EGGS AND LARVÆ OF FISHES AND THEIR ROLE IN SYSTEMATIC INVESTIGATIONS AND IN FISHERIES

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The stages of fishes that will be discussed in our presentation are those that are collected by hauling plankton nets in the ocean. These are the eggs, larvae, and less frequently, the juveniles of marine fishes. The stages collected by plankton gear are commonly referred to as ichthyoplankton. The collections are usually made on survey cruises or on wider-ranging expeditions.

There are perhaps three principal reasons why ichthyoplankton surveys are made.

Firstly, the surveys are often directed toward a single target species (or a group of closely allied species) in order to use the distribution and abundance of the pelagic eggs to obtain an estimate of the biomass of the adult spawning population.

Secondly, the larvae of a target species are studied in order to estimate the success of the year brood resulting from its spawn and hopefully to understand the factors underlying fluctuations in survival.

The third reason is to use ichthyoplankton surveys to evaluate fish resources in general. The plankton net is not selective — it collects the eggs and larvae of all kinds of fishes with pelagic egg and/or larval stages. It provides information on unexploited resources as well as on exploited resources. In fact, with a few exceptions, it provides information on the whole spectrum of fishes in the area being surveyed.

Whether the surveys are made to assay a single exploited population or to provide information on all the kinds of fishes being sampled as eggs and larvae, the ichthyoplankton technique, if properly planned and executed, is one of the more rewarding.

If a worker hopes to use fish eggs and larvae surveys for any of the above purposes, a primary consideration is that the investigator be able to identify the eggs and larvae of target species with complete certainty. Although this requirement would appear to be obvious, its fulfilment is not always easy, and sometimes requires detailed and even sophisticated research. The eggs and larvae of some of our important commercial fishes are among the more difficult to identify, particulary if they co-occur with related species. This applies, for example, to larvae of clupeids, engraulids, scombrids, istiophorids, and gadids, in other words to the very core of our important commercial fish resources. Hence, when dealing with the eggs and larvae of a target species, such as the Pacific sardine, it is necessary to know what other clupeids could be in the area, where and when they spawn, and how to distinguish among their early life history stages.

Estimates of egg abundance.

If eggs are to be used for obtaining population biomass estimates, it is important to completely cover both the spatial distribution of spawning and its temporal distribution — i.e., to have a complete coverage of spawning of the target species in space and time. In order to completely delimit the spatial and temporal distribution of the eggs and larvae of a target species, exploratory surveys are often necessary and these alone could require 1 or more years.

Of course, the frequency of coverage of a known spawning area depends on vessel resources. It may require several research vessels rather than one, even to obtain monthly coverage of the spawning area of a pelagic species, such as the Pacific sardine or the northern anchovy.

Our basic data are egg numbers obtained from a grid of stations that cover the spawning area, during a series of cruises cover below the spawning season. The number of eggs taken at any given station are standardized to represent the number under a unit area of sea surface (such as 1 m^2 or 10 m^2). For each station we need to know the average number of eggs spawned per day in order to integrate our egg numbers over time.

Most pelagic fishes spawn during a limited period each day. The Pacific sardine, for example, spawns principally between 8 p.m. (20.00 Naval time) and midnight. Because spawning occurs for only a brief time each day, the eggs of the several day's spawnings present in a sample represent different and separated stages of development. By utilizing stages of development, it is possible to determine the egg count for each spawning day represented, and from this the average number of eggs spawned per day. It was found that there is a rather precise relation between the water temperature and the number of hours spent in the egg stage. This relation was demonstrated originally for the Pacific sardine by relating the temperature obtained at a station with the egg stages obtained (AHLSTROM, 1943). The temperature relation itself can be used to determine the number of days spawning potentially represented in a sample, and from this the average number of eggs spawned per day (SETTE and AHLSTROM, 1948). ZWEIFEL and LASKER, (1976) have developed a precise mathematical model to express the relation between temperature and stage of development in a variety of pelagic species.

Once the average count of the number of eggs is determined for each station, an estimate of the number of eggs spawned during the year simply involves integration of these values over area and time. There are several methods of doing this which are well documented in the literature (SETTE and AHLSTROM, 1948 ; AHLSTROM, 1954 ; TANAKA, 1955, 1974 ; SAVILLE, 1964).

