate is the simulation of the temperature-induced inshore-offshore migrations of mackerel and horse mackerel, their relationship to El Niño events, and the resulting changes in the overlap anchoveta and mackerel/horse mackerel distributions. Model parameters were estimated from a variety of sources, including ichthyoplankton and echo-acoustic surveys, catch statistics and miscellaneous field data, covering the years 1964 to 1986 on the growth, mortality, diet composition and anchoveta consumption of mackerel and horse mackerel. Overall, results indicate that these two fishes, especially mackerel are far more important anchoveta predators than the guano birds, bonito or marine mammals, and that their anchoveta consumption, except for the 1961-1971 period, either exceeds or is similar to the fishery catches. The implications for research are pointed out.

Introduction

The present contribution is an attempt to estimate the consumption of anchoveta *(Engraulis ringens)* by mackerel (*Scomber japonicus* or "caballa", Fam. Scombridae) and horse mackerel (*Trachurus murphyi* or "jurel", Fam. Carangidae), two important pelagic fishes of the Peruvian upwelling ecosystem. Beyond catches, ichthyoplankton samples and some scattered biological information, very little is available on the stocks of mackerel and horse mackerel before 1977, when echo-acoustic surveys aimed at stocks other than anchoveta began.

Thus, a model was constructed which simulate biomasses and overlap with anchoveta as a function of sea surface temperature (SST), and anchoveta consumption as a function of predator biomass, a temperature and size-dependent ration and estimates of anchoveta vulnerability and availability. The presentation of the data used for parameterization of the model also provides an opportunity to review some major aspects of the biology of mackerel and horse mackerel off Peru, and to present some previously unpublished data.

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*PROCOPA Contribution No. 43.

Food and Feeding Habits of Mackerel and Horse Mackerel, with Emphasis on the Role of Anchoveta

Stomach contents of mackerel off Peru have been studied by Miñano and Castillo (1971), Chavez (1976), Ojeda and Jaksio (1979) and Mendo (1984), among others; the same has been done for horse mackerel by Rosario (1970), Videla (1976), Konchina (1981) and Sanchez and Muck (1983, 1984).

From these studies, it clearly emerges that both species are opportunistic predators, feeding exclusively on anchoveta when these are abundant and vulnerable and switching to a diet dominated by zooplankton (mainly copepods and euphausids) when anchoveta are less abundant and/or vulnerable (Fig. 1, Tables 1 and 2). Predator size is also important; mackerel switches from planktivory to piscivory (given that anchoveta are both abundant and vulnerable) at a length of about 28 cm (i.e., 300 g and 3 years), horse mackerel at a length of about 30 cm (i.e., 400 g and 2.7 years). Between these sizes and their maximum sizes of about 40 and 70 cm, respectivey, mackerel and horse mackerel consume anchoveta with sizes such as also caught by the purse seine fishery (Fig. 2), as is also the case for the other predators in the Peruvian upwelling ecosystem (see Muck and Pauly, this vol., Muck and Fuentes, this vol. and Pauly, Vildoso et al., this vol.)

Anchoveta egg predation by these two species, although not quantified here may be substantial. Thus, off Chimbote, where such predation appears to be highest, 40% of the stomachs sampled between September and December 1967 were positive for anchoveta eggs, with a mean of 517 ± 427 (s.d.) eggs per stomach.

Anchoveta predation by mackerel and horse mackerel appears to occur with about equal intensity along the coast of Peru, except for the area off Paita, i.e.,north of the area where anchoveta concentrate (Table 3 and see Pauly and Tsukayama, this vol.).

Note, however, that during the 1982-1983 El Niño, the diet of mackerel and horse mackerel along the whole Peruvian coast resembled that off Paita (at any time) in that it consisted overwhelmingly of macrozooplankton (Fig. 1). Overall, from south of Paita to the Chilean border, anchoveta provided in 1979, a non-El Niño year, about 40% of the food of mackerel and 75% of the food of horse mackerel.

Table 1 shows that the value of 40% for mackerel in 1979 is intermediate between the high value for 1976 (79%) and the low value for 1982 (2%), and that the trend itself is a function of relative anchoveta biomass (see below).

Daily Food Consumption of Mackerel and Horse Mackerel

Table 4 presents data for 1976-1982 on the weight of anchoveta in "anchoveta positive" mackerel stomachs from which a mean anchoveta food bolus of 23.5 g can be derived,

Table 1. Percent anchoveta in the diet of mackerel, 1976-1982.

Year	Number of mackerel sampled	% mackerel stomachs with anchoveta remains	% anchoveta in mackerel stomachs[b]	Relative anchoveta biomass[c]
1976	105	79[a]	16.4	32.4
1977	–	–	–	–
1978[d]	340	44	10.1	17.1
1979	501	40	7.7	11.9
1980	230	26	8.9	10.0
1981	388	13	4.2	8.6
1982	230	2	0.3	7.1

[a] This value would be 100% if anchoveta eggs were counted.

[b] % of stomach content weight.

[c] % of maximum annual mean biomass (1967: 21 x 10^6 t) in Table 3 of Muck and Pauly (this vol.).

[d] In 1978, off Callao, 22% of the "anchoveta positive stomachs" contained 4 or more anchoveta, with a maximum of 7, weighing a total of 86.4 g in a 827 g mackerel. The maximum % of anchoveta weight *vs.* predator weight was 15.4 and occurred in a mackerel of 543 g.

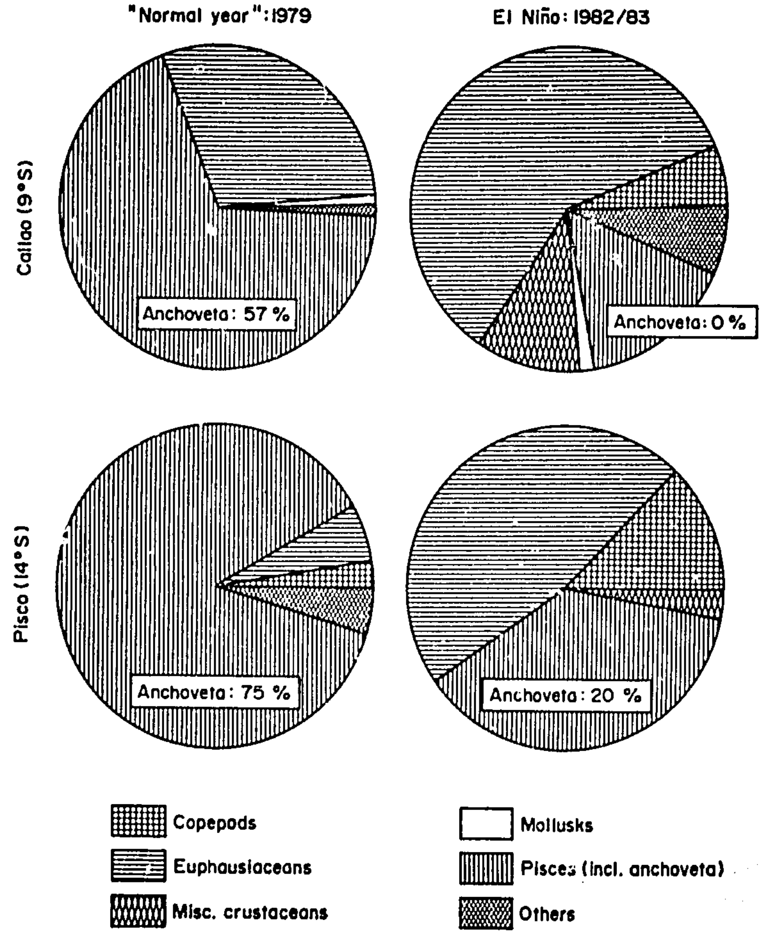

Fig. 1. Diet composition of mackerel *(Scomber japonicus)* during a "normal year" and an El Niño event, off two areas of the Peruvian coast. Note decrease of anchoveta (in % of total weight composition) and increase of Euphausiaceans.

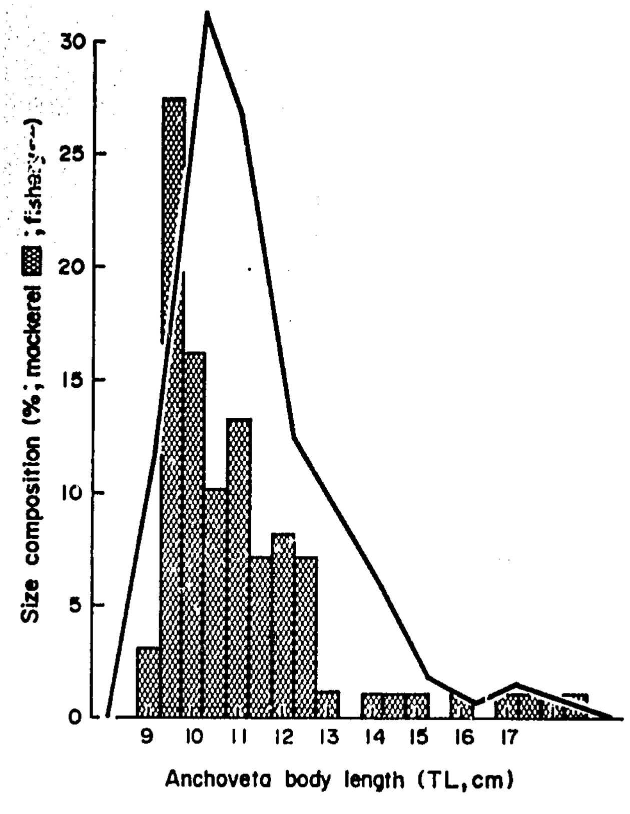

Fig. 2. Size-frequency distribution of anchoveta *(Engraulis ringens)* ingested by mackerel *(Scomber japonicus)* (28-64 cm) off Chimbote (1976), compared with size-frequency distribution of catch samples from the purse seine fishery (June-July, adapted from Table 24 in Tsukayama and [illegible]omares, this vol.).

Table 2. Summary of data on feeding and diet composition of mackerel/horse mackerel sampled in 1979 along the Peruvian coast. Note that % diet composition refers to weight and that the % contribution of "other" items can be obtained by subtraction.

Location Parameter	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Paita (5°S)												
Sampled fish (n)	80 / 3	75 / 8	25 / 20	100 / –	150 / 15	50 / –	75 / 3	– / 18	– / 31	– / 24	– / 56	–/–
Mean individual weight (g)	342 /472	399 /602	463 /997	441 / –	441 /543	400 / –	412 /494	– /531	– /948	– /791	– /915	–/–
Mean stomach content (g)	2.7/ 2.0	7.0/ 2.2	7.9/ 25.4	10.0/ –	3.6/ 1.7	14.3/ –	15.0/ 1.2	– / 15.7	– / 3.7	– / 7.6	– / 23.9	–/–
% diet composition												
Anchoveta	0 / 0	0 / 0	0 / 0	0 / –	5.3/ 0	0 / –	0 / 0	– / 0	– / 0	– / 0	– / 0	–/–
Euphausiacea	34.9/100	1.5/100	24.3/ 95	8.6/ –	20.4/ 79	69.4/ –	0.3/ 5.3	– / 3	– / 55	– / 67	– / 93	–/–
Copepods	27.5/ 0	96.2/ 0	0 / 3.2	73.3/ –	46.0/ 21	0 / –	66.2/ 94	– / 53	– / 45	– / 33	– / 7	–/–
Chimbote (9°S)												
Sampled fish (n)	– / –	– / –	33 / –	44 / –	119 / –	57 / –	57 / –	15 / –	84 / –	28 / –	– / –	–/–
Mean individual weight (g)	– / –	– / –	471 / –	363 / –	558 / –	457 / –	461 / –	412 / –	486 / –	450 / –	– / –	–/–
Mean stomach content (g)	– / –	– / –	6.1/ –	4.4/ –	12.4/ –	4.2/ –	2.5/ –	2.1/ –	3.7/ –	5.0/ –	– / –	–/–
% diet composition												
Anchoveta	– / –	– / –	50 / –	47.4/ –	73 / –	0 / –	46.2/ –	83.2/ –	2.5/ –	0 / –	– / –	–/–
Euphausiacea	– / –	– / –	4.1/ –	2.2/ –	0 / –	0 / –	0 / 0	2.9/ –	1.9/ –	57 / –	– / –	–/–
Copepods	– / –	– / –	27.6/ –	47 / –	23.2/ –	90.7/ –	39 / –	11 / –	50 / –	42.1/ –	– / –	–/–
Callao (12°S)												
Sampled fish (n)	– / –	6 / 24	– / 55	7 / 78	3 / 84	10 / 51	7 /110	12 / 18	– / –	– / –	5 / –	–/–
Mean individual weight (g)	– / –	579 /632	– /480	758 /473	541 /502	491 /435	560 /519	634 /412	– / –	– / –	596 / –	–/–
Mean stomach weight (g)	– / –	14.7/ 8.1	– / 9.1	22 / 10.9	3 / 4.6	15.1/ 13.1	17 / 12.5	25 / 0.8	– / –	– / –	4 / –	–/–
% diet composition												
Anchoveta	– / –	100 / 25	– / 49.3	69 / 28.2	100 / 62.8	100 / 98.2	92 / 76.7	85 / 0	– / –	– / –	0 / –	–/–
Euphausiacea	– / –	0 / 45.3	– / 1.7	31 / 0.2	0 / 18.2	0 / 0	0 / 0	0 / 26.7	– / –	– / –	97 / –	–/–
Copepods	– / 0	0 / 9.4	– / 24.1	0 / 8.7	0 / 1.2	0 / 0	0 / 0	0 / 73.3	– / –	– / –	3 / –	–/–
Pisco (14°S)												
Sampled fish (n)	– / 10	– / 12	– / 16	– / –	– / 4	– / 19	– / 8	– / 11	– / 15	– / –	– / 2	–/–
Mean individual weight (g)	– /991	– /842	– /1,084	– / –	– /1,003	– /877	– /789	– /741	– /760	– / –	– /810	–/–
Mean stomach weight (g)	– / 23.3	– / 3.7	– / 28.4	– / –	– / 19.9	– / 24	– / 23.6	– / 22	– / 29.3	– / –	– / 13.3	–/–
% diet composition												
Anchoveta	– /100	– / 71.5	– / 97.8	– / –	– /100	– /100	– / 97.4	– /100	– / 98	– / –	– / 50	–/–
Euphausiacea	– / 0	– / 18.3	– / 0	– / –	– / 0	– / 0	– / 2.6	– / 0	– / 0	– / –	– / 50	–/–
Copepods	– / 0	– / 10.2	– / 0	– / –	– / 0	– / 0	– / 0	– / 0	– / 0	– / –	– / 0	–/–
Ilo (17°S)												
Sampled fish (n)	– / 18	– / 4	46 / –	– / –	16 / –	– / –	– / 10	– / –	– / –	– / –	– / –	–/–
Mean individual weight (g)	– /540	– /456	488 / –	– / –	473 / –	– / –	– /459	– / –	– / –	– / –	– / –	–/–
Mean stomach weight (g)	– / 2	– / 1.5	13.2/ –	– / –	1.2/ –	– / –	– / 13.2	– / –	– / –	– / –	– / –	–/–
% diet composition												
Anchoveta	– / 21.7	– / 50	100 / –	– / –	12 / –	– / –	– /100	– / –	– / –	– / –	– / –	–/–
Euphausiacea	– / 75	– / 50	0 / –	– / –	0 / –	– / –	– / 0	– / –	– / –	– / –	– / –	–/–
Copepods	– / 3.3	– / 0	0 / –	– / –	0 / –	– / –	– / 0	– / –	– / –	– / –	– / –	–/–

Table 3. Percent[a] anchoveta in mackerel and horse mackerel stomachs sampled along the Peruvian coast in 1979[b].

Sampling area (°S)		Mackerel % anchoveta	Sample size	Horse mackerel % anchoveta	Sample size
Paita	(5)	0.8	555	0.0	178
Chimbote	(9)	37.8	437	no data	
Callao	(12)	48.6	420	78.0	50
Pisco	(14)	no data		90.5	97
Ilo	(17)	39.0	62	57.3	32

[a] % of stomach content weight.
[b] Based on Table 2.

Table 4. Contribution of anchoveta to the diet of mackerel in three areas off Peru, 1976-1982.

Area Month	Year	Mackerel Number examined	Mean weight; g (s.d.)	% mackerel stomach positive for anchoveta	Mean (weight) % anchoveta in all stomachs	Mean (weight) % anchoveta in "positive" stomachs (s.d.)
Chimbote (9°S)						
6	1976	65	469 (89)	60	14.6 (5.9)	19.9 (17.8)
8	1978	152	529 (65)	24	8.9 (4.2)	28.8 (20.3)
6	1979	157	520 (42)	21	5.2 (5.2)	25.3 (15.3)
3	1980	64	673 (110)	35	17.1 (28.0)	47.9 (14.5)
5	1981	183	543 (67)	16	5.8 (12.7)	36.2 (20.7)
4	1982	99	448 (171)	2	0.4 (7.1)	21.3 (19.7)
Callao (12°S)						
2	1978	87	631 (77)	39	13.4 (18.0)	34.0 (18.5)
6	1979	299	440 (101)	42	8.2 (3.4)	14.7 (5.3)
4	1980	141	485 (98)	30	5.5 (3.4)	19.4 (16.1)
5	1981	151	512 (80)	24	6.7 (11.0)	25.6 (12.0)
4	1982	131	300 (–)	1	0.1 (1.0)	13.6 (–)
Ilo (17°S)						
2	1976	40	500 (89)	98	18.1 (16.7)	18.3 (12.7)
4	1978	101	509 (57)	70	7.9 (11.0)	14.6 (10.0)
2	1979	45	479 [illegible]	56	9.7 (12.7)	18.1 (5.7)
1	1980	25	492 (40)	12	4.0 (1.0)	14.0 (0.8)
3	1981	54	–	0	–	–

corresponding to about 4.7% of the mean mackerel weight of 502 g (of 33 cm and 4 years). This value of 23.5 g is not the daily ration (R), however. Rather one can propose, following Backiel (1971),

$$R = 24\ m/t_h \qquad \ldots 1)$$

where m is the mean stomach content and t_h the time (in hours) needed for the stomach to be completely evacuated.

Various factors affect t_h, notably temperature, food type, size of food organisms, meal size and frequency, etc. (Brett and Higgs 1970; Tyler 1970; Jones 1974; Durbin et al. 1983).

Conover (1978), based on data of Tyler (1970) proposed that cod *(Gadus morhua)* stomachs are evacuated, at 19°C, about 17 hours after intake of a meal. Magnuson (1969) reported an evacuation time of 11-12 hours in skipjack tuna *(Katsuwonus pelamis)* kept at 23-26°C. Tyler's lower temperature is near to those occurring off Peru in normal years. We shall use a value of t_h

= 17 hours for both mackerel and horse mackerel whose value of R in fish of 502 g is thus given by

$$33.2 = 24 \cdot 23.5/17 \qquad ...2)$$

Hatanaka and Takahashi (1956) and Hatanaka et al. (1957) conducted growth experiments with *Scomber japonicus* fed *Engraulis japonicus* at a mean temperature of 18.6°C. Using their data (as reported in Conover 1978), the mean mackerel weight and daily ration above 502 and 33.2 g, respectively, we have derived the empirical model

$$R = 0.333\ W^{0.74} \qquad ...3)$$

(d.f. 7, r = 0.71) which can be used to obtain estimates of daily ration (in g/day) as a function of mackerel and/or horse mackerel body weight (in g).

Biomass Distribution and Migrations of Prey and Predators

The Prey

Along the Peruvian coast, anchoveta occurs predominantly from south of Paita to 14°S (Tsukayama 1983; Pauly and Tsukayama, this vol.).

In the 1960s, when anchoveta was abundant, its inshore-offshore ranges changed seasonally, from 40-50 miles in summer to 100-120 miles in winter. To date, however, the bulk of the (smaller) anchoveta biomass is found throughout the year within about 40 miles of the coast (Zuta et al. 1983; Tsukayama 1983). We shall therefore call here "main anchoveta range" (MAR) the 40 nm stretch of the Peruvian coast between 4 and 14°S.

During El Niño events, warm and nutrient-poor waters invade the MAR from the North. Anchoveta usually react to this by hugging the coast, where cold water pockets may remain for some time, or by migrating southward or into deeper waters (Schweigger 1940; Vogt 1942; Fiedler et al. 1943; Jordan and Fuentes 1966; Valdivia 1978; Johannesson and Vilchez 1980; Zuta et al. 1983; Arntz 1986). Thus, during the strong El Niño of 1982-1983, anchoveta (as well as sardine, mackerel and horse mackerel, incidentally) were observed at depths of 100 m and more, apparently in relation to the SST gradient (Muck and Vilchez 1986; Arntz 1986).

Coastward and downward migrations have obvious implications for the purse seine fishery for anchoveta. Valdivia (1978) reports that during the 1972 El Niño, anchoveta were so concentrated along the coast and hence so vulnerable to the fishing that, e.g., the 1st of March, 170,000 t were caught, i.e., 4% of the anchoveta catch of that year. Conversely, the very low catches during the 1982-1983 El Niño suggest a very low vulnerability of pelagic fishes to the fishery, which can reach schools down to only 50 m. No information is available to answer the question whether anchoveta vulnerability to mackerel and horse mackerel (both visual hunters) is reduced at depths of 100 m or more, due to the poor light conditions. This is likely, however.

The Predators

Mackerel and horse mackerel occur all along the Peruvian coast, from 3 to 19°S, and up to 200 miles offshore (Zuzunaga 1986), normally predominating in the outer half of the coastal upwelling system (Barber and Smith 1981). Johannesson and Vilchez (1980) report that the heaviest concentrations of both species were found offshore, in 1978, at a distance of roughly 50 miles. This was confirmed during echo-acoustic surveys conducted in May-June 1986, which located the density maximum of both species 40-50 miles offshore, while echo-acoustic surveys conducted from 1983 to 1985 suggest that an average of 40% of the total biomass of these two predators occurs within the MAR.

Seasonal migrations of mackerel and horse mackerel into the MAR have been reported by Tsukayama (1983), Zuzunaga and Niquen 1985 and Zuzunaga (1986), among others. These migrations generate high densities of the two predators within the MAR during spring and summer, and low densities in autumn and winter. The timing and dependence on coastal SST of these migrations are confirmed through ichthyoplankton surveys (see Muck et al., this vol.), fishery catch data (Fig. 3) and the temperature preferenda of mackerel and horse mackerel (Table 5). Therefore, coastal SST appears to be an adequate parameter for quantification of the distribution overlap between anchoveta and the two predators considered here, i.e., vulnerability of anchoveta to mackerel and horse mackerel.

Mackerel and horse mackerel biomass data are available from echo-acoustic surveys since 1977 (Table 6). The relatively large interannual differences probably do not reflect real changes in total biomass but are consequences of variations in (i) total area covered by the survey, (ii) maximum survey distance from the coast (Johannesson and Vilchez 1980) and (iii) seasonal effects and El Niño-related fish migration.

Thus the highest biomass of 1.8 + 8.9 = 10.7 t x 10^6, detected in 1983, can be interpreted as the result of onshore migration caused by El Niño-induced temperature anomalies; the then following decrease to 6 t x 10^6 in 1984 can, on the other hand, be interpreted as the result of offshore migration that occurred when coastal SST returned to normal.

The notable difference in biomass nearshore (<40 miles = 25%) and offshore (>40 miles = 75%) in 1985 suggests that the low total value of less than 1 t x 10^6 for both species together

Table 5. Temperature preferenda[a] of mackerel, horse mackerel and anchoveta, as related to mean coastal sea surface temperature (SST)[b] off Peru.

	Temperature (°C)
Species	
Mackerel	16 – 25
Horse mackerel	17 – 24
Anchoveta	15 – 20
Mean coastal SST	
Summer	16.9
Winter	19.7

[a] Based on acoustic and other surveys conducted by IMARPE (unpublished).

[b] From Zuta et al. (1983).

Table 6. Echo-acoustic estimates of biomass and catches of mackerel and horse mackerel off Peru, 1977-1986.

Year	Offshore limits of surveys (nm)	Biomass (10^6 t)		Catch (10^3 t)	
		Mackerel	Horse mackerel	Mackerel	Horse mackerel
1977	52 – 80	0.7	1.5	46	505
1978	60 – 80	1.5	4.2	102	387
1979	50 – 82	1.2	3.5	118	152
1980	30 – 80	1.4	4.8	59	123
1981	40	1.4	4.7	33	38
1982	–	–	–	–	–
1983	100	1.8	8.9	20	51
1984	170	0.8	5.2	71	172
1985	80	0.45	0.18	1	10
1986	100	1.9[a]	4.6[a]	–	–

[a] Preliminary estimates.

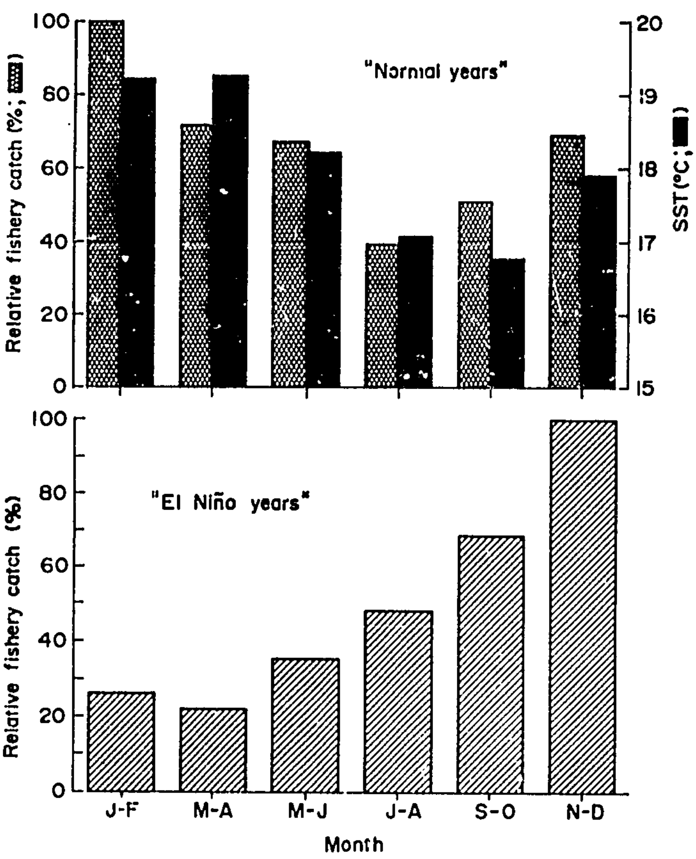

Fig. 3. Above: "normal" seasonality of mackerel catches and SST off Peru (based on data for 1970, 1971, 1974, 1975, 1979, 1980 and 1981) showing how closely (inshore) catches relate to SST. Below: showing how nearshore mackerel biomass builds up in the course of an El Niño with mean SST of 20.0°C (based on data for 1972 and 1976).

represents only a small fraction of the total biomass, the main part of which seemed, in 1985, to be concentrated outside the survey area. Offshore migrating mackerel and horse mackerel schools, leaving the area covered by the survey, were observed during the 1985 cruise (IMARPE 1985).

That fishing mortality could be responsible for the 1983-85 decrease is less probable considering the comparatively low annual catches registered during this period (Table 6).

Results of an echo-acoustic biomass survey conducted in May-June 1986 suggest, for mackerel about 1.9 t x 10^6 and for horse mackerel 4.6 t x 10^6 which are close to the values reported in former years (except for the anomalous years 1983 and 1985) suggesting a mean standing stock of about 1.3 t x 10^6 of mackerel and about 4.1 t x 10^6 of horse mackerel distributed inside an 80-mile band along the Peruvian coast.

The biomass detected in 1983 has been interpreted as close to the true overall total biomass of both species off the Peruvian coast which is assumed in the following as 11 t x 10^6.

Mackerel and horse mackerel biomasses before 1977 are unknown. Catch statistics are available since 1964 but cannot be used for biomass estimation.

We do not know if the drastic change in anchoveta biomass from 1967 to 1973 has affected the population size of mackerel and horse mackerel. The very high biomass of the two predators found in 1983, when anchoveta biomass was negligible, and the results of stomach content analyses in areas and periods when anchoveta availability was very poor support the hypothesis that mackerel and horse mackerel are independent of anchoveta because they can replace them by zooplankton. That the fishery had at any time a significant impact on the stock size of mackerel and horse mackerel is not likely, considering the relatively low annual catches of these two species, of 12,000 and 13,000 t (average for 1953-1975), respectively.

These considerations are supported by the results of ichthyoplankton surveys, which suggest the absence of a correlation between anchoveta biomass and the abundance of mackerel larvae, again implying an independence of the biomasses of predator and prey (see Muck et al., this vol.).

We shall thus assume here that the biomass estimate of about 11 t x 10^6 for mackerel (2t x 10^6) and horse mackerel (9 t x 10^6) off Peru in 1983 also applies to earlier and subsequent years. However, this biomass extends from 3 to 19°S, and to more than 40 miles offshore. Table 7 gives factors which can be used to reduce our biomass estimate to that part that is overlapping with the MAR.

Table 7. Offshore and alongshore distribution of mackerel and horse mackerel off Peru, 1983-1986.[a]

Year	% of mackerel stock: between 4-14°S[b]	% of mackerel stock: < 40 miles offshore[c]	% of horse mackerel stock: between 4-14°S[b]	% of horse mackerel stock: < 40 miles offshore[c]
1983	67	40	71	38
1984	38	45	58	42
1985	76	29	60	19
1986	–	40[d]	–	45[d]

[a] Based on data in GOPA (1985).
[b] Mean for both mackerel and horse mackerel: 62%.
[c] Mean for both mackerel and horse mackerel: 38%.
[d] Preliminary estimates based on incomplete data.

Mean biomass within 80 miles of the coast, of mackerel and horse mackerel in non-El Niño years from 1977 to 1984, was 1.3 resp. 4.1 t x 10^6. We assume, thus, that 1.2 t x 10^6 of these two fishes occur within the MAR, in normal years. Based on fishery catch statistics, we further assume that this biomass varies seasonally by a factor of 2.5 (see Fig. 3, upper panel), and, finally that during El Niño years, the biomass of mackerel and horse mackerel within the MAR is more than doubled (see below and Fig. 3, lower panel).

We shall present below, in addition to model runs based on these various assumptions, the result of model runs which simply use annual fishery catches of mackerel and horse mackerel from 1972 to 1982 as minimum estimates of the biomass of these two species.

Basic Structure of Mackerel/Horse Mackerel Biomass Model

The following equations define a model for estimating, on a monthly basis, the biomass of mackerel and horse mackerel within the MAR as related to seasonal of El Niño-dependent changes of SST.

Key assumptions are:

(i) the density of mackerel and horse mackerel in the inshore-offshore dimension can be approximated by a normal distribution;

(ii) total biomass (in and out of MAR) is 11 t x 10^6;

(iii) during the winter months (July-September), only 10% of the biomass is within 40 miles from the shore; the rest is mainly within 50-90 miles, with a mean of 70 miles (Fig. 4).

Thus, $\bar{X} = 70$ in the normal distribution density function

$$Y = 1/(s.d.\sqrt{2\pi}) \cdot \exp -(0.5)\cdot((X-\bar{X})/s.d.)2 \qquad ...4)$$

In Equation (3), the term "$(X-\bar{X})/s.d.$" can be replaced by the variable "z", which quantifies the area under the standardized normal distribution. Calculated values for these areas, corresponding to different values of z can be found in most statistics text (e.g., Sachs 1978). The 10% biomass assumed above for the 40 mile limit of the MAR corresponds to a value of $z_{10\%} = 1.3$. Thus, the standard deviation (s.d.) can be estimated from

$$s.d. = (40-70)/1.3 = 23 \qquad ...5)$$

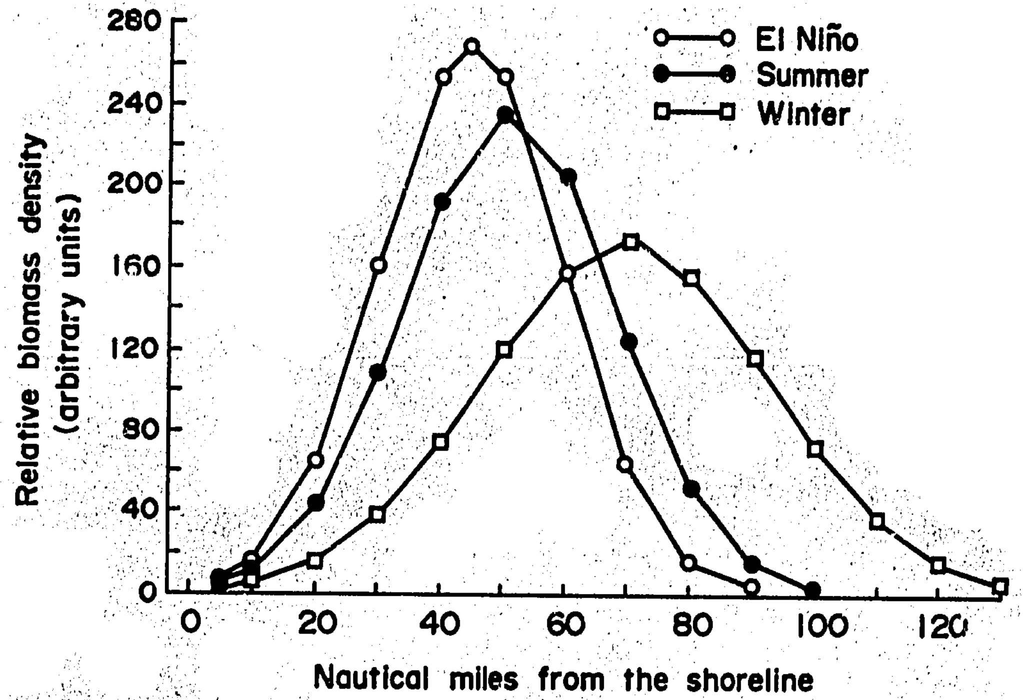

Fig. 4. Example of a model output, showing the density distribution of mackerel and horse mackerel biomass as a function of distance offshore and SST (El Niño > Summer > Winter); see also text.

The coefficient of variation (C.V., here assumed constant) is thus (23 · 100)/70 = 33%.

Seasonal changes between low winter ($\bar{X} = 70$, s.d. = 23) and high summer biomass within 40 miles from the shore are modelled through consideration of the fact that summer biomasses are about 2.5 times higher than in winter (see above). Thus, 1.1 x 2.5 = 2.8 t x 10^6, corresponding to 25.5% of the total biomass of 11 t x 10^6. The value of 25.5% corresponds to $z_{25.5\%} = 0.65$. The density maximum (i.e., $\bar{X}$) thus occurs 51 miles offshore because

$$(40-51)/16.8 = 0.65 \qquad ...6)$$

and the s.d. value is 16.8, because C.V. = 33% (see above).

As mentioned previously, mackerel and horse mackerel move, during El Niño events, very close to the coast and catch statistics for 1972 and 1976 (Fig. 3) suggest that their inshore biomass increased 3.5-fold when temperature was highest. Thus 1.1 x 3.5 = 3.9 t x 10^6 occurred within the MAR, corresponding to 35% of the 11 t x 10^6 stock. This corresponds to $z_{35\%} = 0.36$, with $\bar{X}$ and s.d. estimated, as shown above, as 45 and 14.8 miles, respectively.

Similarly, 4 t x 10^6 of mackerel and horse mackerel occurred within the MAR, in March-May 1983, i.e., during the 1982-1983 El Niño. This corresponds to $z_{40\%} = 0.22$, $\bar{X} = 40$ and s.d. = 14.2 miles. The four estimates of $\bar{X}$ derived are recalled in Table 8, along with the corresponding temperatures.

These data allowed derivation of the equation

$$D_{max} = 1{,}260\ T^{-1.06} \qquad ...7)$$

where D_{max} is the maximum of the biomass density function (i.e., $\bar{X}$ as used previously) and T is the SST, in °C. Thus we have

$$z = (40-1{,}260T^{-1.06})/(1{,}260T^{-1.06} \cdot 0.33) \qquad ...8)$$

which allows estimation of the percentage of the total biomass of mackerel and horse mackerel within 40 miles as a function of SST.

Table 8. Relationship between estimated distance offshore of mackerel concentrations and SST within 40 miles off the coast.[a]

Distance offshore (nm)	SST (°C)	Reference period
70	17.1	July-August, 30 year mean
51	19.3	January-February, 30 year mean
45	19.8	November-December (1972 and 1976)
43	25.5	March-April 1983

[a] Based on unpublished IMARPE survey data.

Table 9 gives values of z, D_{max} and the corresponding % of mackerel and horse mackerel within 40 miles (B%), for temperatures ranging from 16 to 25°C. The regression equations expressing the relationship between temperature and B% is

$$B\% = 0.948 \exp 0.158T \qquad ...9)$$

which can be used to estimate B% from T without using the z-transformation. B% can be turned into absolute biomass for the area ranging from 4 to 14°S, i.e., within the MAR, by using the appropriate factor in Table 7.

As an alternative to this model, which assumes a constant overall biomass of mackerel and horse mackerel, and a highly variable overlap with the MAR, we have also estimated the anchoveta predation that would have been generated by these two fishes, had their biomass within the MAR been equal to their catch, which is largely taken within the MAR. These estimates shall be called here "least predator biomass estimates" to emphasize the fact that they provide lower limits to the biomass that mackerel and horse mackerel may have had during the period considered here.

Food and Anchoveta Consumption By Mackerel and Horse Mackerel

The total daily food intake of a population (R_{tot}) can be expressed as the sum of the intake by each age (or weight) group (R_t), i.e.

$$R_{tot} = \sum_{t=1}^{t_{max}} R_t = \sum_{t=1}^{t_{max}} N_t \cdot c\,W_t^{\,d} \qquad ...10)$$

Table 9. Relationship between coastal SST and distance offshore of main mackerel biomass (D_{max}), z-value and the derived % of overall mackerel biomass occurring within 40 miles of the coast ($B_{\%}$).

SST (°C)	D_{max}	z^a	$B_{\%}$
16	67	1.22	11
17	62	1.08	14
18	59	0.98	16
19	56	0.87	19
20	53	0.75	23
21	50	0.61	27
22	48	0.51	31
23	45	0.34	37
24	43	0.21	42
25	42	0.15	44

[a] From Table 13 in Sachs (1978).

where N_t is the number of individuals with age t, W_t their mean body weight, and c and d constants of the relation linking ration and body weight (Table 10); the equation can be solved in relative terms, by setting $N_o = 1$ for $t = 0$ in the equation

$$N_{t(rel)} = N_o \exp\text{-}Zt \qquad \text{...11)}$$

where Z is the total mortality (Table 10). For a given biomass B, relative abundance of fish of age t can be turned into absolute abundance (N_t) using

$$N_t = B(N_{t(rel)})/(\ N_{t(rel)} \cdot W_t) \qquad \text{...12)}$$

Weight (W_t) at age (t) was estimated using the von Bertalanffy growth equation

$$L_t = L_\infty\ (1\text{-}\exp\text{-}(K(t\text{-}t_o))) \qquad \text{...13)}$$

Table 10. Constants used in model for estimation of food consumption by mackerel and horse mackerel off Peru (equations 9-14).

Parameter (units)	Mackerel	Horse mackerel
Asymptotic length, L_∞ (cm)	40.6[a]	82.6[b]
von Bertalanffy constant K (y^{-1})	0.408[a]	0.15[b]
Theoretical age at zero length, t_o (y)	−0.05[a]	−0.28[b]
Maximum observed age (y)	> 10[c]	15[d]
Maximum observed length (cm)	39[a]	71[b]
a, factor in length-weight rel. (−)	0.0106[e]	0.033[f]
b, exponent in length-weight rel. (−)	3.083[e]	2.758[f]
Ration-weight rel. ($R = c \cdot W^d$)		
c, factor (−)	0.333[g]	
d, exponent (−)	0.74[g]	
total mortality, Z (y^{-1})	0.85[h]	

[a] From Mendo (1984).
[b] From Dioses (1986).
[c] From Tsukayama (1983).
[d] T. Dioses (1983 and pers. comm.).
[e] From Mendo (1983), mean of values for Callao and Chimbote for 1976-1978.
[f] From Sanchez and Muck (unpublished data).
[g] From Hatanaka and Takahashi (1956) and Hatanaka et al. (1957), Conover (1978) and see text.
[h] From Tsukayama (1986).

and the length-weight relationship

$$W = a \cdot L^b \qquad \text{...14)}$$

whose parameters (L_∞, K, t_o, a and b) are given, for mackerel and horse mackerel, in Table 10.

Thus, our model for estimating total daily consumption of a predator population with $t_{max} = 12$, and a total biomass B is

$$R_{tot} = \sum_{t=1}^{12} (((B \cdot N_{t\,(rel)}) / (\sum_{t=1}^{12} N_{t\,(rel)} \cdot W_t)) \cdot (a \cdot L_\infty (1 - \exp - K\,(t - t_o))^b)) \qquad \text{...15)}$$

Table 11 gives a computation example for mackerel, based on a biomass of 2 t x 10^6; note that for actual computations, the values of B used referred only to the MAR, as discussed above. Monthly anchoveta consumption by mackerel and horse mackerel within the MAR may now be viewed as a fraction ($R_{a(i)}$) of their total ration ($R_{tot(i)}$) in month (i). $R_{a(i)}$ can be further viewed as depending on anchoveta availability (A_i), i.e.,

$$R_{a(i)} = R_{tot(i)} \cdot A_i \qquad \text{...16)}$$

Table 11. Steps in estimating the food consumption of a stock of mackerel with biomass = 2 x 10^6 t.

Age (year)	Length (cm)	Weight (g)	Daily ration (% body weight)	Standing stock (N x 10^9)	Daily food consumption by stock (t x 10^3)
1	14.1	37.3	13.0	9.04	43.08
2	23.0	167	8.8	3.86	56.78
3	28.9	338	7.3	1.65	40.66
4	32.8	500	6.6	0.71	23.41
5	35.4	623	6.2	0.30	11.76
6	37.1	733	6.0	0.13	5.71
7	38.3	805	5.8	0.055	2.57
8	39.1	856	5.8	0.024	1.64
9	39.6	890	5.7	0.010	0.51
10	39.9	914	5.7	0.004	0.21
11	40.1	930	5.6	0.002	0.09
12	40.3	941	5.6	0.001	0.04

Anchoveta availability can be viewed, finally, as the product of relative anchoveta biomass ($B_{r(i)}$) and an anchoveta vulnerability index ($Vul_{(i)}$), as in Muck and Fuentes (this vol.) and Muck and Pauly (this vol.), i.e.,

$$A_{(i)} = B_{r(i)} \cdot Vul_{(i)} \qquad \text{...17)}$$

Thus, decreasing anchoveta biomasses and/or decreasing vulnerability reduces anchoveta availability and hence anchoveta consumption by mackerel and horse mackerel. Unfortunately, information is insufficient to treat vulnerability as a true variable; thus, the parameter Vul in Equation (17) has been set constant, assuming that, on the average, the maximum percentage of anchoveta in the diet of the two predators considered here is 80% when anchoveta are very abundant ($B_{r(i)} = 1$). The estimation of $A_{(i)}$ for values of $B_{r(i)} < 1$ was done using the data of Table 2. From these, daily anchoveta consumption ($R_{a(i)}$) and its relationship ($R_{a\%i}$) to daily total consumption ($R_{tot(i)}$) can be computed using Equation (1) with $t_h = 17$ and Equation (2). This leads to the data in Table 12, which show $Ra_{\%(i)}$ values decreasing from 72% in 1976 to 1.5% in 1982, in relation with the decline of anchoveta biomass, and as also observed in Table 1. The data of Table 12 have been used to estimate, for absolute anchoveta biomasses $B_{a(i)}$ ranging from zero to 9 t x 10^6 the empirical equation

$$B_{r(i)} = 0.111\, B_{a(i)} - 0.09 \qquad \text{...18)}$$

with $B_{r(i)}$ set equal to 1 when $B_{a(i)} > 9$ t x 10^6.

Anchoveta consumption by mackerel and horse mackerel of 3 years or more was estimated on a monthly basis, using this and preceding equations, as well as the preliminary anchoveta biomass estimate in Muck and Pauly (this vol.) and the SST values in Table 2 of Pauly and Tsukayama (this vol.).

Additionally, estimates of anchoveta consumption based on the "least biomass estimates" mentioned above were obtained, considering that about 75% and near 100% of the fishery catches of mackerel and horse mackerel, respectively, consisted of fish of ≤ 30 cm, i.e., of potential anchoveta predators (Menz 1983; Tsukayama 1986).

Least annual anchoveta consumption by mackerel and horse mackerel (LC) was estimated from their respective annual catches (Y_{mack} and $Y_{horse\ mack}$) through

$$LC = Y_{mack.} + (Y_{horse\ mack.} \cdot 0.75)) \times 0.05 \times 365 \cdot A_{(i\ mean)} \qquad \text{...19)}$$

where the value of 0.05 is the mean daily ration as a fraction of body weight and $A_{(i\ mean)}$ is the mean anchoveta availability computed, for each year, as the mean of monthly $A_{(i)}$ values.

Table 12. Model estimates of anchoveta consumption by mackerel in relation to anchoveta biomass.

Year	Mackerel weight (g)	Weight of anchoveta in mackerel stomachs (g)	Daily anchoveta consumption (g)[a]	% anchoveta in mackerel diet	Relative anchoveta biomass (%)[b]
1976	486	16.4	23	72	0.74
977	–	–	–	–	–
1978	556	10.1	14	39	0.39
1979	480	7.7	11	34	0.27
1980	550	8.9	12	33	0.22
1981	528	4.2	6	18	0.19
1982	374	0.3	0.4	1.5	0.16

[a] $R_{a(i)}$ in text.
[b] $B_{r(i)}$ in text.

Results and Discussion

Tables 13 and 14 give our estimates of monthly anchoveta consumption by mackerel and horse mackerel, respectively, for the years 1953 to 1982.[a] These data are also plotted for both species combined, on an annual basis in Fig. 5, which also shows, for comparison, annual fishery catches of anchoveta and anchoveta consumption by the birds. As might be seen, our estimates of anchoveta consumption by mackerel and horse mackerel are, throughout, well above the anchoveta consumption estimates for the birds, and *ipso facto* well above the corresponding estimates for bonito (see Pauly, Vildoso et al., this vol.), and dwarf those for the seals (Muck and Fuentes, this vol.). This is also true for the "least consumption estimates" based on catches instead of biomasses (Table 15), and which have been also plotted onto Fig. 5, for the years 1974-1982, i.e., for the period with an aimed fishery for mackerel and horse mackerel.

It thus appears that mackerel and horse mackerel jointly create an enormous predatory pressure on anchoveta - an interesting finding in view of the fact that anchoveta predation by the guano birds of Peru has generated to date a considerable literature, to which there is no equivalent as far as *Scomber japonicus* and *Trachurus muphyi* are concerned.

Some details on the seasonal and interannual variability of anchoveta predation by these two species are provided by Fig. 6, which shows species-specific anchoveta consumption on a monthly basis. As might be seen, anchoveta predation by mackerel is far below that for horse mackerel, but both species react similarly to changes of SST, thus reflect El Niño events in similar fashion.

We also ran our model for the period from January 1983 to July 1986, using the SST data in Table 4 of Muck et al. (this vol.). There was a reasonable agreement between the model estimates of D_{max} (50 and 70 miles for the summer and winter seasons, respectively) and the maxima of the observed density distribution (Fig. 7).

On the other hand, our model, although it suggested a biomass reduction, failed to predict the extremely low mackerel and horse mackerel biomass of 57×10^3 observed during a survey conducted by IMARPE in March-May 1985. This is probably due to the extremely cold water (<16°C) observed during this period.

Overall, we interpret these findings as supporting our concept of a temperature-mediated inshore-offshore migration and its implication concerning changes in anchoveta predation.

Ursin (1980) suggested anchoveta predation on the eggs of their potential predators as a possible key regulatory mechanism in the Peruvian upwelling ecosystem, and Muck et al. (this vol.) have confirmed this for sardine (*Sardinops sagax*). Sardine spawn from 5 to 12°S, within 40 miles off the coast (Santander and Flores 1983), i.e., well within what we have termed here the Main Anchoveta Area (MAR). This is not so for mackerel and horse mackerel (see references above) and indeed the abundance of their larvae from 1964 to 1982 has been shown

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[a] Intermediate results such as monthly mackerel and horse mackerel biomass within the MAR, their estimated total food consumption and related statistics are available on 5.25' microcomputer diskettes. Please contact the senior editor of this volume for details.

Table 13. Estimated monthly anchoveta consumption of adult mackerel *(Scomber japonicus)* off Peru (4-14°S; < 40 nautical miles) in t x 10^6, 1953 to 1982.

Year	Month J	F	M	A	M	J	J	A	S	O	N	D
1953	.11	.15	.19	.16	.12	.09	.09	.08	.08	.08	.08	.09
1954	.10	.11	.10	.08	.07	.06	.07	.05	.06	.06	.06	.09
1955	.14	.12	.09	.10	.08	.08	.07	.07	.07	.06	.07	.08
1956	.10	.12	.13	.10	.09	.09	.09	.08	.07	.07	.07	.07
1957	.09	.18	.18	.17	.18	.15	.13	.10	.09	.09	.09	.14
1958	.17	.18	.17	.13	.10	.09	.09	.08	.08	.08	.08	.08
1959	.11	.15	.14	.12	.10	.09	.08	.07	.08	.08	.09	.10
1960	.11	.12	.11	.09	.08	.08	.07	.08	.07	.07	.07	.09
1961	.11	.14	.11	.10	.09	.08	.07	.06	.07	.07	.07	.07
1962	.11	.11	.09	.08	.09	.08	.07	.07	.07	.07	.07	.07
1963	.08	.10	.11	.09	.10	.09	.09	.08	.08	.08	.08	.09
1964	.11	.12	.11	.09	.07	.06	.06	.09	.06	.07	.07	.07
1965	.09	.12	.13	.15	.14	.12	.11	.10	.09	.08	.09	.10
1966	.12	.13	.11	.09	.08	.08	.07	.07	.06	.07	.07	.08
1967	.10	.12	.11	.09	.08	.07	.07	.06	.06	.06	.06	.07
1968	.09	.09	.10	.07	.07	.06	.06	.07	.07	.07	.07	.08
1969	.10	.11	.13	.14	.15	.12	.08	.08	.08	.08	.08	.09
1970	.11	.12	.13	.11	.10	.09	.08	.08	.08	.08	.08	.08
1971	.09	.11	.12	.12	.10	.09	.09	.09	.08	.08	.08	.08
1972	.10	.14	.15	.13	.11	.11	.09	.07	.05	.06	.07	.10
1973	.13	.13	.09	.06	.05	.04	.04	.03	.04	.04	.05	.04
1974	.05	.06	.06	.07	.07	.08	.06	.06	.05	.05	.06	.06
1975	.07	.08	.13	.10	.08	.06	.06	.05	.06	.07	.06	.07
1976	.08	.15	.15	.12	.12	.11	.09	.08	.06	.05	.06	.06
1977	.06	.04	.05	.05	.04	.04	.04	.04	.04	.04	.05	.05
1978	.05	.06	.06	.05	.04	.03	.03	.02	.02	.03	.03	.02
1979	.04	.04	.04	.04	.03	.02	.02	.02	.02	.02	.01	.01
1980	.02	.02	.02	.02	.02	.02	.02	.02	.02	.02	.02	.03
1981	.03	.03	.02	.02	.02	.01	.01	.01	.01	.01	.01	.03
1982	.02	.02	.02	.01	.01	.01	.01	.01	.01	.02	.03	.05

Table 14. Estimated monthly anchoveta consumption of adult horse mackerel *(Trachurus murphys)* off Peru (4-14°S; < 40 nautical miles) in million metric tonnes (1953 to 1982).

Year	Month J	F	M	A	M	J	J	A	S	O	N	D
1953	.54	.72	.90	.75	.56	.43	.42	.37	.38	.36	.37	.41
1954	.47	.51	.46	.38	.33	.29	.31	.25	.27	.27	.31	.45
1955	.68	.56	.42	.46	.37	.36	.35	.31	.33	.30	.32	.36
1956	.46	.58	.61	.49	.45	.42	.41	.37	.35	.33	.34	.33
1957	.42	.86	.83	.79	.84	.72	.62	.48	.41	.43	.43	.65
1958	.79	.84	.82	.61	.49	.45	.43	.37	.37	.38	.40	.37
1959	.51	.72	.65	.56	.48	.42	.36	.35	.36	.38	.41	.48
1960	.51	.55	.52	.43	.38	.38	.35	.36	.35	.35	.35	.41
1961	.51	.65	.53	.48	.45	.39	.35	.27	.34	.34	.34	.34
1962	.51	.52	.44	.39	.41	.37	.35	.34	.35	.32	.34	.34
1963	.39	.49	.54	.45	.46	.43	.41	.39	.39	.37	.37	.43
1964	.51	.55	.52	.42	.33	.30	.28	.41	.31	.32	.33	.33
1965	.41	.56	.63	.73	.65	.55	.51	.46	.41	.40	.43	.48
1966	.59	.53	.52	.44	.40	.36	.34	.33	.30	.33	.34	.36
1967	.46	.56	.52	.41	.36	.33	.32	.29	.29	.27	.27	.34
1968	.41	.41	.47	.35	.34	.29	.31	.32	.34	.32	.35	.38
1969	.48	.51	.63	.64	.70	.55	.39	.39	.38	.39	.39	.42
1970	.52	.58	.60	.52	.48	.42	.36	.36	.36	.39	.37	.38
1971	.45	.51	.56	.58	.48	.43	.43	.43	.39	.36	.38	.38
1972	.48	.64	.72	.61	.54	.53	.42	.34	.25	.29	.32	.48
1973	.63	.60	.45	.28	.24	.20	.18	.16	.17	.18	.22	.20
1974	.23	.28	.31	.33	.32	.36	.29	.26	.24	.25	.30	.30
1975	.32	.39	.61	.49	.40	.30	.28	.25	.29	.31	.30	.34
1976	.38	.70	.73	.56	.55	.52	.44	.39	.27	.26	.26	.30
1977	.28	.21	.23	.25	.21	.20	.19	.18	.18	.19	.21	.24
1978	.23	.30	.29	.23	.17	.14	.13	.11	.11	.12	.14	.15
1979	.18	.19	.19	.17	.14	.12	.10	.10	.08	.08	.07	.07
1980	.08	.08	.10	.10	.09	.09	.08	.07	.08	.09	.12	.14
1981	.12	.14	.11	.09	.08	.06	.04	.04	.03	.05	.06	.08
1982	.08	.09	.08	.07	.07	.05	.05	.03	.04	.07	.15	.22

Table 15. Minimum estimates of mackerel and horse mackerel capable of feeding on anchoveta, and their estimated anchoveta consumption, as used to provide a lower limit to estimates of anchoveta withdrawals by these two fishes, from 1974 to 1982.