In order to convert egg numbers to population biomass, several biological parameters must be taken into account. It is necessary to know the proportion of males and females in the spawning population. For some pelagic fishes such as the Pacific sardine, this is approximately the same, 50 % females, 50 % males. It is also necessary to know if males and females of the same age are of similar weights. In terms of biomass, is one male equal to one female ? If either the weight of males or the proportions of males in the population relative to females changes as fish grow older either becoming less or more, then it is essential to know the age composition of the spawning population. For commercially exploited species, the age structure of the commercial catch usually is determined season-by-season. For unexploited or little-exploited resources, such information must be obtained by other means. Next is the problem of fecundity of females as related to age or weight. For species whose fecundity has been rather intensively investigated, such as the sardine, a relation has been found between the number of eggs spawned and body weight, hence, it is possible to express fecundity as the number of eggs matured and spawned per batch per gram body weight. For the sardine, the average number of eggs spawned per batch is 263 eggs per gram body weight (MAC-GREGOR, 1957). We make the assumption that the average female sardine will spawn three batches of eggs during the spawning season. MAC-GREGOR (1957) has shown that this is not a static value, but one that could be modified by such factors as condition factor of females (whether they are fat or thin at the time of maturation) and by external environmental events.

Success or failure of year broods.

Now to the second major problem, that of using egg and larva surveys to get an estimate of the success of the year brood from the spaun. It is usually assumed that the major mortality of a year brood occurs during the early life history stages, and particularly during the period when the larva first obtains food, after using up its yolk. For larvae that survive the critical transition stage from yolk to particulate feeding, their survival will depend both on obtaining adequate food and escaping predation. A further consideration, and one of the critical problems in fishery research, is how the abundance of the spawning population itself affects the strength of incoming year classes.

The Report on a Colloquium on Larval Fish Mortality Studies held at the Southwest Fisheries in La Jolla during January 1975, has just been published (HUNTER, Ed., 1976). It was the concensus of the Colloquium "that the major causes of larval mortality are starvation and predation, and that these may interact". Relative to these two subject areas, larval research has been weighted toward studies on food, feeding and starvation in fish larvae, whereas relatively little work has been done on predation. This balance needs to be rectified. Furthermore, a principal concern of larval fish mortality studies should be to study the density-dependent aspects of starvation and predation because these aspects of mortality are most likely to provide the understanding of the stock and recruitment relation.

Age and size of larvae as related to water temperatures.

In discussing problems relative to survival of fish larvae, we will choose most of our examples from the northern anchovy, the species being most intensively investigated at our Center.

Larvae of the northern anchovy, *Engraulis mordax* are the most abundant taken on CalCOFI surveys (AHLSTROM, 1968). They represent a considerable size range from newly hatched at about 2.5 to 3.0 mm to larvae about to transform at 20 mm. Above this size, anchovies avoid plankton nets through agility. Also, more larger larvae are taken in night hauls than in daytime hauls. Anchovy larvae are routinely measured, hence we have counts by size for each cruise and season. For mortality estimates, however, we need to know abundance of larvae in terms of age rather than size. Ideally, we desire the ability to age sea-caught larvae in increments of a day. Attempts to age sea-caught larvae by following size modes on successive cruises has proved less than successful. A complication is simply that larvae, like embryos, will grow faster at higher temperatures, hence it is necessary to know the growth rate of larvae in relation to temperature. This requires laboratory work.

KRAMER and ZWEIFEL (1970) reported on the growth of anchovy larvae reared in the laboratory at two constant temperatures, 17° and 22° C. The growth rate at 22° C was considerably faster than at 17° C. The best fit for the growth curves (two experiments at 17° C, one at 22° C) was made by using the Laird-Gompertz equation. The largest larvae in their experiments were about 20 mm in length and 34 days old. Wild plankton was used as the basic food. HUNTER (1976) repeated the culture and growth experiments of anchovy at temperatures of about 16° C (one experiment at 17.7° C). His fifth experiment was the most successful, made at 16.2° ± 0.33° C, using as food a mix of laboratory-cultured organisms. In this experiment, Hunter was able to rear anchovy through metamorphosis at a length of about 35 mm and age of 74 days with a minimum survival of 12.5 %. Throughout the experiment, larvae were sampled on alternate days for both length and weight determinations. These data give excellent fits to the Laird-Gompertz growth equation.

Similar experiments have been continued at several other constant temperatures, including 13° and 19° C. These experiments give good fixes on the temperature-age relation of anchovy larvae within the size and temperature ranges sampled on CalCOFI survey cruises. The question of how well these laboratory-determined values apply to larvae in the sea is being tested from otolith daily increment studies.

Assessment of age of larvae in the sea.