Year	Least predator biomass ($t \times 10^3$)[a]	Mean annual anchoveta availability index[b]	Least annual anchoveta consumption ($t \times 10^6 \times y^{-1}$)[c]
1974	176	0.54	1.73
1975	56	0.66	0.67
1976	84	0.61	0.9[illegible]
1977	540	0.34	3.35
1978	463	0.31	2.62
1979	238	0.21	0.91
1980	168	0.17	0.52
1981	63	0.13	0.15
1982	67	0.11	0.13

[a] Equivalent to catch of mackerel and horse mackerel within the MAR (see text).

[b] Estimated as in variable biomass model, see equations (15-17) and text.

[c] From equation (18).

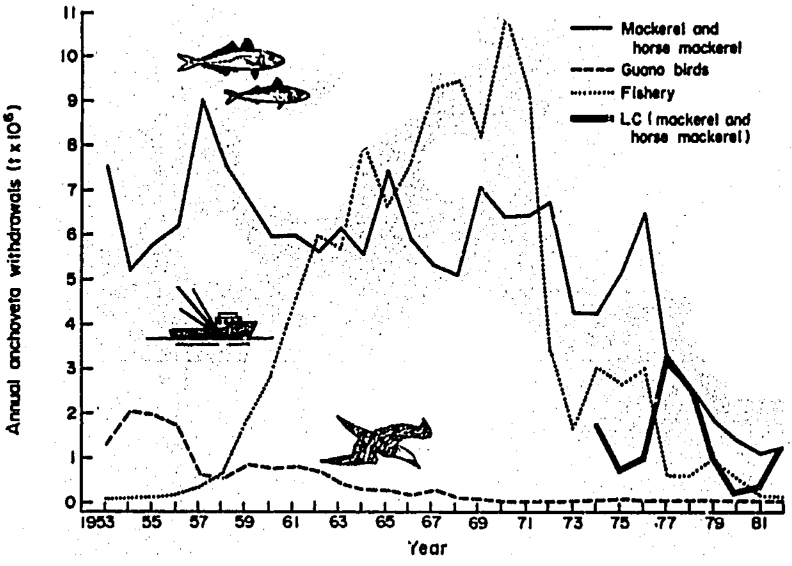

Fig. 5. Annual estimated consumption of anchoveta by mackerel and horse mackerel, compared with the bird consumption, the fishery catches and minimum estimates of mackerel and horse mackerel predation (LC).

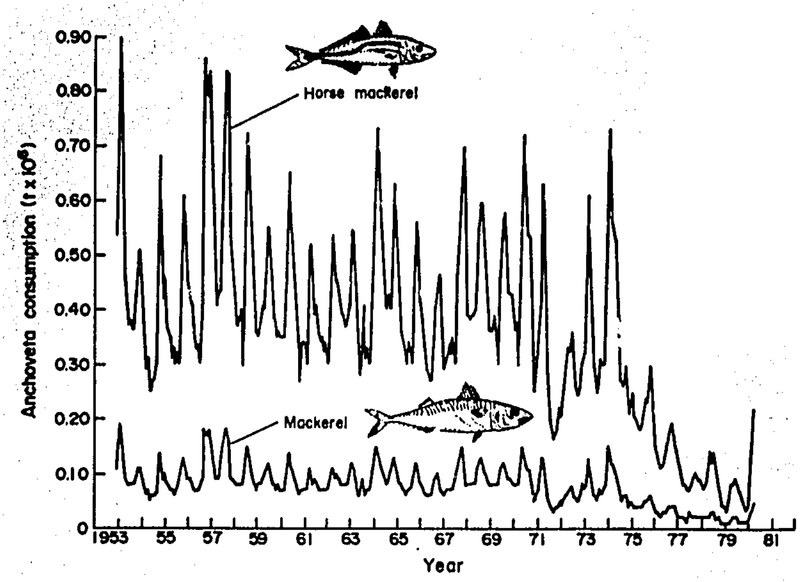

Fig. 6. Seasonal and interannual variability of anchoveta consumption by mackerel and horse mackerel.

Table 16. Variability of biomass and catches of three pelagic fishes in Peruvian waters, 4-14°S, within 40 nautical miles of the coast, 1983-1986.

Year	Biomasses (t x 10^6) Mackerel	Horse mackerel	Anchoveta	Annual catch of anchoveta (t x 10^6)[a]
1983	0.39[b]	1.99[b]	about 1[a]	0.12
1984	0.26[b]	0.54[b]	1 – 1.5[a]	0.02
1985	0.03[b]	0.03[b]	6.2[b] – 9.5[c]	0.82
1986	0.60[d]	1.60[d]	3.6[d]	–

[a] IMARPE catch and landing statistics.
[b] GOPA (1985) based on echo-acoustic surveys conducted by IMARPE.
[c] IMARPE egg survey.
[d] IMARPE echo-acoustic estimates.

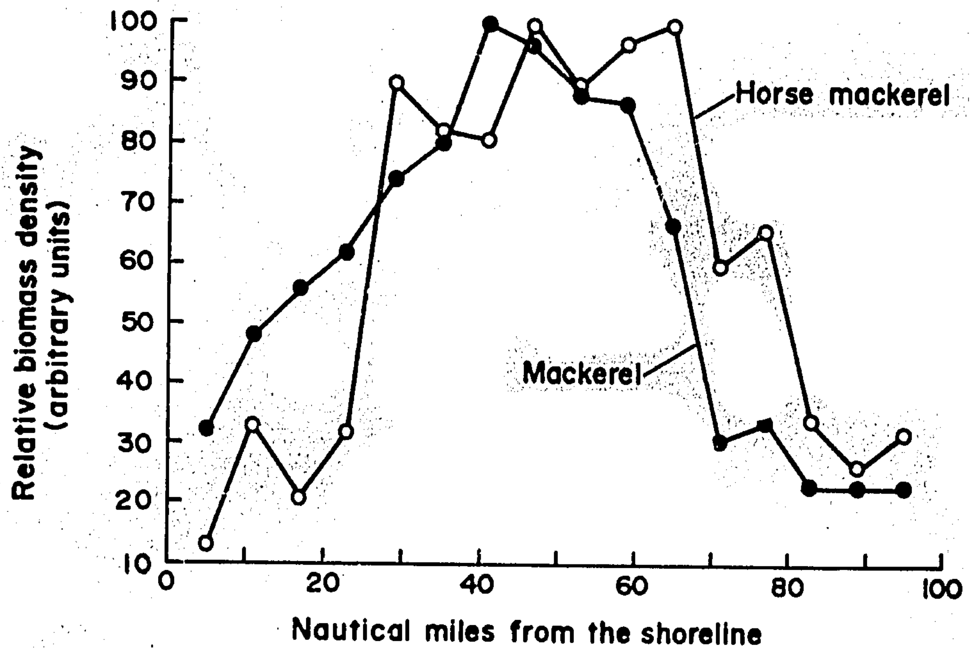

Fig. 7. Density distribution of mackerel and horse mackerel as recorded during an echo-acoustic survey conducted off Peru from April to May 1986. The biomass model predicted for the winter and summer seasons density maxima at 50 and 70 miles, respectively (see also text).

by Muck et al. (this vol.) to be independent of anchoveta biomass. This provides strong support for our assumption that the overall biomass of mackerel and horse mackerel may have been fluctuating around 11 t x 10^6 during the whole period considered here (1953-1983).

It is highly probable, on the other hand, that the predation by mackerel and horse mackerel on anchoveta or the absence of predation may explain (at least in part) the very strong fluctuations of anchoveta, e.g., their massive increase from 1984 to 1985, at a time when mackerel and horse mackerel within the MAR was very low (Table 16).

From this, and the foregoing results, it appears that mackerel and horse mackerel will have to receive far more attention than hitherto in models of the Peruvian ecosystem, in which they now appear to be to most important top predators.

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Exploratory Analysis of Anchoveta Recruitment off Peru and Related Environmental Series*

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Abstract

An exploratory analysis of monthly anchoveta *(Engraulis ringens)* recruitment estimates and associated biological and environmental series for the years 1953 to 1981 was performed with the aim of investigating the possibility of forecasting anchoveta recruitment three months ahead of time. While the high degree of autocorrelation in the monthly recruitment series prevented the identification of causal models, yearly models combining pairs of adjacent months were identified which appear promising as a means to forecast future trends in anchoveta recruitment. These models, however, do not appear to conform to any of the conventional hypotheses providing mechanisms to explain recruitment fluctuations.

Introduction

Recruitment is one of the most important but least understood components of fish population dynamics. Several authors have tried to empirically relate larval survivorship with environmental parameters (Bailey 1981; Lasker 1981). These efforts to relate recruitment variability with environmental variability have not been notably successful due to the very short data series generally available for empirical analysis (Bakun 1986). Major recent studies have indicated environmental-biological linkages for pelagic and demersal species of the California Current, Canary Current and Guinea Current (see Bakun 1986). Wind induced Ekman transport, a turbulent mixing index (wind speed cubed) and temperature also have been used in several studies of environmental effects on fish stocks (e.g., Collins and MacCall 1977; MacCall 1980; Bakun and Parrish 1980; Mendelsohn and Cury 1987).

Similar studies have yet to be done for the Peruvian anchoveta (*Engraulis ringens*) which in the early 1970s generated the highest catch of any single-species fishery in the world (Tsukayama and Palomares, this vol.; Castillo and Mendo, this vol.), and whose biomass was well over 20 t x 10^6 by the end of the 1960s (Pauly, Palomares and Gayanilo, this vol.). The collapse of the anchoveta fishery has been attributed both to overfishing and to the influence of El Niño which may have changed the usual spawning patterns of the anchoveta (Santander 1980).

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*PROCOPA Contribution No. 53.

The biology of the anchoveta is rather well documented (see relevant contributions in this vol.). Spawning in anchoveta tends to have two peaks per year - one in the austral winter-spring and the other in austral summer. The major spawning concentrations usually occur near the coast up to around 105 km offshore. Since the 1960s, the Instituto del Mar del Peru (IMARPE) has carried out anchoveta egg and larval surveys (see Santander, this vol.), but these data do not necessarily indicate variations in anchoveta recruitment due to density-dependent egg cannibalism, other sources of egg mortality and fluctuations in survival of the larvae (see Pauly, this vol.).

Several authors (Santander 1980; Mendiola and Ochoa 1980; Tsukayama and Alvarez 1980; Santander and Flores 1983) have presented evidence showing that during El Niño years, primary productivity decreased and the periods of peak spawning changed resulting in lower recruitment. These two factors have been thought to be the major environmental influences on recruitment variability.

In this paper we perform an exploratory data analysis of the estimated recruitment and biomass series of Pauly, Palomares and Gayanilo (this vol.), of the egg production series in Pauly and Soriano (this vol.) and of several of the various environmental series gathered in this volume. Our interest is in determining if it is possible to forecast anchoveta recruitment at least three months ahead of time, a forecast that would be useful in managing the fishery.

Exploratory data analysis has the advantage in this situation where little is known in that we do not try to force the data into models that may not agree with the structure of the observed data. Despite the variety of fisheries models available, there is no "physics of fisheries" in the sense of known laws that have been experimentally verified. Letting the data lead us to a model structure leaves us open to alternative causal explanations as well as providing a check on the realism of the estimated series, identifying outliers in the data and flagging data points that may be overly influential in the analysis.

The Data

The anchoveta population data used are the estimates presented by Pauly, Palomares and Gayanilo (this vol.). The environmental series consisted of sea surface temperature (SST) and oceanic wind speed cubed and offshore transport derived by Bakun (this vol.), as well as hourly wind direction and intensity recorded at Trujillo and Callao airports by CORPAC (Corporacion Peruana de Aviacion Comercial). The Trujillo and Callao data are described further in Mendo et al. (1987) and Mendo et al. (this vol.).

Offshore transport at both Trujillo and Callao were calculated as in Bakun (1973 and this vol.), as was wind speed cubed for both locations. Peterman and Bradford (1987) report using an index reflecting Lasker's hypothesis (1978) to predict the survival of anchovy *Engraulis mordax* larvae off California. A similar index was computed for both Trujillo and Callao; it measures the number of 4-day periods during which the wind speed did not exceed 5 m/sec. These 4-day periods are here called "Lasker events", as suggested by D. Pauly (pers. comm.).

Spectral analysis showed that the Trujillo and Callao wind series were not significantly coherent at all frequencies. The Trujillo wind series were only coherent with the oceanic wind series at a frequency of 6 months (though out of phase) and at frequencies longer than a year. The oceanic series show a pronounced seasonal cycle, the Callao series a smaller seasonal cycle and the Trujillo series showed essentially no seasonal cycle. The general impression is of strong local differences suggesting the need for care in choosing what variables to use in the analysis.

The Lasker events were problematic at best. At Callao, the wind always satisfied the criteria, while at Trujillo most months had a zero incidence of the necessary periods of calm, especially during 1955-1970, when recruitment was at high levels (see below and Table 1). The estimated recruitment following the periods of zero counts vary greatly, making Lasker events of little use for these periods. For the periods where numerous Lasker events occurred, examination of the data revealed that a high number of events tended to precede low rather than high recruitment. Lasker's hypothesis is based on experience in California where turbulence disperses the food necessary for larval survival; in Peru the food concentration in the mixed layer may be high enough for turbulence not to have that great an effect. All that can be said with certainty from this is that the situation in Peru appears to differ from that in California.

Table 1. Monthly occurrence of "Lasker events" near Trujillo, 1953-1985.[a]

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	0	7	2	0	0	1	6	19	2	2	0	0
1954	0	6	20	0	0	0	0	0	0	0	0	0
1955	0	0	0	0	0	0	0	0	0	0	0	0
1956	0	0	0	0	0	0	0	0	0	0	0	0
1957	0	0	0	0	0	0	0	0	0	0	0	0
1958	0	0	0	0	0	0	0	0	0	0	0	0
1959	0	1	0	0	0	0	0	0	0	0	0	0
1960	0	0	0	0	0	0	0	0	0	0	0	0
1961	1	3	2	0	0	0	0	0	0	0	0	0
1962	0	0	0	0	0	0	2	0	0	0	0	0
1963	0	1	0	0	0	2	1	0	0	0	0	0
1964	0	0	0	0	0	3	0	0	0	0	0	2
1965	3	0	1	0	0	0	0	0	0	0	0	0
1966	0	0	0	0	0	0	0	0	0	0	0	0
1967	0	0	0	0	0	0	0	0	0	0	0	0
1968	0	0	0	0	0	0	0	0	0	0	0	0
1969	0	0	0	0	0	0	4	0	1	0	0	0
1970	0	0	0	0	0	0	0	0	0	0	0	0
1971	0	2	8	0	0	0	3	0	0	0	0	0
1972	2	1	0	0	0	0	0	0	0	0	0	0
1973	0	0	0	0	0	0	0	0	0	0	0	1
1974	20	27	22	6	3	0	6	5	0	0	0	0
1975	3	6	4	1	0	0	0	0	0	0	0	0
1976	0	1	0	0	0	0	0	0	0	0	0	1
1977	0	0	0	0	1	0	3	0	0	0	4	0
1978	0	0	0	0	12	4	3	3	0	4	11	1
1979	0	0	7	6	2	8	7	2	0	0	0	1
1980	0	0	1	0	0	0	0	0	0	0	0	0
1981	0	2	5	0	5	10	8	1	1	0	1	6
1982	14	12	6	1	21	30	30	31	30	31	30	5
1983	0	0	12	12	4	0	7	0	0	0	0	0
1984	3	1	0	0	0	1	17	3	0	0	2	1
1985	6	1	2	6	2	0	0	2	0	0	0	0

[a] Based on data in Mendo et al. (1987); a "Lasker event" is a period of calm (wind speed below 5 m/s) lasting 4 days; periods of 5 days are viewed as two partly overlapping 4-day events, etc. (see Peterman and Bradford 1987, note 16).

Based on this preliminary analysis of the environmental series, we restricted our attention to the wind variables at Trujillo. The Trujillo station has no nearby topographic interference, such as mountains, and the coastline from one degree north of Trujillo to one degree south of Trujillo is almost straight. The area off Trujillo also is one of the major anchoveta spawning areas (Santander and Castillo 1973; Santander 1980, this vol.).

Localized trends were calculated using the "lowess" algorithm of Cleveland (1979) for recruitment, egg and total biomass as well as for offshore transport and wind speed cubed at Trujillo. Both the recruitment and total biomass series exhibit three periods with distinct mean levels. A pre-1960 period with low levels of biomass and recruitment, a period from 1960 to 1972 when both biomass and recruitment were at high levels, and a post-1972 period following the collapse of the fishery (see Pauly, Palomares and Gayanilo, this vol.). On a log scale, for the 1960-1972 period, the trend line for both recruitment and total biomass is almost flat, suggesting random variation around a fixed mean level.

Recruitment Series

For our initial look at anchoveta recruitment we examined the dynamics of the recruitment series by decomposing it into three components - localized trend, seasonal and autoregressive (AR) components (Fig. 1), using an algorithm of Gersch and Kitigawa (1983). The variation in recruitment is dominated by longer-term behavior captured in the estimated trend, as the AR component is an order of magnitude smaller than the recruitment series and the seasonal component is almost two orders of magnitude smaller.

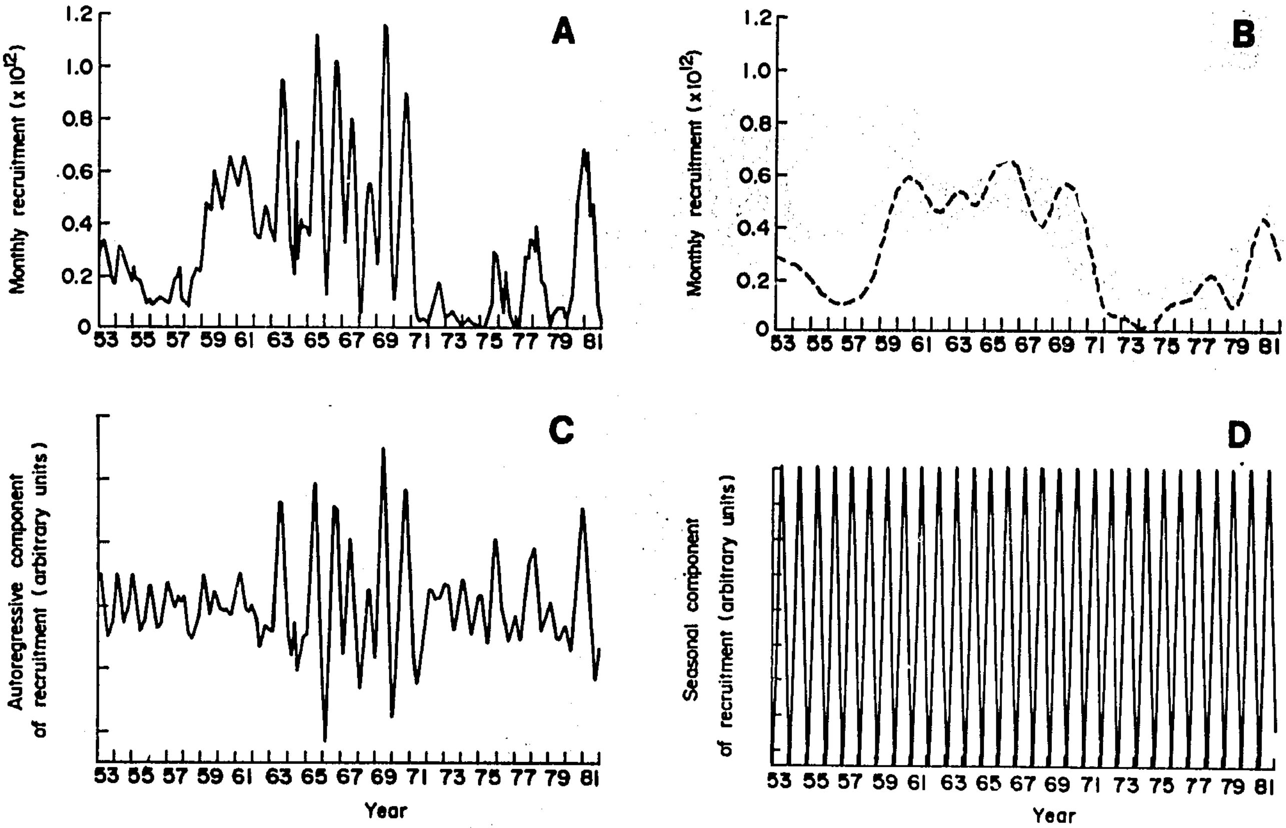

Fig. 1. Decomposition of the anchoveta recruitment time series into its component parts: (A) observed data; (B) estimated trend; (C) autoregressive component; (D) seasonal component (see text for details).

The estimated local trend (Fig. 1B) suggests three different periods: a low level of recruitment from 1953 to 1958, a higher level from 1959 to 1969 or 1970, followed by a sharp drop in recruitment which *preceded*: (i) the El Niño even to 1972-1973, (ii) the collapse of the fishery, (iii) and by a year, the drop in total biomass. This suggests that the effects of El Niños on the population dynamics of anchoveta may be more complex than previously thought. The 1971 recruitment collapse must have been due to overfishing or environmental effects the previous years since the collapse of the fishery appears to have begun before the El Niño.

The seasonal component (Fig. 1D) is very regular but of such small magnitude as to be almost unnoticeable in the overall variation in recruitment. The autoregressive component (Fig. 1C) also suggests three periods: a period from 1953 to 1961 of relatively small variations, a period from 1961 to 1972 of large variations coinciding with the growth of a large-scale fishery and a period from 1972 or so onwards following the collapse of the fishery which is also a period of smaller variations in recruitment. The period of high variability from 1961 to 1972 also is a period of high estimated total biomass.

The autocorrelation function of recruitment both on the normal and the log scale is highly nonstationary and dominated by a value of .95 at a lag of one month. A simple model that includes an autoregressive term of recruitment on itself at lags 1, 2, 6 and 12 months explains almost 96% of the variance in the monthly series. This agrees with the decomposition of the time series: monthly estimates of recruitment have not increased our degrees of freedom as the series is not independent at monthly time spans; rather, the important variation is between years.

The high degree of autocorrelation in the monthly recruitment series is probably caused by (i) the fact that the sampled length-frequency data may not be accurate enough to resolve monthly differences in population structure so that the size information tends to be "smeared" across months, (ii) the fact that Virtual Population Analysis (VPA) uses a series of recursive equations that estimate the present biomass levels from the data from successive periods; these equations will tend to smooth the observed data towards low-order autoregressive behavior, reducing the independence of the monthly data and (iii) the fact that the version of length-structured VPA used by Pauly, Palomares and Gayanilo (this vol.) increases the inherent tendency of VPA to smooth data across months (D. Pauly, pers. comm.).

There are several approaches for analyzing the recruitment series given this high degree of autocorrelation. We can low-pass filter the series and then decimate the results to one or two representative values a year and use these data points as the new time series. Alternatively, we can form separate annual series of seasonal segments of the annual cycle and fit separate models across years for each of the aggregate series, comparing the results of the different models. This second approach has an added advantage that it allows us to check for time-dependent relationships in the data. In what follows we restrict ourselves to this second approach.

Bimonthly Recruitment Series

As an initial examination of the data by months across years, we constructed box plots (Velleman and Hoaglin 1981) for each of the series (Fig. 2). A plus marks the median of the data, the I's mark the hinges plus or minus 1.5 times the H-spread, where the hinges are the medians of the two halves of the series defined by the median and the H-spread is the difference between the two hinges. The lines beyond the boxes show the outer normal range of the data which is defined as the hinges plus or minus 3 times the H-spread. Values somewhat outside this range are marked with dots and values far outside this range with open dots. Finally, the parentheses denote a confidence limit on the medians.

Recruitment (Fig. 2A) starts out in January at a relatively lower level, increases gradually to a recruitment peak around May-July and then slowly decreases to the end of the year. Egg production, however, has a relative peak around February-March and a much larger peak around September-October. Parent biomass (Fig. 2C) has a large peak in February-March concurrent with the relative peak in egg production but usually has relatively low value during the September-October period. Thus assuming the recruits to be 3-4 months old (see Palomares et al., this vol.), the larger recruitment in June-July would stem from the lesser spawning of February-March, which is based on a large parent biomass. Conversely, the lesser recruitment in the beginning of the year would stem from the major spawning in September-October, which is based on a relatively small parent biomass. The wind-related environmental series (Figs. 2E and 2F) are at a relative minimum during the February-March period, but are at their maxima during the September-October period and thus generate unfavorable environmental conditions. Parrish et al. (1984) also comment on the large austral spring spawning during unfavorable conditions. One possible explanation for a large spawning during unfavorable conditions is that the conditions during this period are favorable for the adults (it is the upwelling period). A. Bakun (pers. comm.) has suggested that such a low degree of apparent adaptation of spawning effort to the normal seasonality of larval survival prospects might be in some way due to the fact that detrimental El Niño effects may exert strongest impact during the warm austral summer period; thus the effects of intermittent reproductive failures during summer, associated with El Niño anomalies may have tended to counter adaptive tendencies to concentrate spawning in the normally favorable summer season.