Recent work on otoliths of larvae and juveniles of *Engraulis mordax,* following up the lead of PANNELLA (1971), has shown that daily growth increments are indeed laid down in laboratory-reared specimens. These experiments by BROTHERS, MATHEWS and LASKER (1976) used larvae and early juvenile fish of known age. The rings on otoliths are first laid down on anchovy larvae of about 5 days old, after the completion of yolk-sac absorption and the beginning of particulate feeding. These workers showed that daily rings may be used to estimate the age of anchovy larvae and juveniles with great precision up to 100 days old. The experiments were repeated on other laboratory-reared species including the grunion, *Leuresthes tenuis.* In larvae of this species, daily increments appear at hatching rather than at yolk absorption. Hence, the exact timing of the initiation of daily increment formation varies from species-to-species and must be independently determined for each one. STRUHSAKER and UCHIYAMA (1976) using another engraulid, the nehu, *Stolephorus purpureus* from the Hawaiian Islands area, also demonstrated daily growth increments on otoliths.

With these encouraging results, scientists at our Center are actively pursing a program of aging sea-caught anchovy larvae. These also have daily growth increments on their otoliths that can be counted as readily as on laboratory-reared specimens. It should be pointed out that otoliths are lost in specimens preserved in formalin. Initial studies have been carried out on fresh specimens, frozen material, or material preserved in an alcohol-glycerine mixture.

Bioassay experiments.

It has been pointed out by a number of workers (as for example, LASKER *et al.,* 1970) that the average density of larval food in the sea is usually too low to support larval growth and survival. If larvae are to survive, it almost requires that their food concentrates into patches of some extent and persistence and that the newly-feeding larvae locate such patches. LASKER (1975) set out to find if such concentrations or patches of larval food did occur in the sea, and if so what was their extent and persistence. He was using first-feeding anchovy larvae as test animals, placing them in samples of Los Angeles Bight water from the surface and from chlorophyll maximum layers. Feeding of larvae in water from the surface was minimal in all experiments, but extensive feeding occurred in water from the chlorophyll maximum layer when the test samples contained phytoplankters with minimum diameter of approximately 40 μm in densities of 20 to 40 particles/ml. On the initial cruise the chlorophyll maximum layer, which extended along the southern California coast for at least 100 km, was dominated by a bloom of the naked dinoflagellate, *Gymnodinium splendens,* a food organism known to support the growth of anchovy larvae. A storm which caused extensive mixing of the top 20 m of water obliterated the chlorophyll maximum layer and effectively destroyed this feeding ground of the larval anchovy. This work has been continued on a number of subsequent cruises. Recent observations have supplied additional evidence concerning the influence of abiotic factors, such as wind strength, on the persistence of food patches. If good survival of anchovy larvae occurs in food patches, as seems highly probable, then years with environmental conditions which favor stability in inshore waters can be classified as favorable for anchovy larval fish feeding, whereas those that cause instability should be considered to be detrimental to larval survival (LASKER, in press).

Assessment of starvation in the sea, using larval condition.

In several widely separated laboratories criteria are being developed to identify starving larvae using histological, morphological, chemical, or other criteria (EHRLICH, 1974 ; EHRLICH, BLAXTER and PEMBERTON, 1976 ; UMEDA and OCHIAL, 1975 ; O'CONNEL (1976). O'CONNEL (1976) has studied the starving condition of early-stage anchovy larvae, using larvae

reared with or without food up to an age of 9 days. He studied a number of histological characteristics (11) and found that the state of emaciation could be shown by using a combination of four of these : pancreas condition, trunk muscle fiber separation, intermuscular tissue, and liver cytoplasm. UMEDA and OCHIAI (1975) at Kochi University, made similar studies on early-stage larvae of the yellowtail, *Seriola quinqueradiata*. They continued their experiment for 10 days after hatching. The digestive organs of starved larvae became strikingly degenerated by the 6th to 9th day. Using older stages of herring and plaice larvae for experimentation, EHRLICH, BLAXTER and PEMBERTON (1976) were able to show several external morphological changes in larvae starved to the point-of-no-return, including a marked concavity of the head caused by shrinkage and a sharp angle at the ventral junction of the cleithra, resulting from the collapse of the digestive tract. These authors suggest that buoyant fatty tissue is being utilized catabolically from the herring's head causing the shrinkages, and this may explain why starving larvae tend to hang their head down in the water. Such external morphological characters as these are the kind that could readily be observed on larvae collected at sea. Histological characters, such as those studied by O'CONNELL or UMEDA and OCHIAI, require considerably more work and preparation to apply to ocean-caught larvae, but probably will give more accurate diagnoses of starvation.