After examination of the recruitment series and the environmental series we decided on bimonthly aggregation of the recruitment series as follows: February-March, April-May, June-July, August-September, October-November and December-January. Note that the December-January aggregate crosses years: December 1953 is combined with January 1954, etc. These pairs of months vary across years in a similar manner and at similar levels (Fig. 3). For

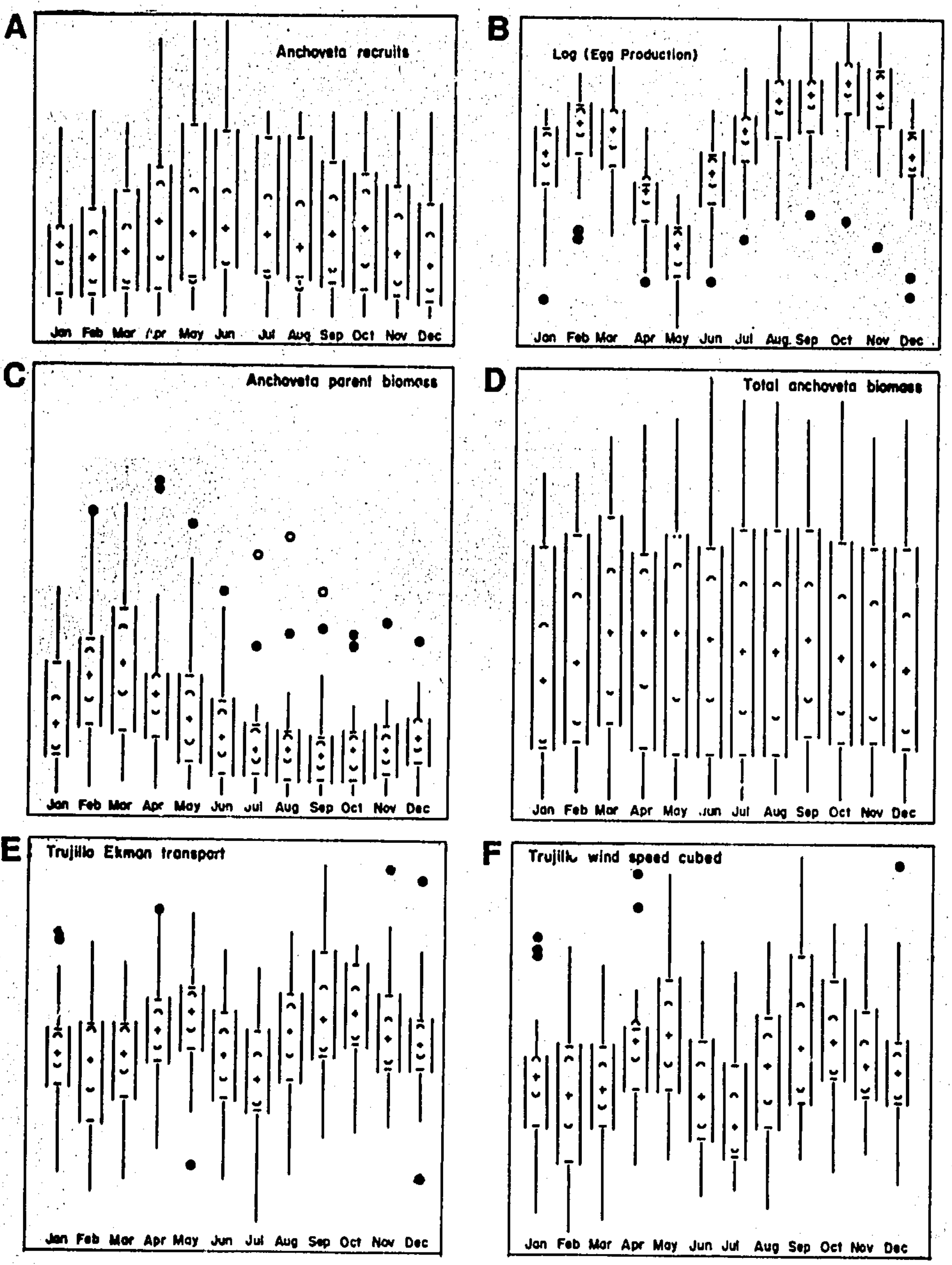

Fig. 2. Boxplots of the monthly anchoveta and wind-based environmental series: (A) recruitment; (B) log of egg production; (C) parent biomass; (D) total biomass; (E) Trujillo offshore transport; (F) Trujillo wind speed cubed (see text for definition of ordinate and data sources).

predictors we considered parent biomass and egg production lagged 3 and 4 months (the spawning period) as well as the monthly offshore transport and wind speed cubed at Trujillo. Spectral analysis of the transport and wind speed cubed at Trujillo shows that these series are highly coherent (> .9) at all frequencies and thus have essentially the same dynamics due to limited variability in the wind direction (Mendo et al., this vol.). We therefore arbitrarily restrict our attention to offshore transport, though similar results can be found using wind speed cubed, i.e., turbulence.

Cross-correlation matrices as well as generalized partial correlations were calculated as in Tiao and Box (1982). Model and variable selection were also examined using the multivariate subset autoregression procedure of Akaike et al. (1979). As it is likely that the relationships between recruitment and the environment is nonlinear, final model selection and identification was done using the AVAS procedure (Tibshirani 1987). This procedure is a modification of the optimal transformation algorithm ACE (Breiman and Friedman 1985) which appears to correct

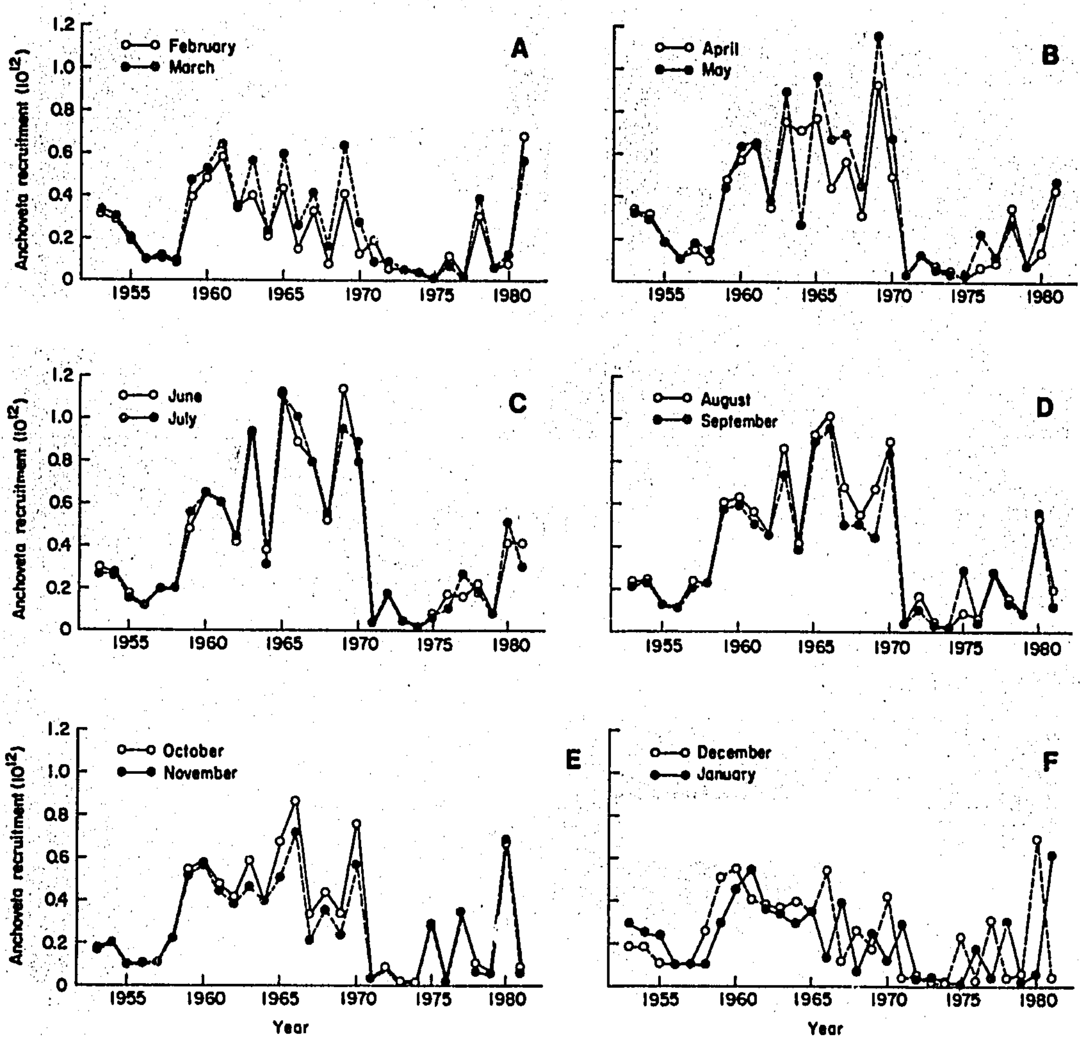

Fig. 3. Monthly anchoveta recruitment across years, 1953 to 1981: (A) February-March; (B) April-May; (C) June-July; (D) August-September; (E) October-November; (F) December-January.

some of the problems with that algorithm, by restricting the transformation of the dependent variable to be monotone and variance stabilizing (Efron 1982).

Both the approach of Tiao and Box (1982) and the subset autoregression procedure suggested the same behavior in all the series. Each of the bimonthly recruitment series had a significant relationship with recruitment two years hence. Parent biomass 3 and 4 months earlier appears to have no significant effect on recruitment. Except in one case to be discussed below, environmental conditions during the spawning period also do not appear to be strongly related to recruitment. Egg production was not examined for all the bimonthly series; however, for the models in which egg production was used as a variable it also was not significantly related to recruitment 3-4 months later.

For all six bimonthly series, offshore transport during the austral spring period September-November was identified as the important predictor of recruitment, and that the strongest relationship appeared to be with September transport. To obtain our models, the AVAS algorithm was used on each of the six bimonthly recruitment series, using recruitment two years earlier and September-November transport as variables. The variables were selected in a stepwise fashion by first identifying the best single variable, then by finding the second variable that when added to best single predictor produces the most increase in r-square value, etc. As a partial check on our procedure, monthly transport series were chosen at random for inclusion in our analysis; at no point did any of these series produce a significant result. Since AVAS produces transformations that can improve the relationship between variables if the relationship is nonlinear, we also tested the inclusion of parent biomass and environmental conditions 3-4 months previous to recruitment. Again, with one exception, none of these series added significantly to our results.

The models estimated by AVAS all had estimated r-square values in the range of .75 to .80. Given the relative short length of our time series as well as the amount of searching we did over variables, it would not surprise us if this value is inflated as a measure of prediction r-square, that is of expected error in forecasting future data rather than the error from the data used to estimate the models (see also Efron 1986; Hastie and Tibshirani 1986). AVAS finds relationships by using smoothers to estimate condition expectations, and the parameters for these smoothers are chosen using generalized cross-validation which at least asymptotically should reflect prediction error (Friedman and Stuetzle 1982; Breiman and Friedman 1985; Hastie and Tibshirani 1986). Also, as we discuss below, the models tend to fit the series by measures other than r-square, particularly in anticipating turning points in the series.

The estimated transformations (Fig. 4) are similar for each of the six models for all variables. (AVAS calculates empirical transformations so the form of the transformation is determined by plotting the transformed variable against the original variable. All transformations are standardized to have zero mean and variance of 1; this is necessary for identification of the transformations.) Recruitment at time t is transformed to a form very close to a log transformation. This agrees with our observation of the decomposed recruitment series that the series appears to have increased variance at higher levels; the log transformation stabilizes the variance in this instance. A log transformation also means that environmental effects are on a proportional rather than an absolute basis, which, *a priori,* appears to be more sensible.

The estimated transformation for recruitment at time t-2 suggests two separate regimes - periods of relatively lower recruitment and periods of higher recruitment. The transformations suggest that the behavior is almost like an indicator function - the group, rather than the exact level, being the important information. At first glance, a 2-year lag in recruitment would seem to reflect the effect recruitment has on the spawning biomass for the recruits at the present time period. However, as previously mentioned, parent biomass during the spawning period is not a good predictor and adds little to our model. The mechanistic interpretation of the 2-year lag in recruitment therefore is an open question.

The transformation of transport during the previous September generally increases to a peak at around a value of 2.5, which corresponds to a wind speed of roughly 6 m/sec, decreases to a minimum with a value of 3, roughly corresponding to a wind speed of 7 m/sec and then increases again. Note that wind speeds between 6 and 7 m/sec correspond to the transitional level at which water changes from being hydrodynamically "smooth" to being hydrodynamically "rough" (Deacon and Webb 1962).

The transformation of transport in November generally increases, but behaves differently between the same values of 2.5-3. The model appears to be contrasting the September and November conditions. Optimal conditions occur when there is some transport in September followed by a high level of offshore transport in November. Again, the mechanistic interpretation of these variables is not clear.

The model for December-January recruitment also contains a term for September transport three months earlier, corresponding to the spawning period. The estimated transformation decreases monotonically, with a particularly sharper slope as wind speed exceeds the 6-7 m/sec range. This term appears to explain why the large egg production during the August through October period does not produce a large number of recruits: egg and larval mortality may be much higher. It is interesting that this is the only period during where conditions during spawning are important to the model.

On the whole, the model predictions (Figs. 5, 6 and 7) of transformed recruitment appear to be quite satisfactory. As the estimated transformations are close to being log transformations, the values are similar to taking the log of recruitment and then standardizing the variables. This will not change relative peaks and troughs and trends in the data. As is clear from both the fits and the residuals, none of the models do a very good job for the first five years, 1955-1959. After that, the models appear to track the major turning points quite well, in particular by anticipating the major decline in recruitment during the 1969-1971 period and the subsequent increase in recruitment later on in the 1970s. Apart from the first five years, the residuals are fairly well behaved except for the April-May residuals which show a definite trend throughout the model

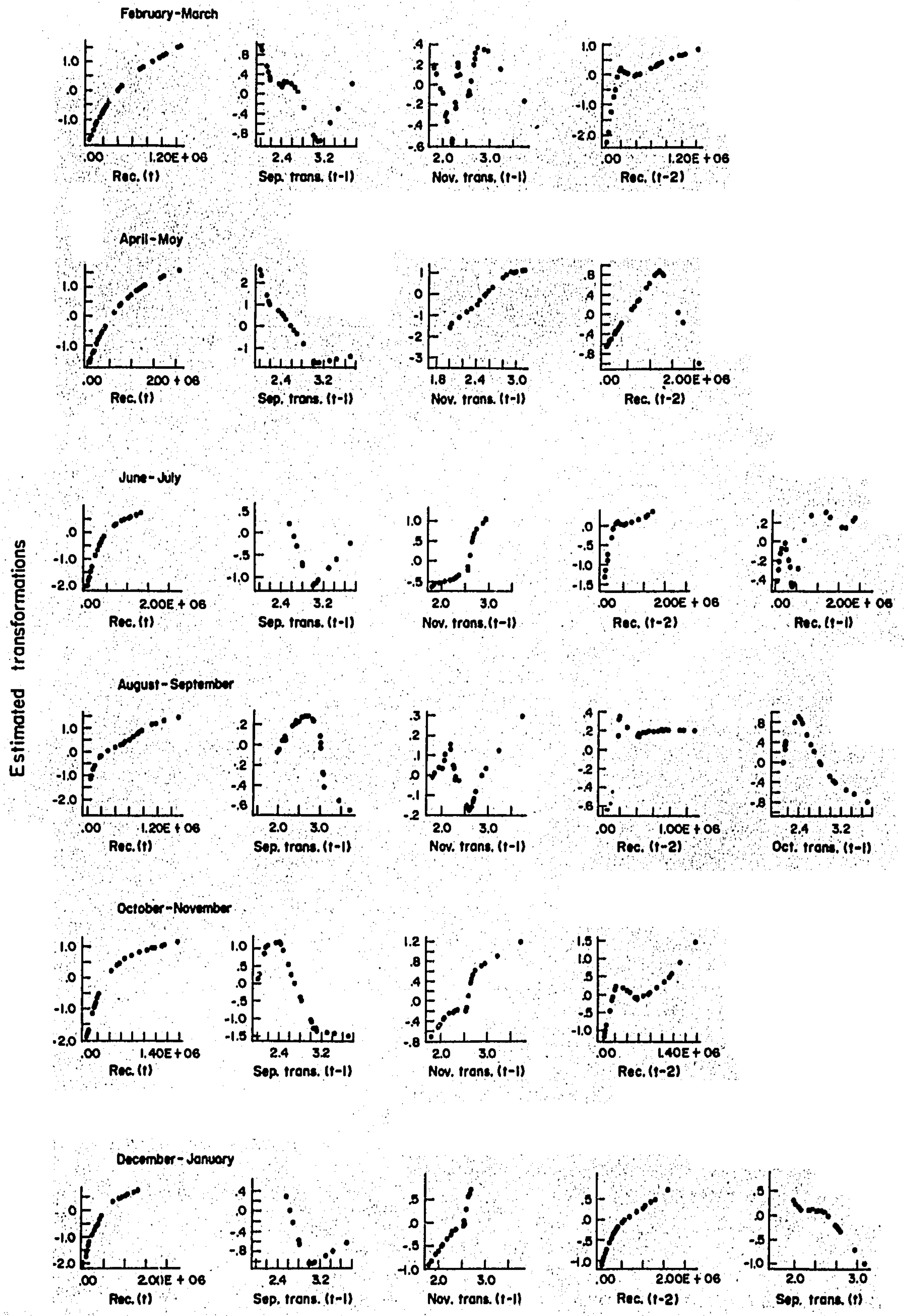

Fig. 4. Estimated transformations for predicting anchoveta recruitment for successive 2-month periods (see text).

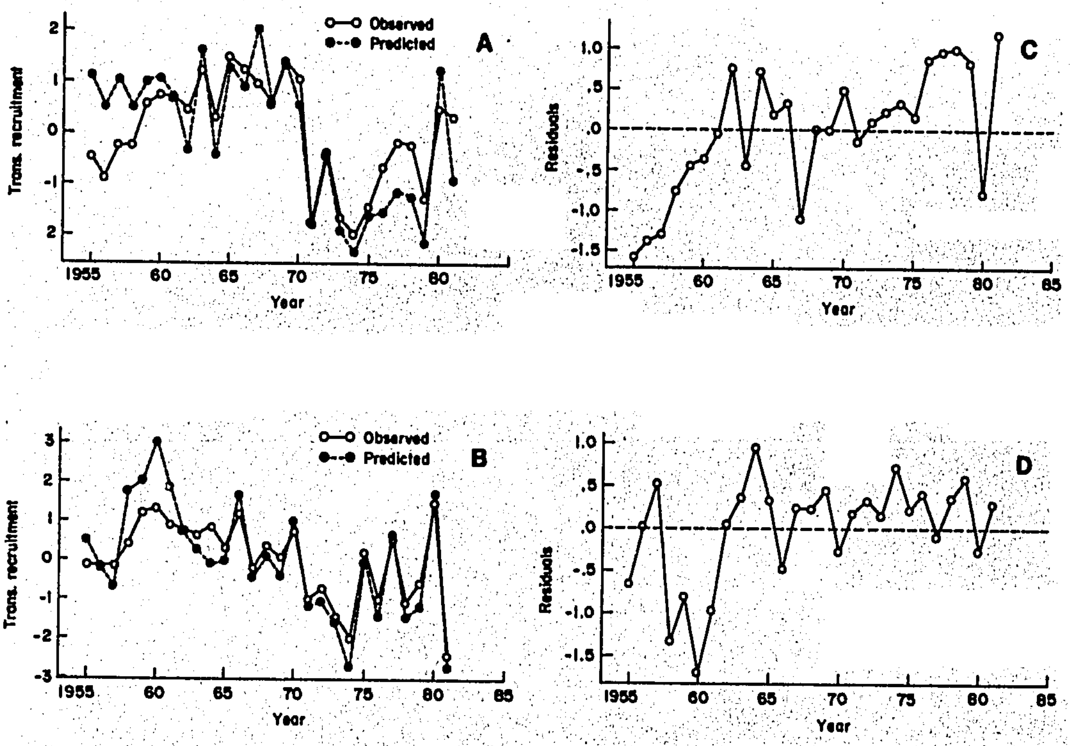

Fig. 5. Observed and predicted February-March (A) and April-May (B) anchoveta recruitments, with residuals (C, D).

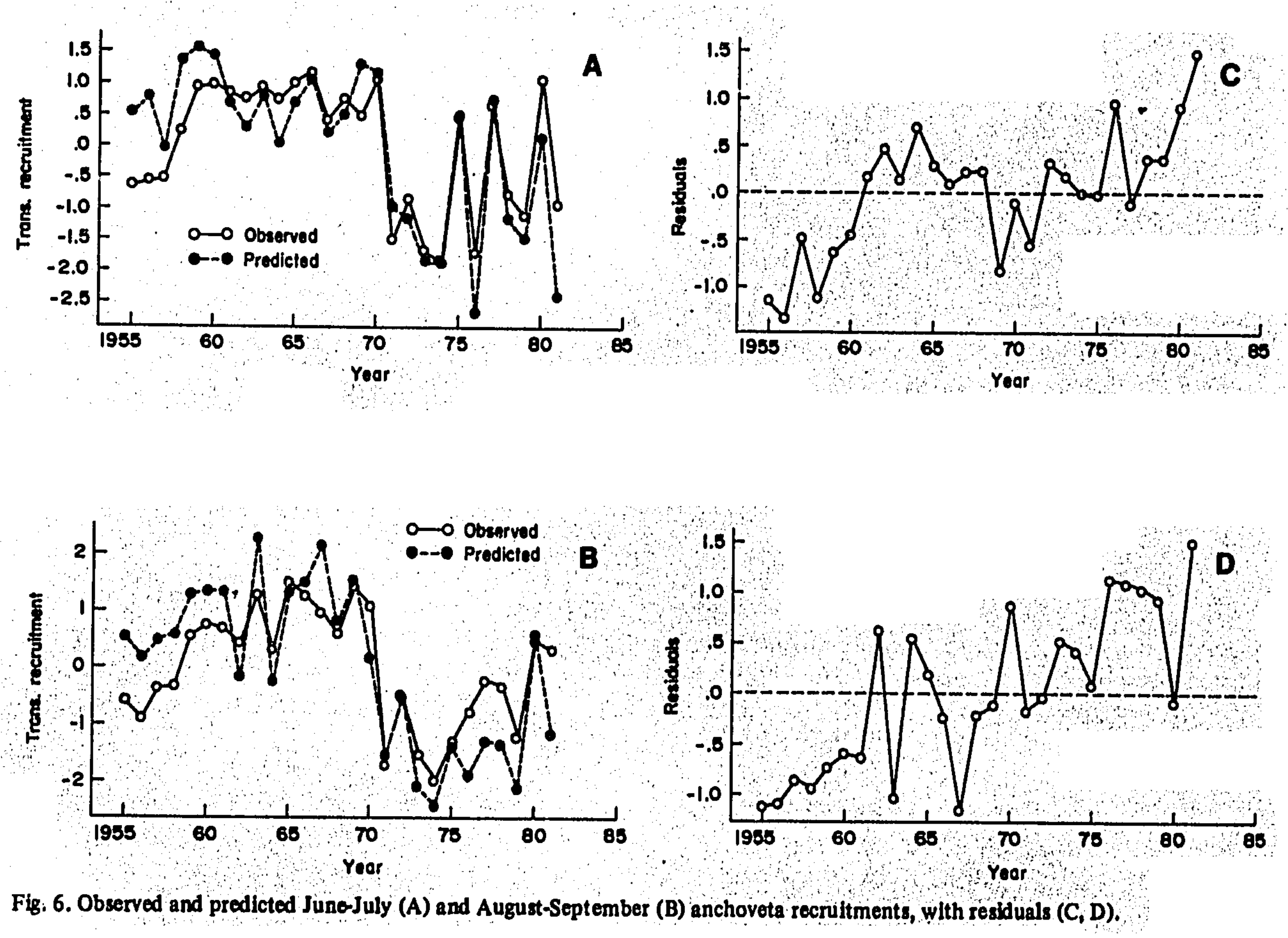

Fig. 6. Observed and predicted June-July (A) and August-September (B) anchoveta recruitments, with residuals (C, D).

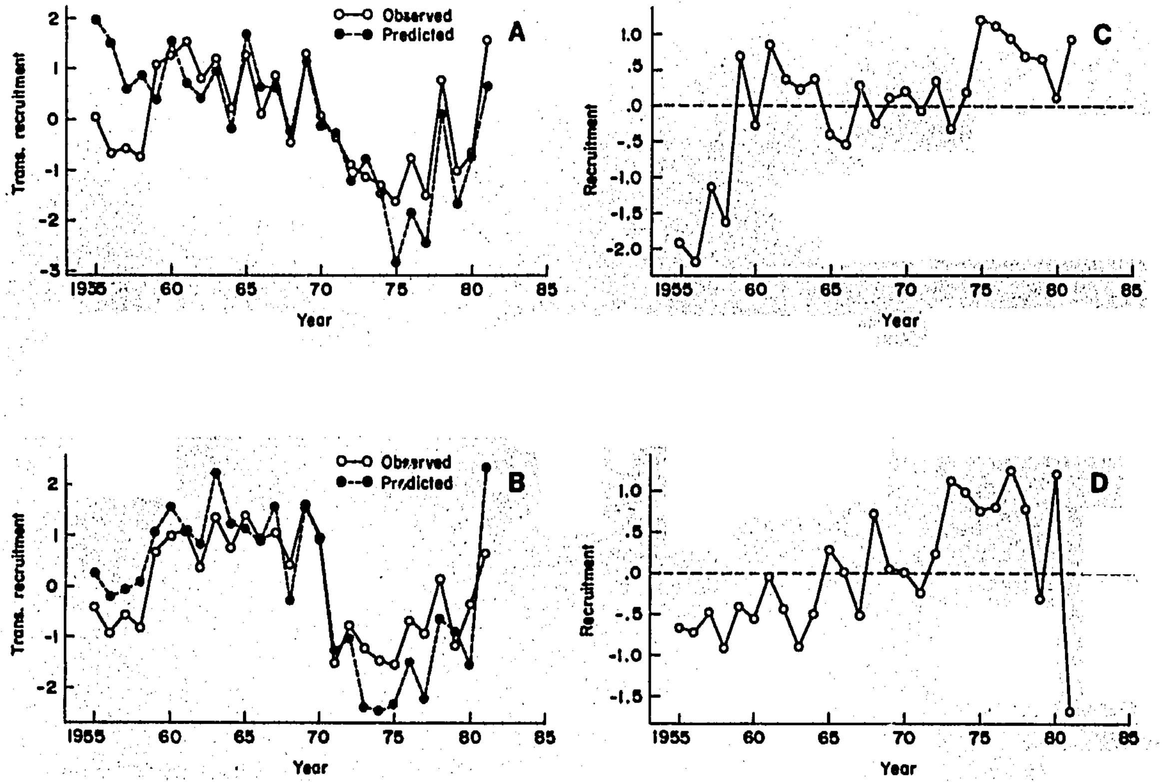

Fig. 7. Observed and predicted October-November (A) and December-January (B) anchoveta recruitments, with residuals (C, D).

period. The June-July and August-September models, when recruitment appears to be at or near a maximum, appear to anticipate changes in recruitment quite well.

The biomasses and the recruitment estimates for the period 1953 to 1959 were obtained through VPA using values of residual natural mortality (M_O) which could not be calibrated against independent biomass estimates; moreover, during this period, a large proportion of the withdrawals used for the VPA were estimates of anchoveta consumption by birds and bonito (see Pauly, Palomares and Gayanilo, this vol.). These appear to be sufficient reasons for differences between this period and the succeeding ones and thus explain why, in terms of our models, recruitment during this time period behaved in a manner different from the rest of the model period (see also Pauly, this vol.).

Discussion and Conclusions

We have shown that while the high degree of autocorrelation in the monthly recruitment data makes it difficult to identify causal models of anchoveta recruitment, we could, however, identify yearly models for bimonthly recruitment series. These models tend to have a similar structure, predict recruitment with approximately equal success and appear promising as a means to forecast future trends in anchoveta recruitment.

The pattern of the cross and partial correlation matrices, as well as several different modelling approaches, have all suggested the same basic models. Thus we feel confident that the relationships described in our models reflect the basic structure of the data. However, there is no clear biological interpretation of this structure. As we have done an extensive amount of searching through different sets of variables and estimating transformations to increase model fit, it is likely that our estimates of the goodness of fit of our models and of the ability of the models to predict future data is somewhat inflated. We would therefore recommend to implement the following steps before attempting to implement a model similar to the one analyzed here:

(i) Attempt to calibrate the estimated recruitment series with independent data (i.e., data not used in obtaining the estimates) to further verify that the estimated recruitment reflects the actual changes in recruitment, at least on a yearly basis;

(ii) Calculate offshore transport and wind speed cubed from other stations near Trujillo to check on the accuracy and consistency of this data set;

(iii) Develop a better mechanistic understanding of the underlying models. We are distrustful of forecasting models that do not have a clear biological interpretation and for which there is no independent evidence for the relationships developed in the exploratory analysis;

(iv) For log recruitment, use techniques that estimate transformations without transforming the dependent variable, and that allow for greater testing of model parameters, such as GAIM (Hastie and Tibshirani 1986); and finally

(v) Use generalized cross-validation or related techniques to test the stability of both the transformations and the degree of fit of the models, in order to get a better idea of the predictive capability of the models for data to be obtained in the future.