Neuston net as an aid in mortality studies.

AHLSTROM and STEVENS (1977) report on neuston (surface) collections made on an extended CalCOFI cruise during May 1972, in which neuston net hauls are compared with regular oblique plankton hauls taken simultaneously. The neuston hauls sampled a different segment of the anchovy larvae population. Only about 2.5 % as many small larvae, 2.0 to 6.0 mm, were taken in neuston hauls as in oblique plankton hauls ; conversely, only 2.5 % as many large larvae, 14.5 mm and longer, were taken in oblique plankton hauls as in neuston net hauls. These are striking differences ; obviously, larger larvae tend to congregate in the surface layer. It should be mentioned that only about 1 % of the total anchovy larvae collected by the standard CalCOFI net hauled obliquely are in the size range of 14.5 mm and larger (AHLSTROM, 1965 *b*). Hence, the neuston haul does provide a much larger sample of anchovy larvae in the part of the survival curve that is rather poorly sampled in oblique hauls. If the neuston net does this consistently (and we are currently testing this), the neuston hauls could be used to provide estimates of changes in relative abundance of larger anchovy larvae from year-to-year, information essential for evaluating success of survival of cohorts of anchovies. HUNTER and SANCHEZ (1976) provide evidence of why larger anchovy larvae do congregate at the surface during a period of each day. They were following up the observation of UOTANI (1973) that larvae of the Japanese anchovy, sardine, and round herring have expanded swim-bladders when captured at night in the sea and deflated ones when captured during the day ; these species feed only during daylight hours. HUNTER and SANCHEZ found that larger anchovy larvae move to the surface at dusk to fill their swim-bladder by swallowing air at the surface. This increases the buoyancy of the larger larvae hence reduces their energy expenditure at night. The diel movement of anchovies to the surface, provides a ready explanation for the surface neuston haul containing so many more larger anchovy larvae than the regular oblique hauls.

Predation.

As was pointed out in the Colloqium report, predation studies have been so neglected that the participants found it difficult to specify in any detail the work needed to be done.

The first obvious step is the need to identify potential predators. Several of the more revealing studies on predation were made half a century ago by LEBOUR (1922, 1923, 1925). She showed

that a variety of zooplankters fed on young fish larvae including medusae, ctenophores, chaetognaths and crustacea (phyllosome larvae of *Panilurus* and the pontellid copepod, *Anomolocera pattersoni*), and the annelid *Tomopteris*. Most of her observations on predation in the laboratory were made with medusae, which could be kept alive for extended periods and which were voracious predators on fish larvae as well as on chaetognaths, ctenophores, and even other medusae. FRASER (1969) made further observations on feeding of medusae and emphasized the importance of their predation on fish larvae. Most reports in the literature dealing with predation on fish eggs and larvae by zooplankton organisms are incidental observations that lack quantitation.

What is now needed is an approach that combines field and laboratory studies. Considerable information on potential predators could be gained by observing which of these co-occur in plankton collections with the eggs, larvae and juveniles of target species, and especially by examining the gut contents of suspected predators. The laboratory studies of predators should establish what size larva are preyed upon, what effect larval condition (i.e., whether larvae are starved or well-fed) has on vulnerability, what are the search patterns, feeding behavior and food capacities of the predators, and the like. Also needed are laboratory studies on larval avoidance mechanisms, recovery from predatory attacks and residence time of identifiable eggs and larvae in guts of predators. Once the potential predators have been identified and their predatory potential evaluated, special sea studies should be made to determine both spatially and temporally the density and distribution of predators in relation to eggs and larvae of target species.

A few of the needed laboratory studies have recently been made on predation, using young anchovy larvae as the objects of predation and several kinds of plankton crustacea as the potential predators. LILLELUND and LASKER (1971) showed that a variety of marine copepods could injure or capture and ingest yolk-sac anchovy larvae. Particularly effective predators were the pontellid copepods, *Labidocera jollae*, *Labidocera trispinosa*, and *Pontellopsis occidentalis*. THEILACKER and LASKER (1974) showed that most developmental stages of the abundant euphausiid shrimp, *Euphausia pacificia*, were effective predators on young stages of anchovy larvae.

Evaluation of fish resources by ichthyoplankton surveys.

If we were to single out one aspect of egg and larvae surveys as of prime importance, it would be their use in fish resources evaluation.