Despite these reservations, we feel we have shown that the series of recruitment estimates produced by Pauly, Palomares and Gayanilo (this vol.) have properties which enable them to forecast far enough in advance for consideration in the formulation of management actions. Further, we have indicated the importance of including variables that reflect environmental processes. However, the fact that the resulting models do not appear to conform to any of the conventional hypotheses concerning major influences on recruitment success remains unsettling.

Acknowledgements

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A Bioeconomic Model of the Peruvian Pelagic Fishery*

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AGUERO, M. 1987. A bioeconomic model of the Peruvian pelagic fishery, p. 307-324. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

This paper presents an overview of the evolution of the Peruvian fisheries from an economic point of view.

The consequences of El Niño phenomena on Peruvian fleet and processing overcapacity, fluctuations on landings and fish meal production and the need for tools to assess economic consequences of alternative conditions in the fishery system are outlined. A mathematical, conditional programming model structured in terms of a constrained optimization problem is presented. A Fisheries Net Benefit Function (FNBF) is proposed which expresses all activities implying costs and revenues. Assumed functional relationships are based on data obtained from secondary sources and extrapolation from similar fisheries.

Results from the base model representing conditions similar to those prevailing in 1982 show that the Peruvian purse seine fishery for small pelagics is capable of generating a net benefit of approximately US$173 million per year from a total catch of 3.5 million tonnes. Gross annual revenues are about US$371 million, of which US$300 million could consist of export revenues. However, costs are approximately US$200 million. The fleet required to harvest this amount is estimated as 364 vessels operating under normal conditions and an average excess capacity of about 37%.

A sensitivity analysis of the model is presented.

Introduction

Evolution of Peruvian Fisheries

Archeological findings in the Illescas peninsula have shown that a number of fishing communities existed in the pre-ceramic era which already made use of important fishing techniques for preserving and designing fishing materials (dying, netting, etc.) (Kostritsky 1955).

However, the present fishing industry dates back only to the early 1950s when the purse-seine caught anchoveta began to be processed into fish meal (Schaefer 1967). Fig. 1A shows the evolution of landings since that time and the spectacular growth of the industry until 1970 when total catch of anchoveta reached the world record level for a single species of over 12 t x 10^6.

Trends in the following decade were equally spectacular, but in the opposite direction as also seen in the 5-year smoothed curve of Fig. 1B. By 1974, total landings had dropped to 3.8 t x 10^6, to 2.5 t x 10^6 in 1980 and to slightly above 2.8 t x 10^6 in 1984 (Table 1).

Graphs illustrating aspects of the Peruvian fisheries are usually very "spiky", which is a reflection of the instability and dramatic changes that have taken place following the occurrence of various El Niño events (see other contributions in this vol.). Intermediate oscillations due to lagged responses of other elements of the altered system also contribute to the observed instabilities in curves describing biomass, catches, effort, capacity, production, prices, etc.

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*ICLARM Contribution No. 379.

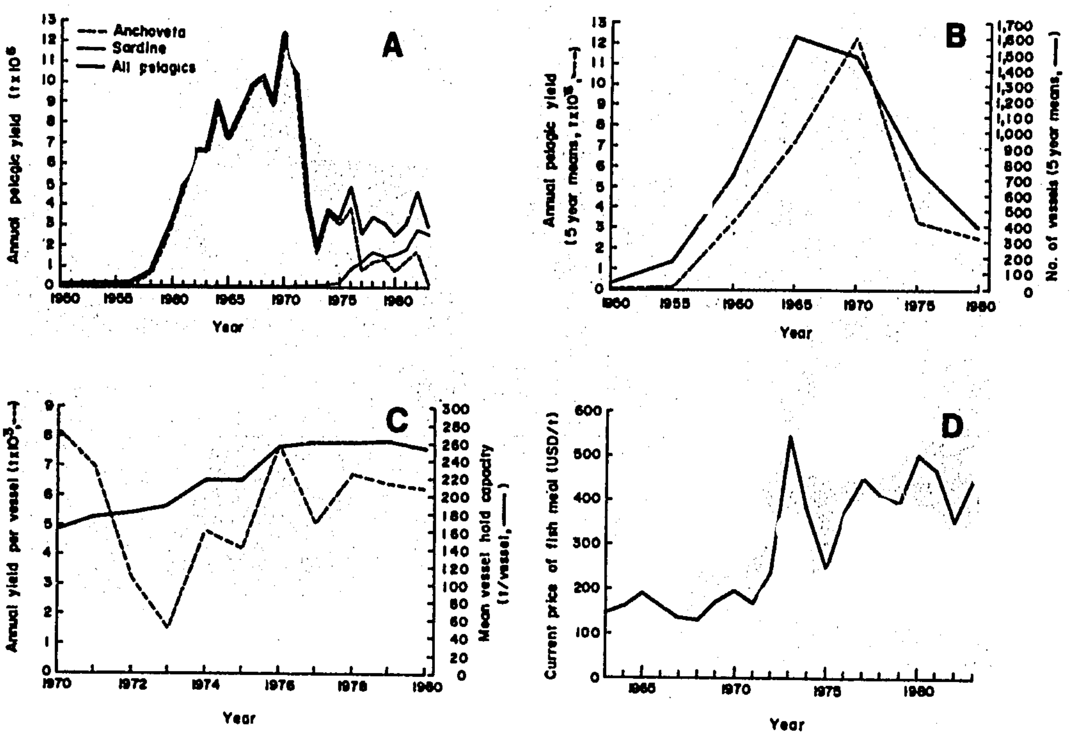

Fig. 1. Basic trends of biological and economic characteristics of the Peruvian purse-seine fishery for the period 1950-1983. A: Annual catch of anchoveta, of sardine and total annual catch, 1950 to 1983. B: Total annual catch and number of vessels, 1950-1980, in 5-year segments such as used in linear programming model. C: Annual catch per vessel and mean vessel hold capacity, 1970 to 1980. D: Current price of fishmeal in adjusted US dollars, 1963 to 1983.

Several institutional changes in public administration have also influenced the development of the fishery (Borgo 1966; Malpica 1976; Chaparro 1983; Peralta 1983) generally through interventions aiming to counterbalance the short-run effects of environmental fluctuations but inconsistent with a long-run perspective of renewable resource management (see also Castillo and Mendo, this vol.; Pauly, this vol.).

Technological developments and improvements in harvesting and processing activities have thus produced negative as well as positive results generating forces for subsequent changes (see Castillo and Mendo, this vol.).

The Management Problem

If management of fishery resources is to provide the highest possible benefits for society, economic evaluation of alternative management interventions as well as changes of the basic characteristics of the fishery system are needed. This is due to the fact that the renewable, stochastic and complex nature of the fishery resource system is extremely difficult to apprehend with simple and elementary conceptualizations. Added feedback loops, such as those created by regulatory measures, makes understanding of a complex system even more difficult.

Nonetheless, methods exist that allow for efficient handling of large, interrelated systems. Programming techniques, simulation and impact analyses are among the available tools which are becoming increasingly applicable, especially through the wide availability of microcomputer hard and software.

This paper discusses the evolution of the Peruvian purse seine fishery from an economic perspective, in order to represent the basic structure of the fisheries as an economic activity and to evaluate the relative costs and benefits of alternative interventions. Following the implicit suggestion of the Second Panel of Experts on the Economic Effects of Alternative Regulatory Measures in the Peruvian Anchoveta Fishery in 1974 (IMARPE 1974), a conditional mathematical model structured in terms of an optimization problem is presented as a tool for modelling the Peruvian purse seine fishery and for assessing possible outcomes of specific changes of key factors.

Table 1. Catches (in t) of the Peruvian purse seine fishery[a], 1950-1983.

Year	Anchoveta	Sardine[b]	Horse mackerel	Mackerel	Mean anchoveta biomass[c]
1950	6,500	n.a.	0	2,300	n.a.
1951	20,300	n.a.	100	1,100	n.a.
1952	24,500	n.a.	100	3,300	n.a.
1953	44,800	n.a.	n.a.	1,900	6,099,459
1954	52,800	n.a.	n.a.	3,500	9,514,038
1955	76,400	n.a.	n.a.	1,300	8,277,176
1956	138,500	n.a.	700	3,700	5,072,786
1957	335,800	n.a.	400	8,600	2,904,439
1958	737,000	2,100	200	12,600	3,751,051
1959	1,953,600	n.a.	400	9,400	7,418,562
1960	3,320,700	2,700	300	9,400	11,921,758
1961	5,010,900	3,000	200	11,700	16,721,428
1962	6,691,500	2,200	700	13,300	14,858,647
1963	6,634,800	10,200	2,000	7,900	13,280,715
1964	8,863,400	7,400	1,700	2,000	14,390,983
1965	7,242,400	1,900	2,600	3,800	13,274,416
1966	8,529,800	2,100	4,300	7,600	15,520,737
1967	9,824,600	1,800	3,100	13,400	18,998,161
1968	10,262,700	1,100	2,800	7,200	11,946,014
1969	8,960,500	500	4,200	7,200	13,591,293
1970	12,277,000	6,100	4,700	8,800	14,737,956
1971	10,276,800	6,200	9,200	10,100	13,745,856
1972	4,447,200	9,900	15,700	3,700	3,159,524
1973	1,768,700	72,605	20,200	18,900	3,143,542
1974	3,583,476	62,851	129,211	63,270	3,458,027
1975	3,078,810	174,701	37,899	23,588	2,823,968
1976	3,863,050	870,903	54,155	40,172	4,262,373
1977	792,106	1,257,948	504,992	46,071	1,254,592
1978	1,187,041	1,727,201	386,793	101,505	3,975,838
1979	1,362,763	1,480,396	151,599	117,953	1,453,747
1980	720,124	1,620,229	123,380	59,062	2,709,939
1981	1,225,168	1,779,782	37,875	32,803	9,175,206
1982	1,720,437	2,823,424	50,013	22,072	n.a.
1983	118,441	2,571,752	76,487	22,579	n.a.

n.a. = not available

[a] FAO Yearbook of Fishery statistics and unpublished IMARPE data.

[b] Prior to 1957 sardines were not separated from anchoveta.

[c] From Pauly, Palomares and Gayanilo (this vol.).

An Overview of the Peruvian Fishing Industry

Fishery Resources

The Peruvian fisheries are based mainly on the exploitation of pelagic resources occurring on 2,800 km of coastline. The resource base of these fisheries is very diverse and consists of about 500 species (Chirichigno 1974). Of these, the most important are anchoveta (*Engraulis ringens*), sardine (*Sardinops sagax*), horse mackerel (*Trachurus murphyi*) and mackerel (*Scomber japonicus*).

Fishing became an important economic activity in Peru in the early 1950s when anchoveta began to be processed into fish meal and oil. Since then, fishing activities centered on anchoveta, grew at spectacular rates until overfishing and unfavorable environmental conditions (i.e., the El Niño of 1971-1972) drove the fishery to collapse (Walsh 1981). The period that followed was characterized by conditions of instability, vulnerability, the occurrence of more El Niño events and the buildup of large biomasses of sardines, mackerels and horse mackerels (Jordan et al. 1978 and see Table 1).

Although the compensatory phenomena reported by Jordan et al. (1978) imply a shift from what was essentially a monospecies to a multispecies fishery, total catches have been fluctuating around a much lower level than those reached during the anchoveta peak of the late 1960s and early 1970s.

Harvesting and Processing Capacity

The characteristics and behavior of fish resources define the technology required for their exploitation. Peruvian anchoveta are harvested by encircling schools with a purse seine of relatively small mesh sizes (10-30 mm) of a length of approximately 300 fathoms and a depth of 35 fathoms, and which is set by purse seiners of 25-30 t LOA driven by diesel motors ranging from 300 to 800 hp. Fishing consists of daily trips with 2 or 3 purse seine sets (Engstrom et al. 1974; IMARPE 1975).

Important changes in the fleet composition and characteristics have taken place since the beginning of the anchoveta fishery. Fig. 1B shows the rapid increase in the number of vessels which took place since the early 1950s, in response to favorable market and biological conditions (Segura 1973), and which began to be reversed after 1964, after a total of 1,623 vessels was reached (Table 2).

Simultaneously, technological improvements such as nylon nets, echo sounder, hydraulic systems, steel vessels and better information on stock distribution (fishing strategies supported by planes, radio communication, etc.) have taken place along with changes of fleet size. Estimates of excess fleet capacity show that the fleet in 1970-1971 was able, under average conditions, to harvest 9.5 t x 10^6 of fish in 130-133 days, which would have amounted to a fishing season of 6.5 months (IMARPE 1974). IMARPE (1974) estimated that the excess capacity of the fleet during that time was about 30% for an expected catch of 9.5 t x 10^6.

Fig. 1C shows, along with the annual catch per vessel, the trends of mean hold capacity in the period 1970-1980, illustrating further the increase in potential harvest (and excess) capacity of the fleet (Berrios 1983).

Catches are used primarily as raw material for fish meal production. Efforts to rationalize the industry performance, to increase aggregated value and make better use of fish for direct human consumption have led in the last few years to increased alternative uses of catches, such as canning and landing of frozen fish, especially with regard to the "new" pelagic species - sardine, mackerel and horse mackerel (Blondet 1986, and see also Table 3).

Processing capacity for fish meal also grew at a disproportionate rate during the "boom" period of the anchoveta fishery. Estimates of excess processing capacity for 1970-1971 are of similar magnitude than those for the harvesting capacity, creating a feedback force to increase effort in order to obtain larger shares of the total catch (IMARPE 1970).

The number of canning plants grew from 16 in 1947 to 69 in 1956, that is, more than 300% growth in less than ten years. During the 1976-1982 period, another large increase in the number of plants occurred, from 34 to 82 plants. Plant use capacity was low, however, near 26% (Peralta 1983).

Products and Market Conditions

Fish meal is a high protein animal feedstuff obtained by cooking, pressing, drying and grinding fish or shellfish. In this process, fish oil and soluble are obtained as byproducts (Fig. 2) which are used in the production of shortening, compound oil, margarine, etc.

Raw material used in manufacturing fish meal and its byproducts is obtained from fish (usually small pelagics) harvested for this purpose. Also, incidental catch and offal obtained during processing of other fishery products (canning, filleting, etc.) are also used for fish meal and related byproducts.

The value of fish meal as feedstuff component is related to several factors of which the content of amino acids, minerals and range of B-complex vitamins are among the most

Table 2. Basic data on the Peruvian purse seines fleet, 1953-1980.[a]

Year	Vessels (no. units)	Average capacity[b]	Total pelagic catch (t)[c]	Estimated of catch per vessel (t/year)
1953	52	n.a.	46,700	898
1954	137	n.a.	56,300	411
1955	192	n.a.	77,700	405
1956	238	n.a.	142,900	600
1957	296	n.a.	344,800	1,165
1958	354	n.a.	75,190	212
1959	414	n.a.	1,963,400	4,743
1960	667	n.a.	3,333,100	4,997
1961	756	n.a.	5,025,800	6,648
1962	1,069	n.a.	6,707,700	6,275
1963	1,655	n.a.	6,654,900	4,021
1964	1,744	n.a.	8,874,500	5,089
1965	1,623	n.a.	7,250,700	4,467
1966	1,650	n.a.	8,543,800	5,178
1967	1,569	n.a.	9,842,900	6,273
1968	1,490	n.a.	10,273,800	6,895
1969	1,455	n.a.	8,972,400	6,167
1970	1,499	161	12,296,600	8,203
1971	1,473	175	10,302,300	6,994
1972	1,399	181	4,476,500	3,200
1973	1,256	188	1,880,405	1,497
1974	795	217	3,838,808	4,829
1975	785	218	3,314,998	4,223
1976	556	256	4,282,280	7,702
1977	514	260	2,601,117	5,061
1978	504	261	3,402,540	6,751
1979	484	262	3,112,711	6,431
1980	403	254	2,522,795	6,260

n.a.: = not available.

[a] Period 1953-1958 (Mills 1969); period 1959-1973 (IMARPE 1974); period 1974-1980 (Berrios 1983).

[b] Berrios (1983).

[c] Sum of first four columns in Table 1.

Table 3. Peruvian fish meal and oil exports, revenues and prices, 1963-1983.[a]

	Fish meal				Oil		
Year	Exports (t)	Revenues (US$)	Price[b] (US$/t)	CIF price (US$/t)	Exports (t)	Revenues (US$)	price (US$/t)
1963	1,041,700	104,755,000	101	145	135,000	9,427,000	70
1964	1,428,600	143,632,000	101	161	117,400	14,748,000	126
1965	1,414,900	155,700,000	110	190	145,500	24,142,000	166
1966	1,304,100	181,914,000	139	160	92,200	15,763,000	171
1967	1,594,800	173,286,000	109	134	194,300	19,738,000	102
1968	2,081,300	204,670,000	98	129	312,200	22,676,000	73
1969	1,711,200	200,464,000	117	172	157,100	14,879,000	95
1970	1,903,400	295,514,100	155	197	200,100	37,849,000	189
1971	1,762,100	277,786,300	158	167	269,000	52,430,000	195
1972	1,625,900	234,402,000	144	239	294,000	37,964,000	129
1973	356,700	137,375,000	385	542	4,600	1,281,000	278
1974	618,000	198,754,000	322	372	74,800	39,005,000	521
1975	783,500	161,680,000	206	245	133,300	37,468,000	281
1976	594,100	185,938,000	313	376	2,900	964,000	332
1977	442,251	183,516,000	415	454	2,788	1,967,000	706
1978	484,752	192,280,000	397	410	2,300	1,620,000	704
1979	530,868	199,311,000	375	395	49,193	21,392,000	435
1980	463,744	207,214,000	447	505	6,151	3,725,000	606
1981	387,184	174,484,000	451	468	3,871	496,000	128
1982	615,880	81,418,000	388	453	2,117	283,000	134
1983	209,601	81,418,000	388	453	2,117	283,000	134

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[a] From FAO Yearbooks of Fishery Statistics for 1981 and 1984 and World Bank (1985).

[b] Estimated from Exports and Revenues.

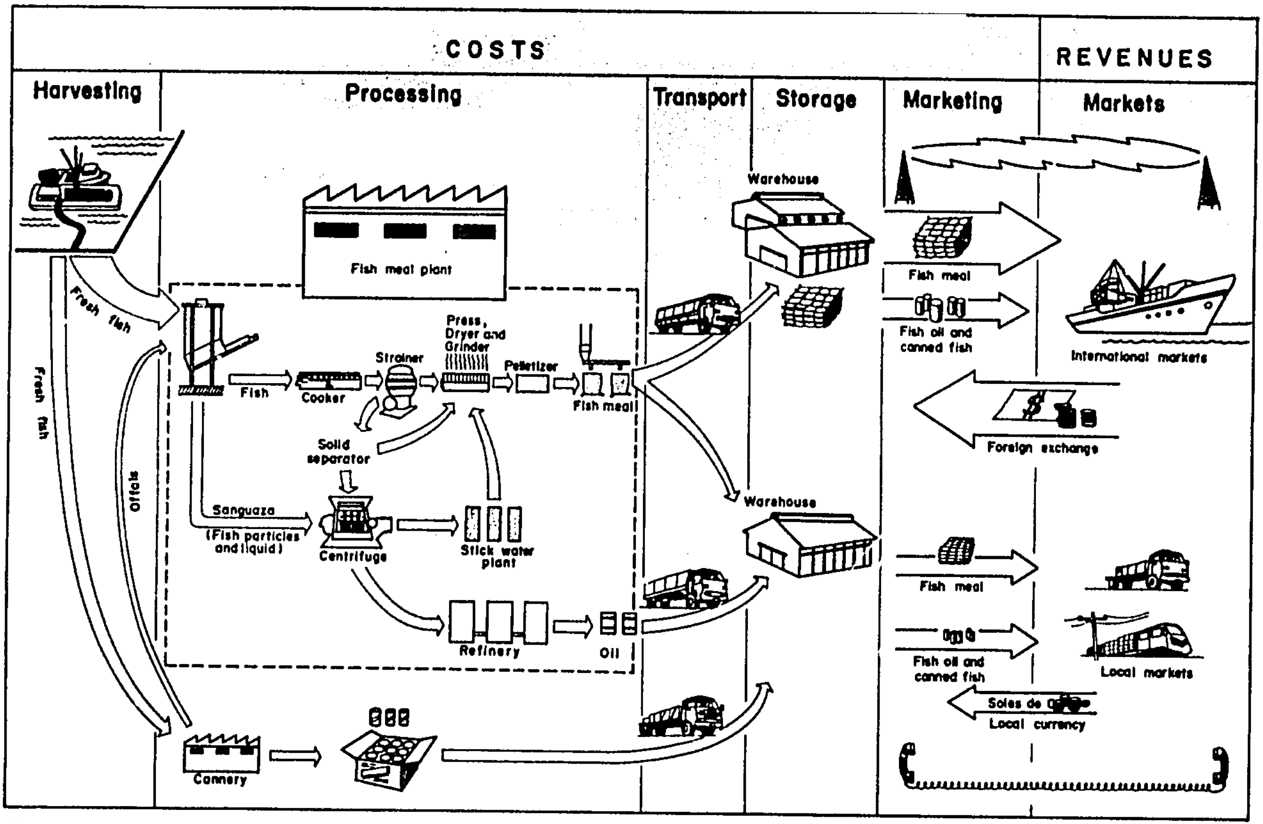

Fig. 2. Schematic representation of major material and money flows in the processing and marketing of Peruvian pelagic fisheries (arrows not to scale, see Tables 1-6 for actual numbers).

important. Fish meal has been shown to have important animal proteins and growth factors (APF and UGF), superior to other vegetable-based proteins, and also to have excellent nutritional balance characteristics (ADB 1983).

Monogastric animals such as pigs and poultry obtain essential amino acids from the breakdown of protein during digestion. In this, fish meal is very superior to vegetable proteins and is thus an excellent feedstuff for these animals.

The demand for fish meal therefore, is a derived demand based on raising animals such as swine and poultry (Capurro 1983). The world feed market is an extremely competitive and complex one and because of its importance on the final consumer demand for animal protein, the outlook for fish meal is favorable over the long run (ADB 1983).

In the pigfeed market, fish meal competes with soymeal as a source of protein; in the poultry industry fish meal is considered a superior product because of its wide spectrum. Finally, in other minor markets such as commercial fish farming, fish meal has little competition.

The demand for fish meal then depends both on the production of these animals and the elasticity of substitution with its competitive products.

Since 1972, the world fish market has undergone dramatic changes. Although the export market is concentrated in a relatively small number of producing countries with sophisticated fisheries industries accounting for a large percentage of the total market, the heterogeneity of the suppliers prevents this oligopolistic industry to behave as expected. The major exporters, for example, have not succeeded in establishing cartels or other types of mechanism in their favor with the exceptions of some bilateral arrangements between Chile and Peru.

Imports, on the other hand, although concentrated in a small number of countries with a large share of the total, do not show the kind of concentration observed in exports and production. Thus, trading patterns depend greatly on transport costs, supply and demand levels as well as quality and traditional buyer/seller relationships (ADB 1983).

Fish meal production in Peru is almost entirely for export. Although a major supplier to the international fish meal market, Peru has been a "price taker" when world market supplies have been normal.

Historically, the prices for Peruvian fish meal have been rather erratic. A dramatic increase in 1973, as a result of the fall in the world market conditions, created in part from the Peruvian shortage of supply (Vondruska 1981), was followed by an equally dramatic fall in 1975, followed by a recovery and fluctuations around a higher average until 1985. The fluctuations between 1963 and 1983 ranged from US$145 to 542/t, which, in constant prices of 1980, corresponds to a range between US$527 and 1,204, the latter value being the peak of 1973. Fig 1D shows the relative instability of Peruvian fish meal prices.

The Mathematical Conditional Model

The analyses and evaluation of the performance of a particular fishery require examination of the key variables expressing dynamic interactions of a set of complex elements of varying importance. Taken as whole, these elements are like links of a chain, with the performance of the chain depending on the strength of each of the components. Information for management purposes must therefore not only identify, describe and quantify these elements (links) but also establish the functional relationships among them. Only in this way is it possible to describe, explain and predict the outcome of specific interventions.

A bioeconomic model, structured in terms of a constrained optimization linear programming problem is presented below. Constraints are of biological, technological and economic nature. Fundamental relationships between biological characteristics of the resource and the technology of capture are incorporated along with relationships between market conditions and fishing effort, processing techniques and harvest levels, product type and demand levels (Fig. 3).

Model Implementation

A Fisheries Net Benefit Function (FNBF) has been established. Each activity of the fishery process impacts the FNBF in a negative or positive way according to whether that activity generates costs or revenues. The absolute difference between total costs and revenues is the net benefit that the fishery generates.

The management problem then is to make FNBF, as great as possible (i.e., to maximize FNBF) without violating the restrictive conditions imposed by the system (i.e., the constraints).

The model is structured into six sequential blocks (Table 4) defining the different activities involved in the fishery within a time period consistent with the validity of the various parameters, functional relationships and constraints. The objective function summarizes all relevant activities into a single value. Thus we have:

$$\text{FNBF} = \text{TOTAL REVENUES} - \text{TOTAL COSTS}$$

or mathematically:

$$\text{FNBF} = + \sum_{i=1}^{3} \sum_{j=1}^{n} (P_{ij} * Q_{ij}) - \sum_{b=1}^{36} \sum_{d=1}^{2} (CPY_{db} * X_{db}) - \sum_{d=1}^{2} (0 * X_d)$$

$$- \sum_{i=1}^{3} \sum_{d=1}^{2} (PUC_{di} * Q_{di}) - \sum_{i=1}^{n} (TUC_i * Q_i^t) - \sum_{i=1}^{n} (CUS_i * Q_i^s) - \sum_{i=1}^{n} (CUM * Q_i^m)$$

subject to:

$(\text{Yield})_{ib} < (\text{BIOMASS})_{ib}$

$b = 1 \ldots\ldots 36$

$(1/y/f) * \text{Yield} <$ Total vessel days available (VDA)

$Q_{di} <$ Total available processing (tonnage) capacity (APC)

$Q_i^t <$ Available total transport capacity (ATT)

$Q_i^s <$ Available total storage capacity (ATS)

$Q_d = \alpha_{di} \cdot X_{db}$

non-negativity constraints:

$Q_{di}, Q_i^t, Q_i^s, Q_i^m, X_d, X_{db}, > 0$

Convex set equations:

$1/\text{Biomass} < 1$

$1/Q_i < 1$

Balance equations:

Harvest to Pivot : $a_d X_{db} - X_d = 0$

Pivot to Processing : $X_d - k \cdot Q_d = 0$

Processing to Transport : $Q_{di} - Q_i^t = 0$

Transport to Storage : $Q_i^t - Q_i^s = 0$

Storage to Marketing : $Q_i^s - Q_i^m = 0$

Storage to Sales : $Q_i^s - Q_{ij} = 0$

a_i = % of species group *d* going into product type i (0.5).

k = reduction coefficient of species group *d* at product type i (4.166).

where:

i = type of product

i_1 = fishmeal
i_2 = fish oil
i_3 = canned fish

j = demand segment

j = 1 .... n

b = yield segments

b_1 = first segment $\leq$ 250 t
b_2 = second segment $<$ 500 t
b_3 = third segment $<$ 1,500 t
•
•
•
•
b_{36} = 36th segment $<$ 9×10^6 t

d = species group composition

d_1 = mix of anchoveta and sardine
d_2 = mix of mackerel and horse mackerel

S = stock size of species mix

S_1 = first segment
S_2 = second segment
S_3 = third segment
•
•
•
S_9 = ninth segment

P_{ij} = Unit price of product type *i* at demand segment *j*
Q_{ij} = Total quantity of product type *i* at demand segment *j*
CPY_{db} = Cost per unit of yield of species group *d* at yield segment *b*
X_{db} = Total quantity harvested of species group *d* at yield segment *b*
X_d = Total quantity of species group *d* transferred into processing
= $(\alpha_{di} \cdot X_{db})$ where α_{di} = is reduction coefficient
PUC_{di} = Processing unit cost of fish of species group *d* into product type *i*
Q_{di} = Quantity of species group *d* processed into product type *i*
TUC_i = Transport unit cost of product type *i* to market place
CUS_i = Storage unit cost of product type *i*
Q_i^t = Quantity of product type *i* transported
Q_i^s = Quantity of product type *i* stored
Q_i^m = Quantity of product type *i* marketed
CUM_i = Marketing unit cost of product type *i*

Harvesting Block

Variables in this block represent catches (in t) as segments of the hypothetical sustained yield function (SY) of the exploitable stock. To each level of sustained yield there is an associated yield per unit of effort (Y/f) which defines a cost per unit of catch (C/Y) coefficient in the objective function.

This block contains the effort capacity constraint defined in terms of available vessel/days (VDA).

Table 4. LP. tableau for Peruvian fishing industry.

	$-\sum_{d=1}^{2}\sum_{b=1}^{36}(CPUC_{db} * X_{db})$						$-\sum_{d=1}^{2}(o * X_d)$		$-\sum_{d=1}^{2}\sum_{i=1}^{n}(PUC_{di} * Q_{di})$					
Activities	Harvesting block						Pivot		Processing block				Constraints	
	CPY_1	CPY_2	CPY_3	CPY_4	—	CPY_{36}	X1	X2	PUC_{11}	PUC_{12}	$PUC_{21/22}$	PUC_{32}		
Stock	+1												<	b1
		+1											<	b2
			+1										<	b3
				+1									<	b4
					—								⋮	⋮
						+1							<	b36
Catch composition	a1	a1	a1	a1	—	a1	+1	0					=	0
	a2	a2	a2	a2	—	a2	0	+1					=	0
Vessel	$1/b_1/f_1$	$1/b_2/f_2$	$1/b_3/f_3$	$1/b_4/f_4$	—	$1/b_{36}/f_{36}$							<	VDA
Convex set h	$1/b_1$	$1/b_2$	$1/b_3$	$1/b_4$	—	$1/b_{36}$							<	1
Balance eq. 1							+1		$-k_{11}$				=	0
Balance eq. 2								0.5		$-k_{12}$			=	0
Balance eq. 3							+1	0.5			$-k_{21/22}$		=	0
Balance eq. 4								0.5				$-k_{32}$	=	0
Plant capacity									+1	+1	+1	+1	<	APC
Balance eq. 1									+1	+1			=	0
Balance eq. 2											+1		=	0
Balance eq. 3												+1	=	0
Transport capacity													<	ATT
Balance eq. 1													=	0
Balance eq. 2													=	0
Balance eq. 3													=	0
Storage capacity													<	ATS
Balance eq. salt													=	0
Balance eq. 1													=	0
Balance eq. 2													=	0
Balance eq. 3													=	0
Convex set 1													<	1
Convex set 2													<	1
Convex set 3													<	1
Balance eq. 1													=	Q_{11}
Balance eq. 2													=	Q_{12}
Balance eq. 3													=	Q_{1n}
Balance eq. 1													=	Q_{21}
Balance eq. 2													=	Q_{22}
Balance eq. 3													=	Q_{2n}
Balance eq. 1													=	Q_{31}
Balance eq. 2													=	Q_{32}
Balance eq. 3													=	Q_{3n}

Table 4. (Continued) LP. tableau for Peruvian fishing industry.

	$-\sum_{i=1}^{n}(TUC_i \cdot Q_i^t)$			$-\sum_{i=1}^{n}(CUS_i \cdot Q_i^s)$			$-\sum_{i=1}^{n}(CUM_i \cdot Q_i^m)$	$+\sum_{i=1}^{3}\sum_{j=1}^{n}(P_{ij} \cdot Q_{ij})$										
Activities	Transport block			Storage block			Market block	Sales block									Constraints	
	TUC_1	TUC_2	TUC_3	CUS_1	CUS_2	CUS_3	CUM_1	UP_{11}	UP_{12}	UP_{1n}	UP_{21}	UP_{22}	UP_{2n}	UP_{31}	UP_{32}	UP_{3n}		
Stock																	≤ ≤ ≤ ≤ ⋮ ≤	b1 b2 b3 b4 ⋮ b36
Catch composition																	= =	0 0
Vessel																	<	VDA
Convex set h																	<	1
Balance eq. 1																	=	0
Balance eq. 2																	=	0
Balance eq. 3																	=	0
Balance eq. 4																	=	0
Plant capacity																	<	APC
Balance eq. 1	−1																=	0
Balance eq. 2		−1															=	0
Balance eq. 3			−1														=	0
Transport capacity	+1	+1	+1														<	ATT
Balance eq. 1	+1			−1													=	0
Balance eq. 2		+1			−1												=	0
Balance eq. 3			+1			−1											=	0
Storage capacity				+1	+1	+1											<	ATS
Balance eq. mkt				+1	+1	+1	+1										=	0
Balance eq. 1				+1				−1	−1	−1							=	0
Balance eq. 2					+1						−1	−1	−1				=	0
Balance eq. 3						+1								−1	−1	−1	=	0
Convex set 1								$1/Q_{11}$	$1/Q_{12}$	$1/Q_{1n}$							≤	1
Convex set 2											$1/Q_{21}$	$1/Q_{22}$	$1/Q_{2n}$				≤	1
Convex set 3														$1/Q_{31}$	$1/Q_{32}$	$1/Q_{3n}$	≤	1
Balance eq. 1								+1									=	Q_{11}
Balance eq. 2									+1								=	Q_{12}
Balance eq. 3										+1							=	Q_{1n}
Balance eq. 1											+1						=	Q_{21}
Balance eq. 2												+1					=	Q_{22}
Balance eq. 3													+1				=	Q_{2n}
Balance eq. 1														+1			=	Q_{31}
Balance eq. 2															+1		=	Q_{32}
Balance eq. 3																+1	=	Q_{3n}

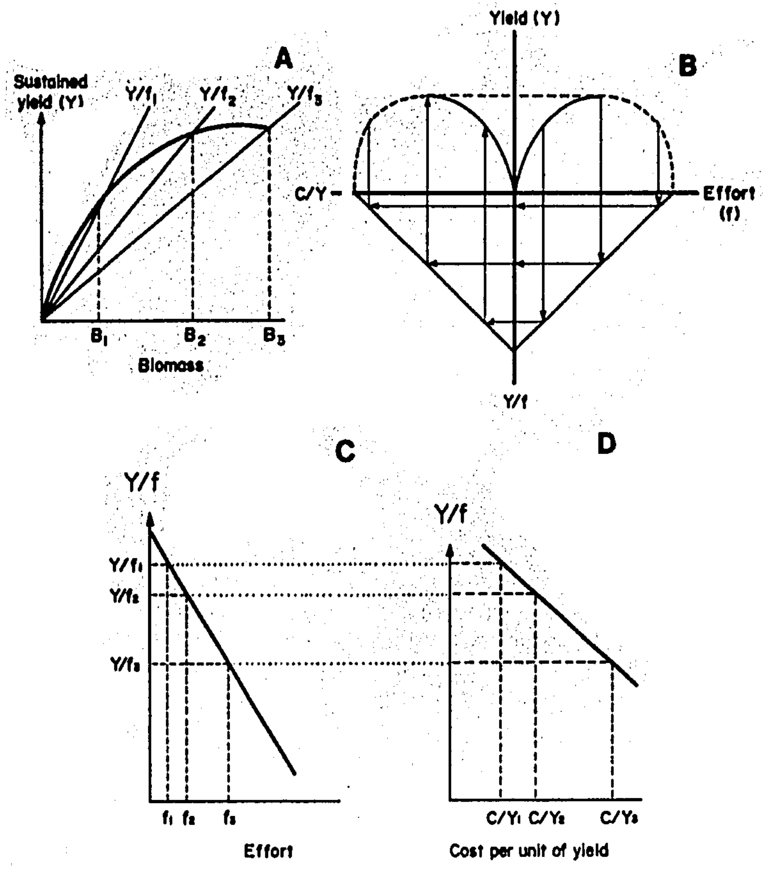

Fig. 3. Fundamental relationships between biological characteristics of fish resources and technology of capture and various cost factors. A: Relationships between yield and the underlying fish biomass (note that $B_1 > B_2 > B_3$). B: Relationships between yield, effort and the quotients cost per unit of yield and yield per unit of effort. C: Relationships between yield per effort, effort and cost per unit of yield.

The functional relationship between sustained yield, effort and cost per unit of effort is consistent with standard bionomic theoretical concepts, as represented in Fig. 3A and 3B. Note that throughout this contribution, the terms "catch" and "catch per effort" are replaced by "yield" (Y) and "yield per effort" (Y/f) such as to avoid confusion with costs (C) and costs per effort (C/f). Note also that using "yield" for *catch in weight* corresponds to the standard notation compiled by Holt (1960).

Processing Block

Variables in this block represent tonnes of fish processed into different product lines with associated yield coefficients and processing unit costs (PUC) in the objective function. This block also contains processing capacity constraints expressed in terms of total available processing capacity (APC, in hours). PUC do not include costs of raw material since these have been incorporated into the harvesting block coefficients of the objective function.

Transport Block

Variables in this block represent tonnes of final products transported from processing plants to storage facilities. Coefficients in the objective function are the transport unit cost per tonne of final product (TUC). Available total transport facilities (ATT) set the constraint for the maximum transport of products per unit time.

Storage Block

Variables in this block represent tonnes of final products stored. Coefficients in the objective function are cost per unit storage (CUS) per tonne of product stored. This block also contains restrictions on available total storage (ATS) in terms of storage per unit of time.

Marketing Block

Coefficients in the objective function associated with this block represent the average cos per unit marketed (CUM) per tonne of final product sold. Balance constraints force all stored products to be sold in order to avoid modelling inventory behavior and accidental losses.

Sales Block

Variables in this block represent total tonnes of products sold into different markets. Coefficients in the objective function associated with this block are the unit prices (UP) per tonne of product.

Balance Equations, Auxiliary Activities and Convex Sets

Balance equations are included in the block structure in order to assure flow of product throughout the matrix while avoiding unaccounted losses.

Auxiliary activities are also used to allow transit and distribution of products throughout the matrix without impacting the objective function. Convex set equations are included as means of assuring compliance with segmentation and grids defined by the piecewise linearization technique used in incorporating nonlinear functions.

Optimal Value

The structure of the problem in terms of activities performed allows for the computation of total expenditures and revenues. All activities implying costs have negative signs in the objective function while activities generating revenues have positive signs. The summation of negative and positive values is the net benefit derived from the fishery.

Implementation of the Model

Data for the conditional model has been obtained from different secondary sources (IMARPE, unpublished data; various FAO statistical yearbooks and extrapolation from similar fisheries, such as the Chilean northern pelagic fisheries (Aguero and Adriasola 1983). The base model was specified to represent the situation prevailing in 1982, which is here used as the reference year (see Table 5).

Several alternative data configurations are presented to represent alternative possible scenarios (Table 6).

The linear programming algorithm in the SOFPES program of Aguero and Lampe (1986), implemented on an IBM PCXT microcomputer was used to run the model.

Theoretical Issues and Devices

Harvesting Block

A hypothetical yield curve was used to simulate alternative levels of sustained yield for the stock of Peruvian pelagics. Linearly decreasing yield per effort coefficients with increasing

Table 5. Summary of data used for base conditional programming model for Peruvian pelagic fisheries (see text for sources).

Variables	Values	Variables	Values
Prices:		Yield rate,	
Assumed demand functions:		– Fishmeal:	
Fishmeal	$P = 644 - 1{,}360\ Q\ [\quad Q < 0.1 \times 10^6]$	* Anchoveta/sardine:	19%
	$= 562 - 248\ Q\ [0.1 \times 10^6 < Q < 1.5 \times 10^6]$	* Mackerel/horse mackerel	24%
	$= 559 - 246\ Q\ [\quad Q > 1.5 \times 10^6]$		
Fish oil	$P = 463 - 700\ Q\ [\quad Q < 0.075 \times 10^6]$	– Fish oil:	6%
	$= 116 - 14\ Q\ [0.075 \times 10^6\ Q < 0.5 \times 10^6]$		
	$= 493 - 710\ Q\ [\quad Q > 0.5 \times 10^6]$		
Canned fish	$= 660 - 1{,}080\ Q$	– Canned fish:	60%
Costs			
Harvest sector:		**Restrictions**	
– Biomass range (t x 10^6):	0.5, ..., 8.5	– No. of boat:	580
– Yield per effort (t per thousand boat-days):	55, ... , 8.0	– No. of fishing days/yr:	240
– Range of cost per tonne (US$):	25, ... , 140	– Total boat-days/yr:	139,200
Processing sector:		– Processing, transport and storage capacity arbitrarily set at unbinding levels	4 t x 10^6
Fishmeal (US$/t)			
* Anchoveta/sardine:	75.00	– Catch composition:	
* Mackerel/horse mackerel	60.00	* Anchoveta/sardine	80%
– Fish oil (US$/t)	0	* Mackerel /horse mackerel	20%
– Canned fish (US$/t)	75.00		
Transport sector:		– Product line:	
– Fishmeal (US$/t):	5.00	* Anchovie/sardine:	Fishmeal & oil (100%)
– Fish oil (US$/t)	10.00	* Mackerel/horse mackerel	Fishmeal & oil (50%) Canned fish (50%)
– Canned fish (US$/t)	15.00		
Storage sector:			
– Fishmeal (US$/t):	5.00		
– Fish oil (US$/t)	8.00		
– Canned fish (US$/t)	6.00		
Marketing costs (US$/t):	5.00		

levels of effort account for the renewable but exhaustible nature of the fishery (Schaefer 1957). The relevant portion of the curve was segmented into discrete steps (grids) of 250,000 t each of which was associated with yield per effort and effort levels as shown in Fig. 3C. Since cost per unit of effort was assumed constant, cost per unit of yield will be an inverse function of yield per unit of effort (Fig. 3D), which in turn will be an increasing function of output.

This technique, derived from piece-wise linearization methods (Duloy and Norton 1975), has been successfully used in integrating nonlinear sustained yield functions using linear programming (Aguero 1983).

Processing Block

Harvested fish were transferred into the processing block through auxiliary activities (which have zero impact on the objective function). Within this block, yield leads to alternative product lines (fish meal and/or canning), each one bearing different processing yields and unit costs.

Balance equations assured that all harvested fish were transferred and processed. Loss factors such as those identified by Castillo and Mendo (this vol.) could easily be added in this block to account for leakage in the system.

Estimates of PUC obtained from a detailed analysis conducted for the northern pelagic Chilean fishery and fish meal industry (Aguero and Adriasola 1983) were used whenever data from the Peruvian fisheries were unavailable assuming that reduction plants operated at half their normal capacity.

Two levels of yield coefficients for fish meal ranging from 19 to 24% were used to allow for variations between the different species groups used as raw material; more species groups could be easily incorporated. Fish oil yield level was estimated at 4%, i.e., the average throughout the industry.

Transport Block

Transport cost coefficients have been determined based on cost estimates of the various means of transport operating between plant and storage/port facilities. Coefficient in the objective function reflect the average cost of transporting 1 t of final product.

Storage and Marketing Block

Both blocks have similar structures and the corresponding coefficient in the objective function represent estimates of average costs incurred in storing and selling 1 t of product. The marketing block does not need to have constraints since its level can be assumed to be indirectly proportional to total production.

Sales Block

This block contains the unit price (free on board or FOB) estimated as an average for a 10-year period (1973-1983) for each product line. It is the only coefficient bearing positive sign in the objective function. It represents gross returns (revenues) to the country.

Although Peru is generally a "price taker" at the international market, the possibility exists that, at very low or very high levels of demand, Peru's share in the world market might have an impact on prices. To reflect this possibility, a hypothetical downward sloping demand curve faced by Peru was assumed and linearized piece-wise. Thus, prices are assumed highly elastic throughout a large portion of the hypothetical demand curve but relatively inelastic at very low and very high levels of supply, specially for fish meal and oil.

Table 6. Sensitivity of Base Programming Model of the Peruvian pelagic fishery to changes of key inputs.

LP results	BASE MODEL	Model 1	Model 2	Model 3	Model 4	Model 5
Remarks	Results of Base Programming Model	25% increase in vessel technology accompanied by decrease in Y/f	25% decrease in vessel technology accompanied by increase in Y/f	25% increase in product prices	25% decrease in product prices	300% increase in vessel technology accompanied by decrease in C/Y
– Net benefit (US$ x 10^6):	172.90	204.40	152.36	271.34	97.47	287.46
– Total revenues (US$ x 10^6):	371.40	371.40	301.00	469.84	202.67	525.81
• Fish meal:	201.62	201.62	150.23	252.31	96.77	304.81
• Fish oil	29.33	29.33	31.58	42.00	23.10	37.61
• Canned fish:	140.45	140.45	119.19	175.53	82.80	183.39
– Total export revenues: (assuming 50% local sale of canned fish)	301.18					
– Total costs (US$ x 10^6):	198.50	167.00	148.64	198.50	105.20	238.35
– Total catch (t x 10^6):	3.50	3.50	2.50	3.50	2.08	5.50
– Total products (t x 10^6):	0.9515	0.9515	0.68	0.9515	0.5669	1.4968
• Fish meal:	0.6157	0.6157	0.44	0.6157	0.3669	0.9686
• Fish oil:	0.1259	0.1259	0.09	0.1259	0.0750	0.1980
• Canned fish:	0.2099	0.2099	0.15	0.2099	0.1250	0.3302
– Boat capacity used:						
• No. of boats:	364.00 (63%)	291 (50%)	278 (48%)	364.00 (63%)	170 (29.26%)	382 (66%)
• Total boat-days (x 10^3):	87.42	69.93	66.68	87.42	40.73	91.70
– Product processing capacity used (t x 10^6):	0.95 (35%)	0.95 (35%)	0.68 (25%)	0.95 (35%)	0.57 (21%)	1.50 (55%)
– Market prices (US$/t):						
• Fish meal:	327.00	327.00	341.00	410.00	264.00	315.00
• Fish oil:	267.00	267.00	351.00	334.00	308.00	190.00
• Canned fish:	670.00	670.00	794.00	836.00	662.00	556.00

Results and Discussion

Base Model

Conditions assumed in the base model for the Peruvian pelagic fisheries are described in Table 5. Prices and cost structure resemble those of the early 1980s. A summary of the results (LP solution) for the base model is presented in Table 6 under the column heading BASE MODEL. It shows that (given the conditions in Table 5) the Peruvian pelagic fishery is capable of generating a net benefit of approximatly US$173 million per year from a total catch of 3.5 t x 10^6. Gross annual revenues are about US$371 million of which US$300 million would be export revenues. However, it costs about US$200 million to harvest the corresponding yield (3.5 t x 10^6) and to send it to the market as final product through processing, transporting and storage intermediaries.

The fleet capacity required is 87,000 boat-days of fishing. This is equivalent to 364 vessels, operating full time for 240 days per year, i.e., reflecting an excess capacity of about 37%.

Sensitivity Analysis

In order to foresee possible outcomes of alternative conditions, five different scenarios were modeled (Table 6).

Two types of changes were assumed:

- increase/decrease in vessel technology with related changes in cost structure.
- increase/decrease in product prices.

Results obtained are presented in Table 6 under the column heading Model 1 to Model 5.

The results of Model 1 indicate that a 25% improvement in vessel technology (accompanied by a decrease in cost per unit of yield) would bring an increase in net benefit from the fishery of about 18%, while harvesting the same amount of fish as in the base model. The entire increase of the net benefit in this case would come from the decrease in total cost of aproximatly 16%. However, this would create more idle fleet capacity (50%) as compared to 37% in the base model.

On the other hand, results of Model 2 (25% decrease in vessel technology, accompanied by increase in C/Y) would reduce total catch to 2.5 t x 10^6 (29% decrease) per year. This would reduce net benefit to US$152 million (a decrease of 12%) and fleet size to 278 boats. Total costs would also be 25% lower (US$120 million).

Models 3 and 4 show the effects of a change in prices by 25% (increase and decrease, respectively). Price increase has no effect on total catch, fleet size or costs. The only effect observed (for Model 3) is an increase in net benefit of 56%.

The fact that vessels and catch do not respond to increase in price is probably due to the range of optimal values for prices in the objective function. This suggests that the model should incorporate a finer segmentation in the harvesting and processing blocks to allow the algorithm to find a cost/price combination consistent with the proposed price change. Otherwise, a larger increase would be necessary to generate a response of fleet size and yields.

Price decrease, on the other hand, shows an impact on number of vessels, yield, revenues and costs, as shown in Table 6. This shows that the model will respond if the price change is large enough to be located outside the range of optimality.

In Model 5, the results of a substantial increase in vessel technology (300% over the base model) are shown. This change would enable an increase of catch by 57% from the level in the base model, using a total of 382 vessels. Net revenues would increase by 66%.

Conclusion

The model presented reflects rather closely the basic behavior of the Peruvian fishing industry. Total catch, total revenues, number of vessels, catch rates, final products, yield coefficients, prices and export revenues are similar to the values of these variables for the 1982 year as obtained from the sources consulted (Blondet 1986, FAO 1986 Catch and Landings Statistics Vol. 58, 59).

Simulated changes in the input values showed movements in expected directions, reflecting consistency and accuracy of the model structure as a tool to predict outcome under alternative simulated scenarios.

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Managing the Peruvian Upwelling Ecosystem: A Synthesis*

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Abstract

A brief review is given of the interrelationships and implications of the findings reported in the contributions included in this volume. Emphasis is given to some questions that now appear crucial, e.g. the cannibalization of anchoveta eggs and biannual cycles in anchoveta recruitment and their possible cause(s). Some suggestions are made for future research on various elements of the Peruvian upwelling ecosystem. Steps are indicated toward an integration of what is now known on the dynamics of the fishes off Peru into a large-scale simulation model that could be used to help formulate a comprehensive fishery management plan for that system.

Introduction

The Oxford English Dictionary provides, as one of its definitions for the word "synthesis", the "action of proceeding in thought from causes to effects, from laws or principles to their consequences". The Dictionary points out, however, that "different logicians and philosophers, though severally applying the term only in a single sense, are still at cross purposes with each other. One calls *Synthesis* what another calls *Analysis*; and this both in ancient and modern times."

And so also here: while attempting to present a synthesis of the preceding contributions in this volume, I shall have to perform some further analyses and in fact constantly switch between these two forms of reasoning. However, one limiting factor - time - shall overall limit the quantity and quality of the analyses and syntheses presented here. The book of which this contribution represents the final chapter is to be presented at the 2nd Latin American Marine Science Congress to be held from 17 to 21 August in Lima, Peru. It is also to provide a background to a workshop on "Models for Yield Predictions in the Peruvian Upwelling Ecosystem", to be held immediately following the Congress. Some of the contributions included in the present volume had been available to the editors in early 1986; the bulk of them became available in early 1987, however, with a few coming in as late as mid-May. The present contribution, written under considerable time pressure could thus not consider more than a few obvious items; I hope the workshop itself and interested readers will fill the gaps using the time series and other data included in this book.

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*ICLARM Contribution No. 390.

Review of Some Important Questions

On Major Trends in the Data Sets

When referring to the Peruvian upwelling ecosystem, the authors of both popular and scientific papers usually use the 1972 collapse of the anchoveta fishery and some related phenomena (e.g., the collapse of the bird populations) as illustrations of the key changes that occurred in that system (see Fig. 1 and Walsh 1981). However, as demonstrated by the contributions of Bakun (this vol.) and Mendo et al. (this vol.), the winds off Peru have intensified since the 1950s, resulting in increased turbulence ("bad" for first-feeding larvae?) and increased upwelling ("good" for adult anchoveta?). These trends, and their possible consequences (reduced anchoveta recruitment and biomass, improved conditions for the growth of adults) are matched, overall by our findings regarding the biology of anchoveta - but the mechanisms are not obvious.

Thus, mean annual anchoveta recruitment does not correlate directly with any of the wind-derived indices presented in this volume (see Mendelsohn and Mendo, this vol.). There is on the other hand a correlation of $r = 0.359$ between log upwelling index (mean annual values, from Table 5 in Bakun, this vol.) and the annual values of the anchoveta growth performance index ϕ' (from Table 3 in Palomares et al., this vol.), which, with 27 d.f. is close to being significant (critical value is $r = 0.367$ for 5% level). This is much less than the value of $r = 0.433$ for the correlation of ϕ' against anchoveta biomass discussed in Palomares et al. (this vol.), but indicates the possibility - which should be followed up - of interactions between various trends, and that decadal increase in anchoveta growth performance may be due to more than strict density-dependence. Further investigations along these lines should consider, moreover, competition with sardine, whose egg abundance is closely related to anchoveta abundance (Fig. 2), more so than suggested by Fig. 1 in Muck et al. (this vol.) which shows untransformed variables.

On Equilibria and Multiple Steady States

None of the contributions included in this volume is structured around the assumption that the Peruvian ecosystem is in "equilibrium", or had reached at some point a "steady state" (although this assumption has been used in some cases to estimate ancillary variables, e.g., the gear selection curve for anchoveta, see Palomares et al. (this vol.) or fishing effort on bonito in Pauly, Vildoso et al., this vol.). It is apparent, on the other hand, that the period from 1972 to the present differs from the period say from 1958 to 1971: not only were the anchoveta egg standing stocks, the survival of the prerecruits (Fig. 3) and the biomasses different, but the structure of the ecosystem itself appears to have changed (Walsh 1981). Thus, a system overwhelmingly dominated by anchoveta was replaced by a system in which anchoveta and sardine compete for dominance as regulated by small temperature shifts (Zuzunaga 1985; Villavicencio and Muck 1985) in a fashion reminiscent of the description of Skud (1982). This suggests the existence of at least two possible "states" for the Peruvian ecosystem, each with its own "ascendency" and related properties (Ulanowicz 1986 and see Table 1).

Temperature Dependence of Development Time in Anchoveta Eggs

Santander and Castillo (1973) reported that, at temperature between 14.9 and 16.9°C, fertilized anchoveta eggs need 50 hours to develop and hatch; they also noted that off the Peruvian coast, anchoveta eggs occurred from 13.5 to 18.5°C, with a pronounced maximum from 15 to 17°C.

In fishes, egg development time depends on temperature (see Hempel 1979) and egg size, among other things. Pauly and Pullin (1987), based on a data set covering 84 species of teleost fishes, temperatures ranging from 2.8 to 29.5°C and egg diameters ranging from 0.6 to 3.4 mm established, for spherical marine fish eggs, the empirical relationship

$$\log_{10} D = 7.10 + 0.608 \log_{10} E_{\phi} - 4.09 \log_{10}(T+26) \quad \text{...1)}$$

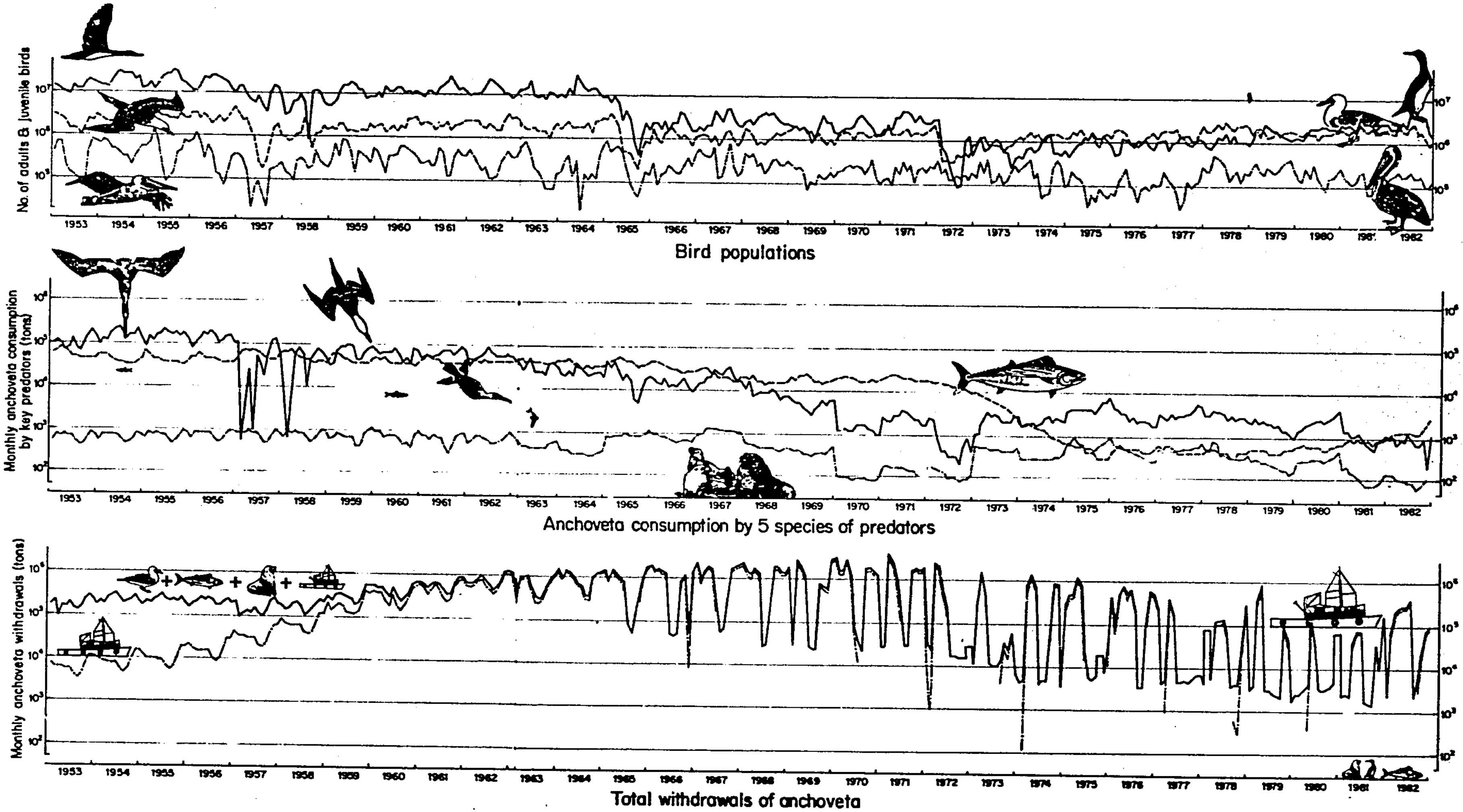

Fig. 1. Selected monthly time series on the Peruvian upwelling ecosystem, 4 to 14°S, 1953 to 1982 (see text for various data sources used). *Above:* populations of cormorants ("guanay", *Phalacrocorax bougainvillii* ————), boobies ("piquero", *Sula variegata* — — —) and pelicans ("alcatraz", *Pelecanus thagus* — · — · —). Note that change in the relations of the three species have gone along with the large decline affecting these birds. *Center:* estimates of anchoveta consumption by cormorants, boobies and pelicans (aggregated from the results of three species-specific models ———), by bonitos (*Sarda chiliensis* — — —) and two species of sea mammals (-- · — · —), the fur seal (*Arctocephalus australis*) and the sea lion (*Otaria flavescens*). The models upon which the consumption estimates are based used among other temperature (and anchoveta biomass for the birds and seals) to regulate food requirements and anchoveta accessibility. Hence, they reflect the occurrence of El Niño events. *Below:* Withdrawals of anchoveta (*Engraulis ringens*) by the fishery (— · — · —), and by the fishery plus key predators (seabirds, bonitos and seals ———). Note that the fishery, which at first took an insignificant proportion of total anchoveta production ended up taking the overwhelming part of that production except, obviously in months with no fishing ("*veda*").

This graph, taken from Pauly et al. (1986) does not consider predation by mackerel and horse mackerel; the absolute values (note log scales!) would be higher, but the trends similar, were these two fishes considered, because Muck et al. (this vol.) found them to have consumed more anchoveta in the 1950s-1960s than in the 1970s-1980s.

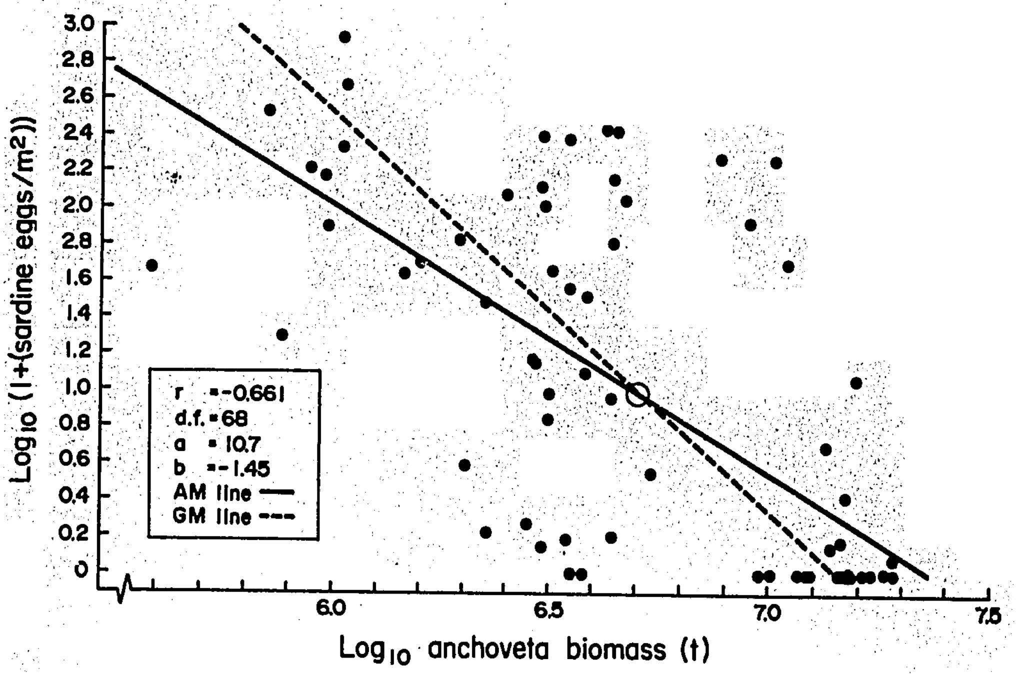

Fig. 2. Relationship between sardine egg density and anchoveta biomass of Peru (based on data in Table 1 of Muck et al., this vol. and Pauly, Palomares and Gayanilo, this vol.). The correlation is much higher than that obtained by Muck et al. (this vol.) due both to the use of improved biomass estimates and especially to the logarithmic transformation applied to both variables, which generates normally distributed residuals.

Table 1. Whole-system properties derived from box models in Walsh (1981; Fig. 1: a budget for the flux of carbon ($g\ C\ m^2\ yr^{-1}$) through the Peru food web *before* (≈ 1966-1969) and *after* (≈ 1976-1979) overfishing of anchoveta), using the BASIC program in Ulanowicz (1986).

Property[a]	Before 1972[b]	After 1972[b]
Total system throughput	2,660	2,485
Full development capacity	5,857	5,279
Full ascendency	3,595	3,408
Overhead on inputs	132	282
Overhead on exports	140	62
Overhead on respiration	1,422	930
Internal capacity	4,446	3,966
Internal ascendency	1,158	597
Tribute to other systems	380	1,100
Dissipation	2,338	1,671
System redundancy	569	597

[a] See Ulanowicz (1986) for definitions.

[b] These numbers imply that the Peruvian upwelling ecosystem was before 1972 "better organized" than thereafter; see footnote a.

where D is the development time, in days, E_ϕ the egg diameter in mm and T the water temperature in degrees centigrade. Anchoveta eggs are not spherical, however, and hence this equation cannot be used directly. Rather, the equation can be solved for 50h = 2.083 days and 15.9°C (=midrange of the temperatures given by Santander and Castillo 1973, see above), i.e.,

$$(\log_{10}2.083-7.10+\log_{10}(15.9+26))/0.608=\log_{10}0.574 \qquad ...2)$$

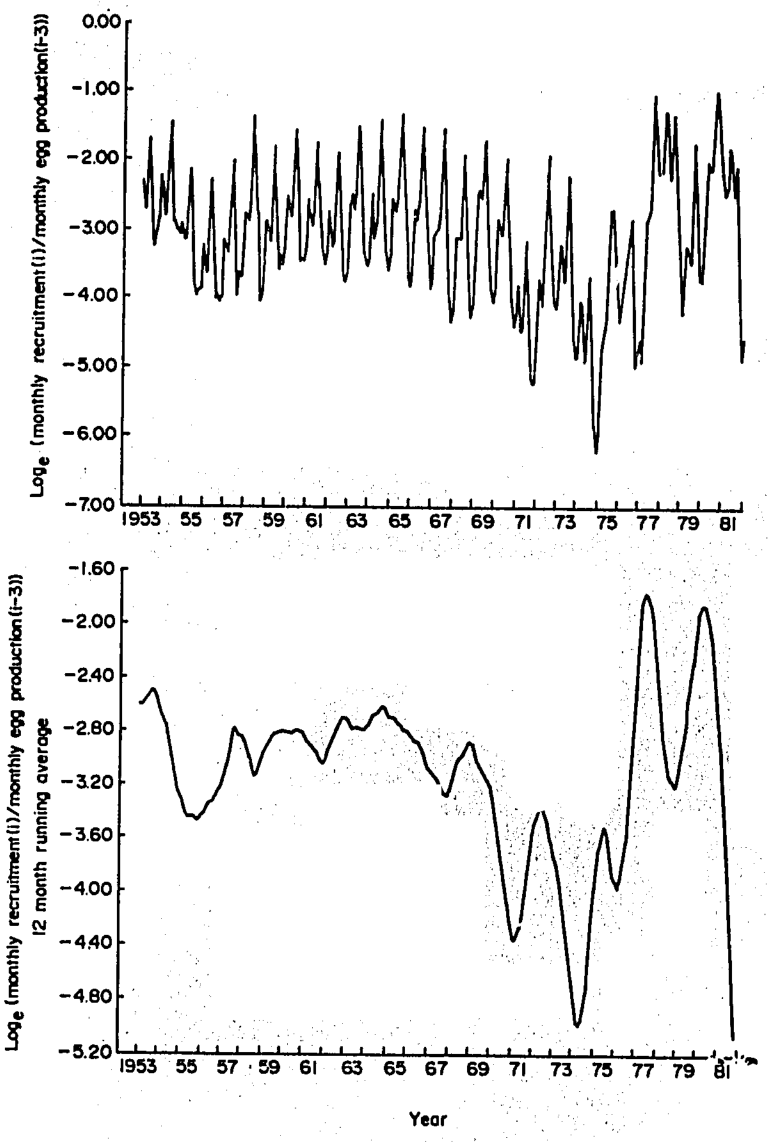

Fig. 3. Time series of an anchoveta prerecruit survival index (i.e., $\log_e$ monthly recruitment in month (i)/egg production in month (i-3)), 1953-1981. *Above:* original monthly series, based on data in Pauly and Soriano (this vol.) and Pauly, Palomares and Gayanilo (this vol.). *Below:* Smoothed series (12 months running means), showing major difference between 1953 and 1969 (high values showing little fluctuations) and 1970 to 1981 (highly variable values).

which gives 0.574 mm as the diameter of a sphere equivalent - in terms of equation (1) and of the data available here - to an oblong anchoveta egg. Solving equation (1) for 0.574 mm and simplifying gives

$$\log_{10}D=6.953-4.09\log_{10}(T+26) \qquad ...3)$$

which can be used to predict development time in anchoveta eggs at any temperature likely to be occurring off Peru.

On the Cannibalization of Anchoveta Eggs

That *Engraulis ringens* cannibalize their eggs has been demonstrated by a number of authors (e.g., in Sharp 1980). There is too some evidence that anchoveta also cannibalize their larvae, the reason for the scarcity of evidence concerning the latter probably being that they are digested faster than eggs (MacCall 1980).

The data in Table 3 of Santander (this vol.) allows quantification of anchoveta egg cannibalism, via the definition (from Gulland 1969)

$$\text{mean age in a stock} = 1/Z \qquad ...4)$$

where Z is the instantaneous rate of mortality (t^{-1}) and the mean "age" in a stock of eggs is the mean time eggs have from spawning until they either hatch or die through predation (including cannibalism).

Using the data in Table 3 of Santander (this vol.) the mean age of anchoveta eggs can be estimated, for different ranges of parent stock sizes, as the slope linking the estimated number of eggs produced by the anchoveta stock (as estimated by Pauly and Soriano, this vol.) and the number of eggs observed (i.e., as recorded on H. Santander's maps) and corrected for the temperature-dependent hatching time. Results obtained through this approach are given in Table 2. As might be seen, the Z estimates obtained in this fashion range from less than 1 d^{-1} to over 4 d^{-1}, and, in fact, allow separation of anchoveta egg mortality into density-dependent and density-independent components. Fig. 4 suggests an extremely strong impact of parent stock size on anchoveta egg survival, and may thus provide a mechanism for the two-year cycles of anchoveta recruitment detected by Mendelsohn and Mendo (this vol.) and further discussed below.

Table 2. Estimates of apparent mean longevity (A) and daily mortality of anchoveta eggs (B) in comparison to their daily egg production estimates based on egg surveys maps and an egg production model.[a]

Range of parent stock ($t \cdot 10^6$)	Mean parent stocks ($t \cdot 10^6$)	n	A Map prod./ theor. prod.[b]	B Apparent mortality[c]
0 – 1.49	0.71	41	1.337	0.75
1.50 – 2.99	2.13	17	0.8325	1.20
3.00 – 4.49	2.64	9	0.3738	2.68
4.50 – 5.99	5.08	4	0.2516	3.98
⩾ 6.00	6.77	3	0.2273	4.40

[a] Based on data in Table 3 of Santander (this vol.).

[b] Map prod. = egg standing stock/egg development time; theor. prod. as estimated by Pauly and Soriano (this vol.). The ratio of the two production estimates expresses mean egg longevity, in days.

[c] Total egg mortality (Z, d^{-1}) is the inverse of mean egg age.

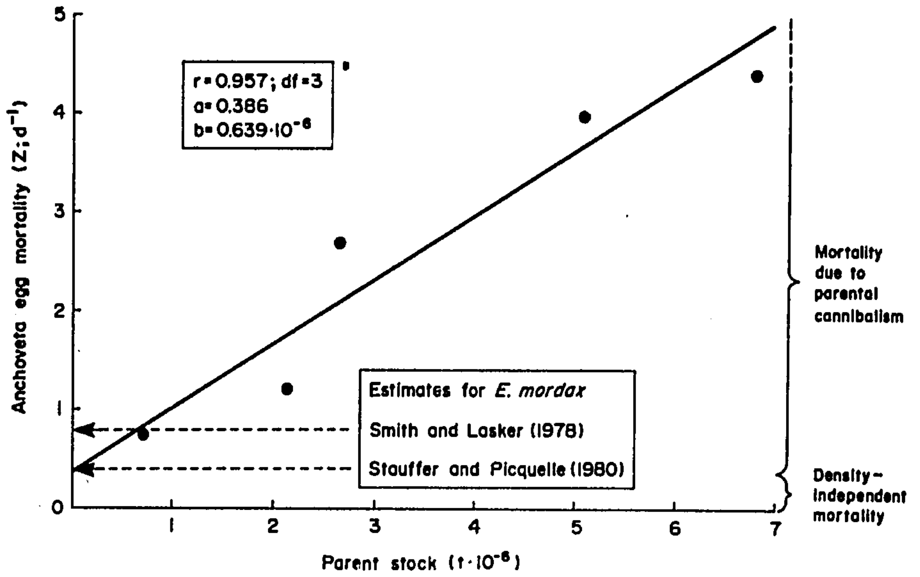

Fig. 4. Relationship between anchoveta egg mortality and parent stock off Peru (based on data in Table 2), with values for the northern anchovy added for comparison. Note extremely high impact of parent stock, and similarity, for low parent stock values, of estimates for Peru and California.

On Biannual Cycles of Anchoveta Recruitment

Although Ricker's (1954) theory of recruitment would imply the occurrence of biannual cycles of anchoveta recruitment (i.e., two times the mean generation time), the first evidence for a two-year lag in the egg-to-recruit relationship was provided, in an entirely non-Rickerian context, by Mendelsohn and Mendo (this vol.). This correspondence of independent evidence (see also Fig. 5), along with the mechanism provided by cannibalism (see above) would be very gratifying, were it not for the fact that sea surface temperature (SST) fluctuations off Peru also have recently been shown to include a strong biannual component (Fig. 6).

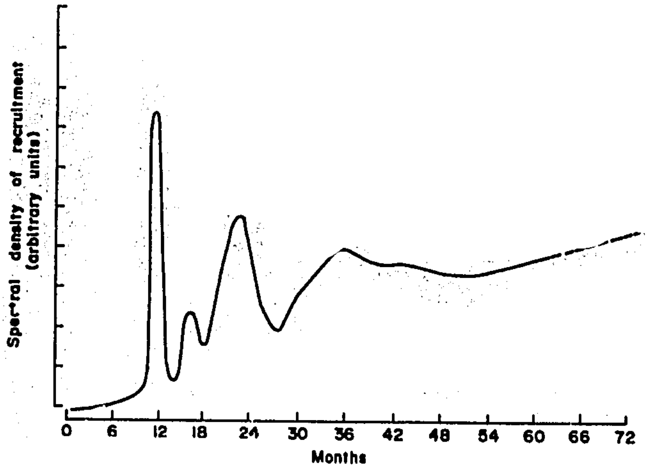

Fig. 5. Spectral analysis of the monthly recruitment time series of Pauly, Palomares and Gayanilo (this vol.) showing (expected) peak at 12 months and (unexpected) peak near 24 months. The analysis was performed using the SPECTRA Procedure in Helwig and Council (1979).

Two possibilities, not mutually exclusive, come here to mind:

i) biannual cyclicity has been artificially introduced into the recruitment data because these were computed based (in part) on anchoveta consumption estimates by predators that are themselves affected by SST,

ii) there are "real" biannual oscillations in anchoveta recruitment.

Obviously, option (ii) can itself be subdivided, i.e.,

a) the biannual oscillations of anchoveta recruitment are directly linked to SST or to another physical phenomenon reflected by SST, or

b) cannibalism (i.e., a Rickerian density-dependent process) generates biannual fluctuations of anchoveta recruitment.

Which of these options (or combination of options) is more realistic cannot be investigated here and now, and in fact should not before a new time series of anchoveta recruitment, explicitly considering mackerel and horse mackerel predation and including missing years (1982 to 1986) has been (re)computed, as discussed below.

On Biases in the Recruitment Time Series

As explained in Pauly and Tsukayama (this vol.) the monthly time series of anchoveta biomass derived in this book may be viewed as a "second iteration", i.e., part of a process which started with a first iteration (represented by the rough biomass estimates in Table 3 of Muck and

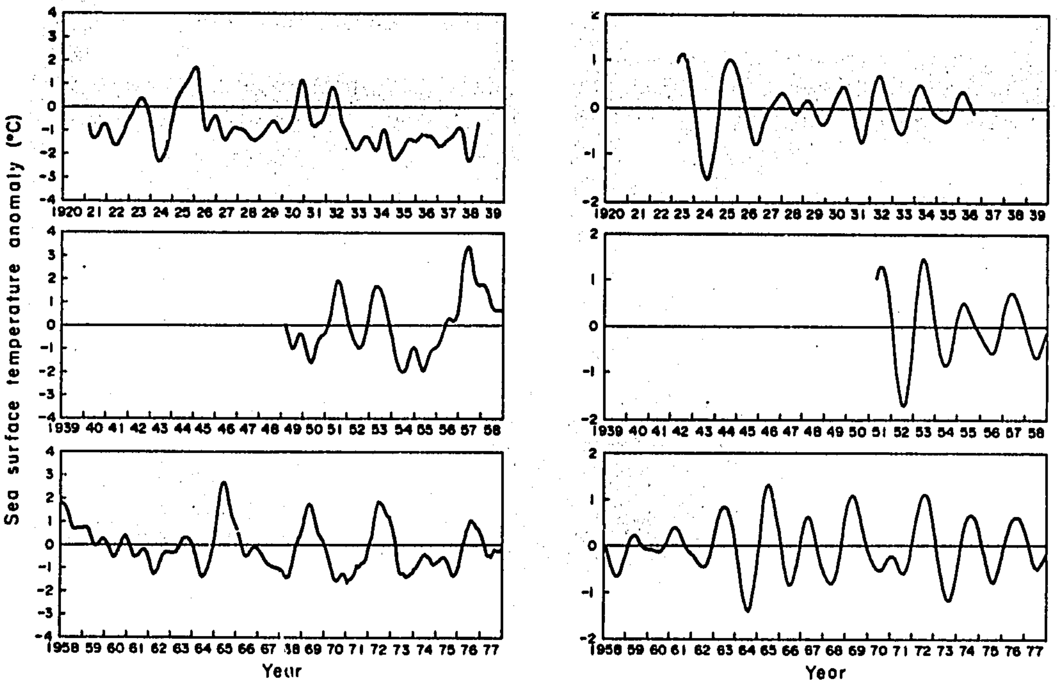

Fig. 6. *Left:* Five-month running mean sea surface temperature anomalies (°C) from ship observations between 4 and 8°S along the ship track parallel for the South American coast. *Right:* Same time-series after band-pass filtering to reveal the biennial component of variability. Filter has full response at 24 months, with one-half power points at 18 and 30 months (E. Rasmussen, University of Maryland, Dept. of Meteorology and C. Ropelewski, Climate Analysis Center, NOAA, pers. comm.).

Pauly, this vol.) and which will eventually lead to reliable series. In this second iteration, the predation by mackerel and horse mackerel was not explicitly considered and its effects were assumed to be part of a residual natural mortality (M_0), set constant for the period 1953 to 1970.

As it turned out, mackerel and horse mackerel consumption of anchoveta during this period was not only substantial (much higher than that of the predators that were explicitly considered) but also drastically declined from the 1950s to the 1980s (see Fig. 5 and 6 in Muck and Sanchez, this vol.).

This implies that Virtual Population Analyses for 1953 to the 1980s that would account for horse mackerel and horse mackerel predation would lead to estimates of biomass (and of recruitment!) higher, for the period 1953 to 1963 than those of Pauly, Palomares and Gayanilo (this vol.). [There would be little change for 1964 to 1982, on the other hand, because of the availability of independent acoustic of biomass estimates for this period]. Moreover since mackerel and horse mackerel tend to invade the nearshore areas and to feed on anchoveta when SST are high (i.e., during El Niño events, see Muck et al., this vol.), there would be a mechanism to (partly) compensate (or overcompensate, as the case might be) for the reduced consumption of anchoveta by birds and seals during warm anomalies (see Muck and Pauly, this vol., and Muck and Fuentes, this vol.).

It can thus be hypothesized that the recruitment and biomass time series that would be obtained would be somewhat smoother, and that the relatively low biomasses and recruitment estimated for the mid- to late 1950s would be closer to the values estimated for the 1960s. This would bring the present outlying point for 1957 in Fig. 6 of Palomares et al. (which illustrates the strong negative relationship between anchoveta growth performance and biomass) in line with the rest of the points. Even more interestingly, it would improve the fit of the models for predicting anchoveta recruitment developed by Mendelsohn and Mendo (this vol.), of which as they write, "none do a very good job for the years 1955-1959".

This is quite encouraging; indeed the specific structure of the bias in our recruitment time series suggests that a third iteration, incorporating mackerel and horse mackerel predation will markedly improve our descriptions and models, although the questions raised above in conjunction with biannual cycles will probably remain.

Fig. 7 shows that, during the years 1953 to 1981, on the average, the anchoveta spawning peak of February to March resulted, three months later, in more recruits than the larger spawning peak of September-November. In terms of Lasker's hypothesis, this would imply that the February-March spawning usually occurs during a period of low turbulence, while September-November should be a period with very few of the well defined periods of calm (see Peterman and Bradford 1987 and Mendelsohn and Mendo, this vol.) which I suggest should be called "Lasker events". As might be seen from Table 1 in Mendelsohn and Mendo (this vol.) this is indeed the case *on the average*. However, as the latter authors point out, the relationship between Lasker events and recruitment success off Peru evanesces upon closer examination. None of the major turning points in the available recruitment time series can be predicted from the available time series of Lasker events.

Mendelsohn and Mendo (this vol.) suggest that this is due to plankton concentration being, off Peru, generally so high that anchoveta larvae may always have enough food, whether plankton-rich microlayers can establish themselves or not, i.e., independently of turbulence.

Their statement clearly implies the need for a re-examination of the available, published information on Peruvian plankton, the re-sorting and re-analysis of the long time series of plankton samples held at IMARPE (as recommended by the IOC/FAO Guiding Group of Experts

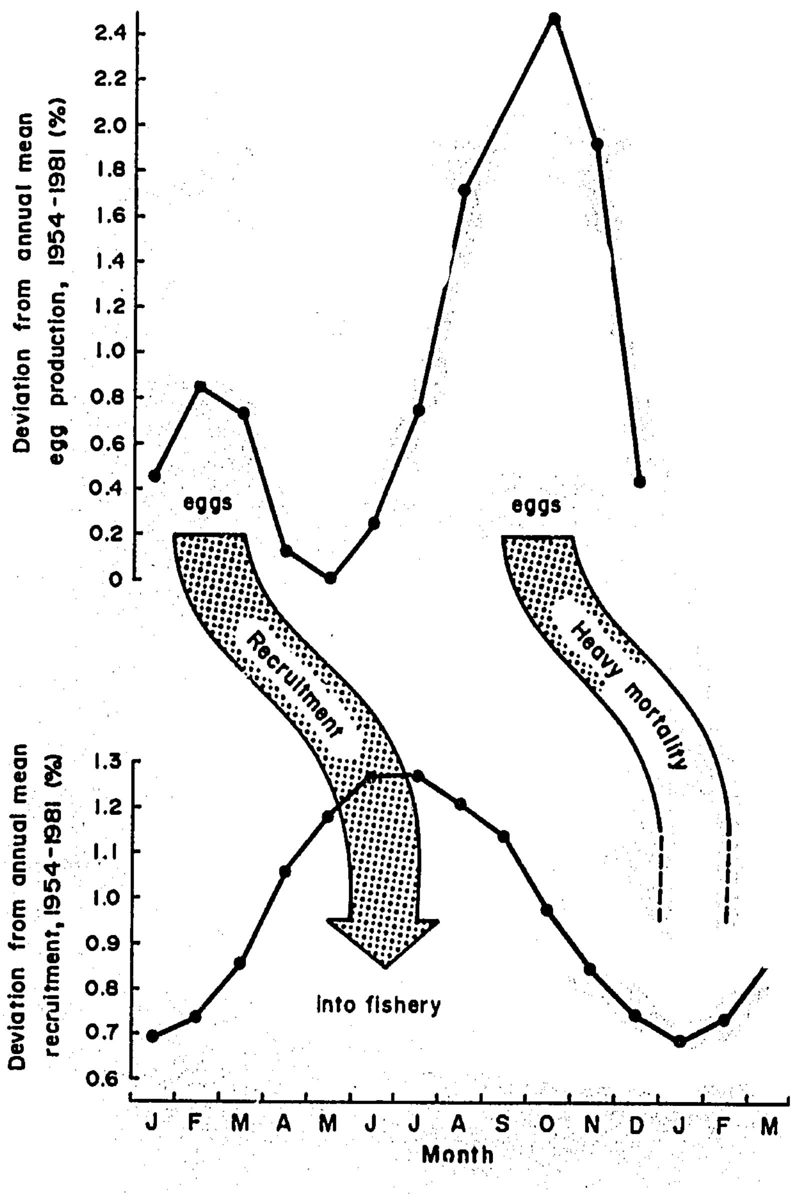

Fig. 7. Demonstrating the existence of an anchoveta "recruitment window": the smaller spawning peak in February-March produces the bulk of anchoveta recruitment (i.e., fish of 3.75-4.75 cm) while the huge spawning peak of September-November corresponds, three months later to a recruitment *minimum*.

on Ocean Science and Living Resources in its 2nd session in Rome, 6-12 June 1987), as well as new data, sampled to specifically address this issue. Haydee Santander's bibliography (p. xi to xii) provides an excellent entry into the Peruvian literature on Peruvian zooplankton, while additional references on this topic, as well as thoughtful analyses may be found in Calienes et al. (1985), Barber and Chavez (1983), Walsh (1975, 1981) and Muck et al. (1984).

Plankton densities affect recruitment not only through their impact on the survival of larvae, however, but also through their effect on the somatic and gonadal growth of the adults, and hence on quantity and quality of spawning products (Nikolskii 1969). Reports on anchoveta stomach contents are available, (see, e.g., Rojas 1953; Mendiola 1966, 1971, 1980; Mendiola and Ochoa 1973; Mendiola et al. 1969; Sanchez et al. 1985) documenting that anchoveta stomachs have been sampled off Peru since the early 1950s. In fact, at the time this is written, the raw data used for the papers cited above are being entered into computer files such that they, too, can be turned into standardized time series similar to those presented in this volume. Hopefully, it will then be possible to address some of the questions left open by our analyses, notably in relation to growth changes, to parental egg cannibalism, as well as to establish links between observed plankton densities, adult anchoveta stomach and fat contents and the survival of anchoveta early stages.

These studies should be complemented, however, by an analysis of the link between phytoplankton standing crop (i.e., the main food of adult anchoveta) and "new primary production". Information on the former is available in the form of numerous maps, both quasi-synoptic and for "average conditions", (see, e.g., Mendiola 1966 and Calienes et al. 1985). The latter can be computed from SST, an upwelling index and a few well-established empirical constants (R. Barber, Duke University, North Carolina, pers. comm.).

On Comparative Studies between Areas, Geological Periods and/or Anchovy Species

Bakun (1985) has recently reviewed the comparative approach as a framework for the interpretation of time series and other data on the recruitment of fish, particularly in Eastern Boundary current systems. Such systems indeed resemble each other both in the physical as in the taxonomic sense, as most dominant species in eastern boundary currents belong to the same genera or even species (Table 3).

For the comparative method to continue to be useful here, however, the subtle differences between these species must be acknowledged, e.g.,that *Engraulis encrasicholus* which range from Norway to West Africa (20°S and beyond if *E. capensis* is a synonym) may not be as well-adapted to upwelling conditions as the more advanced *E. ringens/E. mordax* species pair (Fig. 8). It is in this context that phylogenetic studies, encompassing taxonomy, biogeography (of both recent and fossil forms) and paleontology (i.e., analysis of fish scale abundance and size-frequency distribution in sediment cores) might be most useful. These studies might lead to

Table 3. Dominant anchovy, pilchard, mackerel, horse mackerel, bonito and hake in the four major eastern boundary currents.[a]

Benguela Current	Canary Current	Peru Current	California Current
Engraulis capensis[b]	*E. encrasicholus*	*E. ringens*	*E. mordax*
Sardinops occelatus	*Sardina pilchardus*	*Sardinops sagax*	*Sardinops sagax*
Scomber japonicus	*S. japonicus*	*S. japonicus*	*S. japonicus*
Trachurus trachurus	*T. trachurus*	*T. murphyi*[c]	*T. symmetricus*
Sarda sarda	*S. sarda*	*S. chiliensis*	*S. chiliensis*
Merluccius capensis	*M. merluccius*	*M. gayi*	*M. productus*

[a] After Bakun and Parrish (1980).

[b] Possibly a synonym of *E. encrasicholus* (see Whitehead 1981).

[c] The horse mackerel occurring off Peru was earlier seen as a subspecies, i.e., *T. symmetricus murphyi* (see e.g., Chirichigno 1974).

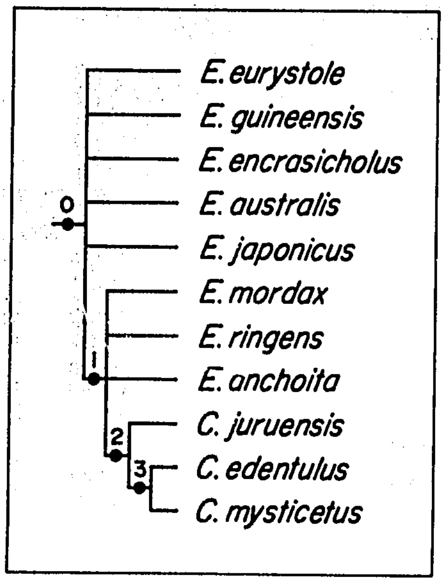

Fig. 8. Interrelationships of species assigned to the genera *Engraulis* and *Cetengraulis*; 0-3, groups for which there is evidence of relationships in the form of shared advanced character (from Nelson 1984).

further generalizations needed for an understanding of the evolutionary biology of *Engraulis ringens* Jenyns (1842) (see Soutar and Isaac 1969; De Vries and Pearcy 1982; Lasker and MacCall 1983; Nelson 1984, 1986; Grande and Nelson 1985; Whitehead, in press and references therein for an entry into the relevant literature).

Some Concluding Remarks on Anchoveta Predators and Other Elements of the Peru Current System

Our analysis of the predation of the guano birds on the anchoveta stocks off Peru suggests that these birds may have less of an impact on the fish stock than proposed by earlier authors (e.g., Furness 1982 and see MacCall 1982). This is in line with the reassessment performed by Bailey (1986) who showed that seabirds may take 5-8%, rather than 20-30% of North Sea fish production. This theme will, in any case, need some re-analyses possibly based on a different model of bird energetics and feeding dynamics than the one used by Muck and Pauly (this vol.), e.g., using some of the new data compiled in Furness and Monaghan (1987).

Sea mammals off Peru - at least as far as sea lions and fur seals are concerned - appear to have a negligible impact on Peruvian pelagic stock (see Muck and Fuentes, this vol., Pauly, Palomares and Gayanilo, this vol.).

Thus, it is not the sea mammals which threaten the Peruvian pelagic fisheries, but rather the converse and indeed more will have to be done toward the conservation of the lesser species of sea mammals. Studies presently conducted in Peru toward this aim are listed in Table 4. Optimal results will be obtained here if those conducting such studies continue to interact with "modellers", thus guaranteeing that their inputs will be considered in future management plans.

The impact of mackerel and horse mackerel on anchoveta, and the error we initially committed of not considering them to be important was discussed above. This error now leads to the question as to which other species may have been neglected.

Hake have been discussed in Pauly and Tsukayama (this vol.) and should be included in future iterations. It is difficult to imagine other fishes (i.e., fishes other than mackerel, horse mackerel, bonito and hake) as having a major impact on anchoveta. This leaves squids (especially *Dosidicus gigas*) as the only fish predators with a potential impact on anchoveta. As mentioned in Pauly and Tsukayama (this vol.) this impact should be limited, however, because the squid in question tend to occur in offshore waters, outside of the range of anchoveta (there are indications that anchoveta in the 1960s ranged further offshore than they presently do, and hence may have been accessible to squid, see Muck and Sanchez, this vol.). A recently available contribution by Benites and Valdivieso (1986), confirms this, both in terms of the distribution of

Table 4. Studies on the biology of small sea mammal presently being conducted in Peru.[a]

Species name Scientific	 Common	Focus of study[b] (investigator(s))
Otaria byronia [= *O. flavescens* (Blainville 1820)]	Sea Lion	population dynamics (IMARPE)
Arctocephalus australis (Zimmerman 1783)	Fur Seal	reproductive biology, feeding habits (P. Majluf)[c], pop. dyn. (IMARPE)
Phocoena spinipinnis (Burmeister 1865)	Burmeister's porpoise	life history (A. Read)[d], feeding habits (J. McKinnon)[e], population discreteness (K. Van Waerebeek)[f], parasites (J. Reyes)[g]
Lagenorhynchus obscurus (Gray 1838)	Dusky dolphin	life history (A. Read), feeding habits (J. McKinnon), population discreteness (K. Van Waerebeek), parasites (J. Reyes)
Tursiops truncatus (Montagu 1821)	Bottlenose dolphin	feeding habits (J. McKinnon), parasites (J. Reyes)
Delphinus delphi (Linnaeus 1748)	Common dolphin	parasites (J. Reyes)

[a] Based on information provided by P. Majluf, J. McKinnon and P. Muck.

[b] Not listed throughout are life histories, and the impact of the fishery on population size and structure, although these are important for all species.

[c] Patricia Majluf, Large Animal Research Group, University of Cambridge, Cambridge, UK.

[d] Andrew Read, Dept. of Zoology, University of Guelph, Guelph, Ontario, Canada.

[e] Jeff McKinnon, Dept. of Zoology, University of Guelph, Guelph, Ontario, Canada.

[f] Koen Van Waerebeek, Museum voor Dierkunde, Rijksuniversiteit Gent, Gent, Belgium.

[g] Julio Reyes, Universitad Ricardo Palma, Lima, Peru.

squid biomass off the Peruvian coast and of their observed diet, i.e., "lantern fishes, crustaceans, other cephalopods, coelenterates and fish eggs". Thus, we have possibly reached here the limit of what needs to be considered in a model of the dynamics of anchoveta.

On Modelling the Peruvian Upwelling Ecosystems

Numerous models of the Peruvian ecosystem as a whole exist (in addition to models of parts of the system, such as presented in this volume). If one disconsiders oceanographic/ meteorological models, they range from conceptual box models (Vogt 1964) to weighted graphs such as in Walsh (1981), simple coupled differential equation models such as Kremer and Sutinen (1975 see Fig. 9) or Aivazyan and Krapivin (1984), all the way to the complex spatial model of Walsh (1975). Whatever their overall complexity, all these models betray, however, through the part that is most detailed, the area of expertise of their maker (e.g., plankton in J.J. Walsh's case), and usually include extremely simplified functions to represent the "lower" (e.g., oceanographic) and "upper" (e.g., fish and/or fishery) interfaces.

We hope that the information presented in this volume will allow the construction of a model of the Peruvian ecosystem in which fish are modelled more realistically than has hitherto been the case, and thus provide, among other things, a basis for refining the bioeconomic model of the Peruvian fisheries presented by Aguero (this vol.).

On Information for Fishery Management

For what it is worth, this volume documents what can be achieved when historical data on a given system are accessed and shared amongst authors. Fishery science is an historical science in

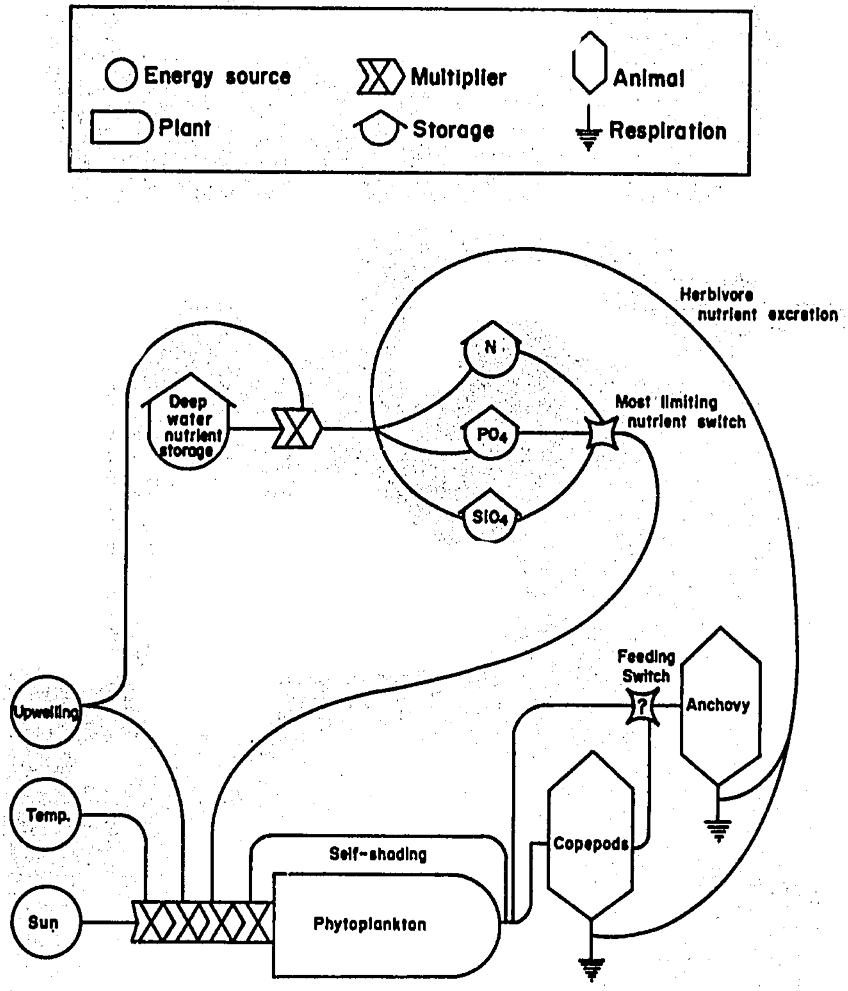

Fig. 9. Flow diagram of the major elements of a simple model of the Peruvian upwelling ecosystem (from Kremer and Sutinen 1975). Note that even in this single model, plankton dynamics are simulated with far more details than the fish, here represented by the "anchovy".

the sense that events are described which are all unique, however much we want to generalize. In our field, this makes the availability of historical information a far more crucial factor than say in chemistry. Indeed, numerous insights, e.g., on the variability of fish stocks or of the intensity of El Niño events, could be gained only because of the availability of old *written* records (see Cushing 1982 and Woodman 1985, respectively). For this reason, an explicit policy to encourage its staff to publish is crucial for any fishery research institution, and some suggestions to this effect are given in Table 5.

Important also are bibliographies, which, while remaining well focused, should be as complete as possible. While having a clear focus, the recently produced bibliography of Mariategui et al. (1985) misses a large fraction of the literature cited in this volume, including classics such as, e.g., Bini (1952), which, however, one finds cited in works such as De Buen (1960) and listed in the bibliography of Stephenson and Hicks (1975).

Equally problematic is the fact that a significant fraction of the literature on the Peru Current was originally published in Russian, and that only a small part thereof was translated into Spanish or English (see, e.g., Aivazyan and Krapivin, 1984 and references therein). Clearly, an effort should be made to have the bulk of this literature translated, e.g., through some cooperative agreement between IMARPE and its sister institution in the USSR, or as part of the "package" enabling Soviet vessels to operate in Peruvian waters. This would both help Peruvian fishery science and management and provide a larger audience for the important work that Soviet fishery scientists and modellers do.

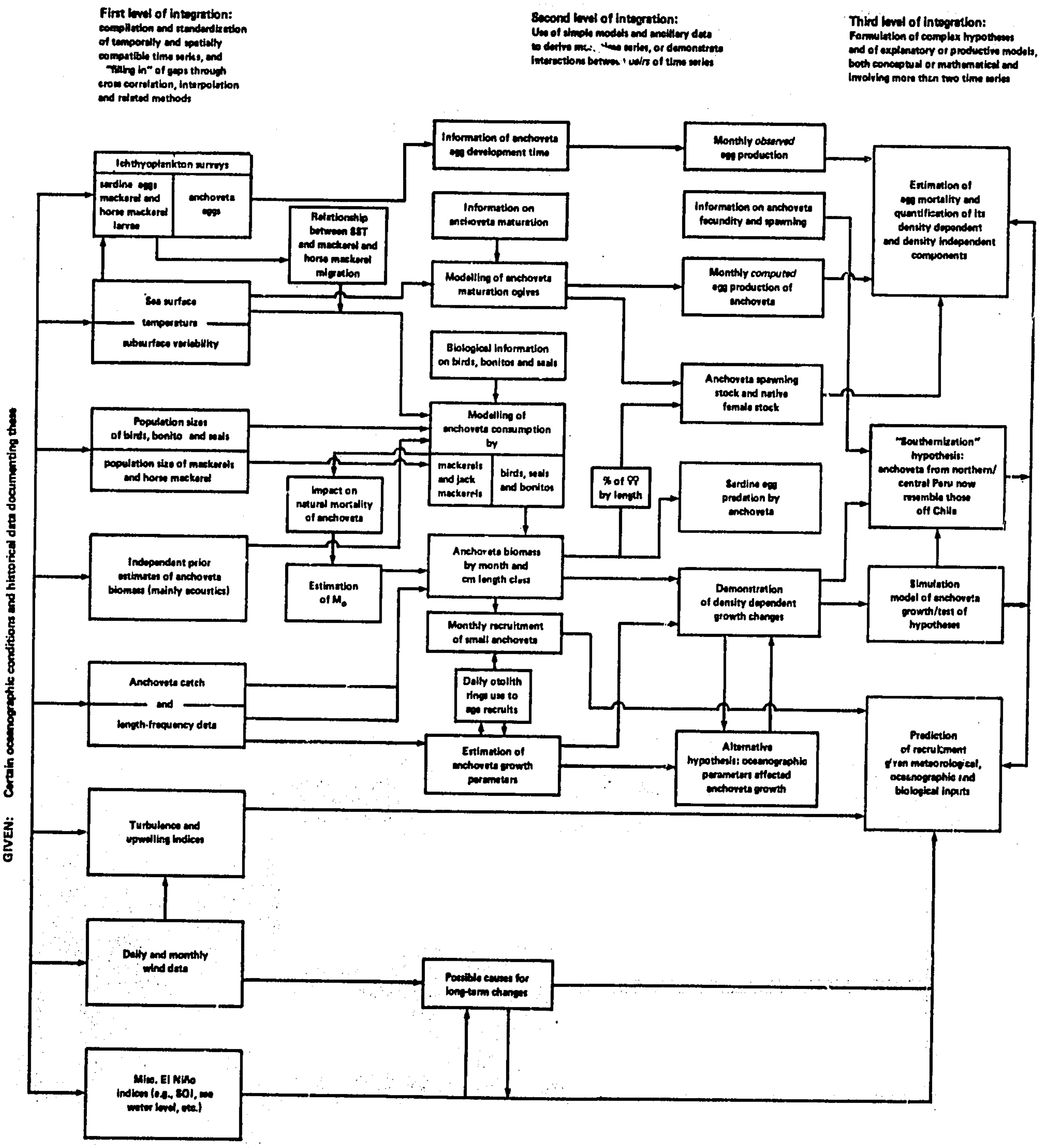

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Fig. 10. Flow chart showing integration of studies included in this volume, along with areas not covered (shaded box), which include fishery-related government policies and "Fourth Level of Integration", not achieved here. Note that arrows (not shown here) should connect the two sides (pages) of this graph.

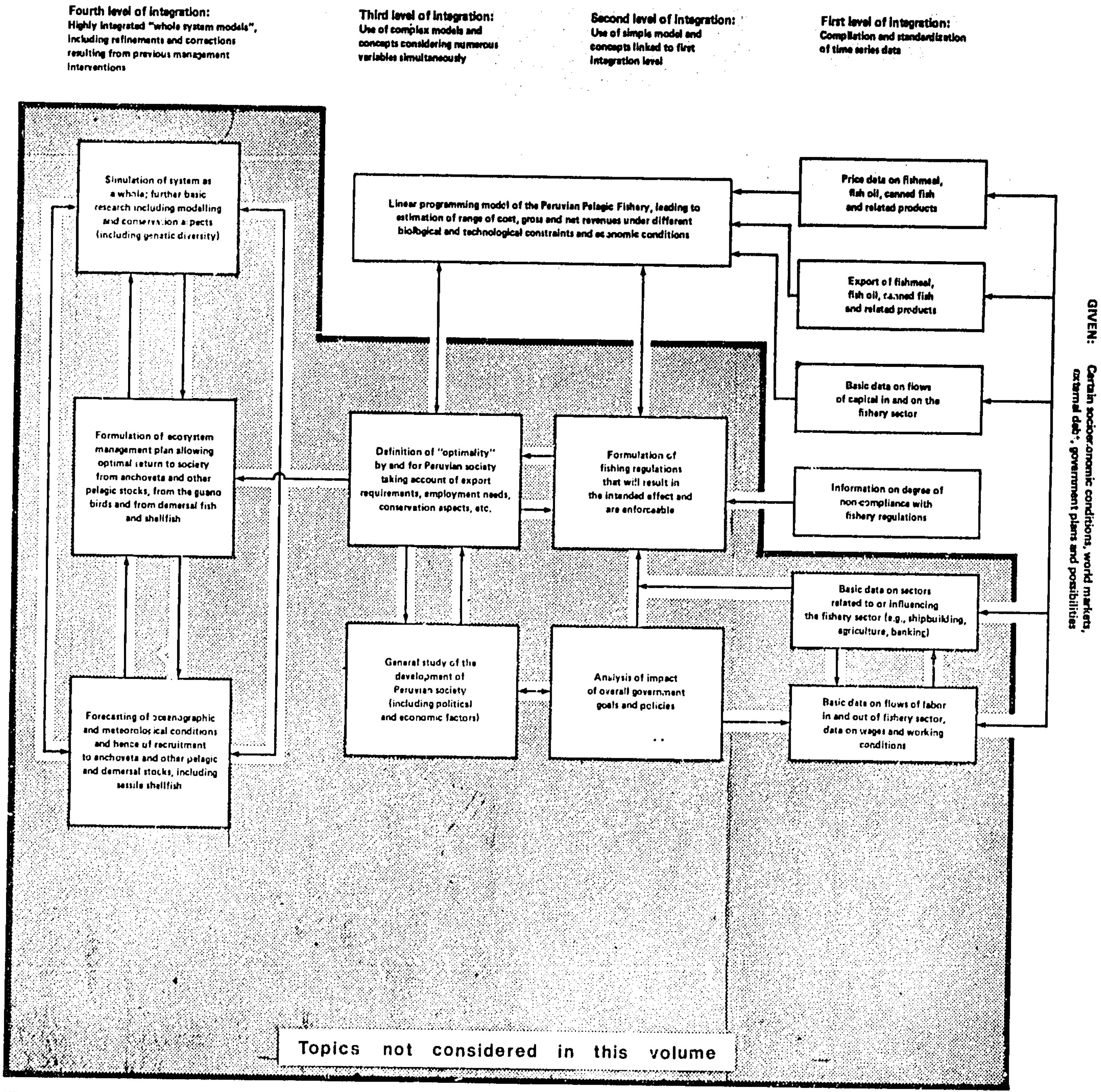

Fig. 10. Continued

Table 5. Some suggestions toward increasing the scientific output of a fishery research institution.

- Produce an Annual Report, with brief accounts of the work in each research group, their findings and published output;
- Produce an annual set of Collected Reprints for exchange with other institutions;
- Give active support to young scientists to publish the results of studies they have carried out under their own authorship;
- Give adequate credit to supervisors and scientific administrators for the scientific output of their subordinates, not only their own;
- Delay as long as possible the promotion of recent Ph.D. recipients to administrative positions;
- Always build reporting and publication costs into the budget of a proposed study;
- Encourage scientific staff to learn the international language of science (English),[a] and to read scientific literature as widely as possible;
- Encourage each scientific staff to submit at least one contribution (however short) a year to an *international journal;*
- Make sure that library has at least one of the current awareness journals (e.g., Aquatic Science and Fisheries Abstract or Current Contents)–cancelling other subscriptions if necessary–and use the titles and addresses in this journal to obtain (free) reprints, which are then circulated to staff;
- Avoid the production of anonymous reports, which give no credit to their author(s);
- Reduce as much as possible (preferably to zero) the production of *technical reports* that are meant to remain confidential;
- Release data and reports as soon as they have outlived their usefulness to real-time management decisions;
- Encourage cooperation, within and between institutions, of staff working on similar or related topics;
- Cooperate with other institutions, e.g., Universities within the country and abroad, partner institutions in neighboring countries, etc.

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[a] N.B.: the author's first language is French.

On Managing the Peruvian Pelagic Fishery

Fig. 10 gives an integrated summary of what was covered by the studies presented in this book, while areas not dealt with are indicated as such (shaded box). As might be seen, we have covered rather comprehensively the oceanographic/biological side of things, while our coverage of the social and economic aspects of fishery management was very limited.

Various contributions in Glantz and Thompson (1981) have highlighted the problems associated with formulating and carrying through a fishery policy with a fixed target (e.g., "MSY") in the face of environmental variability. Clearly, any plan for the management of the Peruvian upwelling ecosystem will have to take environmental variability explicitly into account.

I have termed "Fourth Level of Integration" the level of research and management sophistication required to do this (see Fig. 10). However, Dr. Max Aguero (ICLARM, pers. comm) feels that few studies have been conducted to date which would correspond to this "Fourth Level", one of the few exceptions being the "World Model" of the Club of Rome (Meadows et al. 1972).

Acknowledgements

The synthesis presented here is based in part on feedback received from various colleagues after presentations (in May 1987, at Kiel and Hamburg Universities, Federal Republic of Germany and during the session of the IOC/FAO Guiding Group on Ocean Science in Relation to Living Resources, held in Rome, Italy, 16-21 June 1987), of some of the results presented in this volume. My sincerest thank to these colleagues for their interest and encouragement.

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[a] Page numbers for "*Engraulis ringens*," "Anchoveta" and "anchovy" are omitted due to their occurrence throughout the book.

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