Why are fish egg and larval surveys so useful for fish resource evaluation? Most oceanic fishes have pelagic eggs and/or larvae that are distributed in or just below the photic zone, i.e., within the upper 150 to 200 m of depth. At no other time in their life histories are so many kinds of fishes associated together — mesopelagic and bathypelagic as well as epipelagic fishes — where they can be collected quantitatively with a single type of gear, a plankton net.

The majority of pelagic marine fishes spawn in the open sea in a manner that permits each egg to be a separate free-floating entity that can be readily collected by plankton nets together with the larvae that hatch from these eggs. Inshore fishes that spawn between the shore and about 100 m depth often spawn demersal eggs or build nests and guard their eggs, but their larvae are usually pelagic members of the neritic plankton community. This also applies to larvae of ovoviviparous fishes, such as the speciose genus *Sebastes* in the eastern North Pacific. Hence, the larvae of most marine fishes are members of the plankton community and can be sampled quantitatively with plankton gear.

We wish to provide two examples of the use of ichthyoplankton surveys for fish resource evaluations; the California Current (CalCOFI) surveys and the Eastern Tropical Pacific (EASTROPAC) cruises.

CalCOFI surveys.

It was a fortunate circumstance when we began our CalCOFI surveys (i.e. surveys conducted by the California Cooperative Oceanic Fisheries Investigations) that the spawning of the Pacific sardine, the target species, was found to have an extensive and varying areal and temporal distribution. Because of this, our surveys could not be limited to a part of the year or to a part of the California Current system off California and Baja California. We had to cover an extensive area regularly. Rather than ignore everything but sardine eggs and larvae, we decided to investigate the eggs and larvae of other species as the ecological associates of the sardine. It was through this approach that we were able to assess the fish resource potential of the California Current region.

Species (or genus)	CalCOFI Atlas number	Years covered	Number of cruise charts	Authors Date of publication
Engraulis mordax	9	1951-1965	134	KRAMER (D.) and AHLSTROM (E.H.) (1968)
Merluccius productus	11	1951-1966	95	AHLSTROM (E.H.) (1969)
Trachurus symmetricus	11	1951-1966	91	Same
Sardinops caerulea	12	1951-1966	138	KRAMER (D.) (1970) (eggs and larvae)
Citharichthys spp.	23	1955-1960	64	AHLSTROM (E.H.) and MOSER (H.G.) (1975)
Sebastes spp.	Atlas being prepared	1951-1969	155	AHLSTROM (E.H.), MOSER (H.G.) and SANDKNOP (E.)
Vinciguerria lucetia	17	1955-1960	62	AHLSTROM (E.H.) (1972)
Triphoturus mexicanus	17	1955-1960	61	Same
Stenobrachius leucopsarus	17	1955-1960	50	Same
Leuroglossus stilbius	17	1955-1960	48	Same
Bathylagus wesethi	17	1955-1960	46	Same
Bathylagus ochotensis	17	1955-1960	38	Same

TABL. 1. — *Coverage in CalCOFI Atlases of more abundant kinds of fish larvae taken on CalCOFI cruises.*

As mentioned in AHLSTROM, 1965 a, a few kinds of fishes dominate the California Current collections. In fact, 12 kinds of larvae made up over 90 % of the total larvae, year after year. These 12 kinds involve 10 species and 2 generic groups. Six are of present or potential commercial importance (i.e., *Engraulis mordax, Merluccius productus, Trachurus symmetricus, Sardinops caerulea, Sebastes* spp. and *Citharichthys* spp.) ; 6 have no foreseeable commercial use (i.e., the sternoptychid, *Vinciguerria lucetia,* the myctophids, *Triphoturus mexicanus* and *Stenobrachius leucopsarus* and the bathylagid smelts, *Leuroglossus stilbius, Bathylagus wesethi* and *B. ochotensis*) ; all 12 must be important in the marine food web. All 12 categories have been, or are being included in the CalCOFI Atlas series. For about one-half of the categories, the Atlas covers distribution and relative abundance of larvae by cruise for 15 or more years ; for the remainder, distributions are given for the 6-year period 1955 through 1960 (table 1). Several of the years included in the coverages were highly contrasting with regard to oceanographic conditions ; 1956, for example was a cold year, 1958 and 1959 were warm years. Several of the atlases deal with hydrographic features including temperature and salinity distributions at 10-m, geostrophic flow at the surface and at 200 m, hence it is easy to match up larval distributions with hydrographic features.

Larvae making up the 2nd group of 12 kinds, i.e., larvae ranking between 13th and 24th in the abundance contributed 4 to 6 % of the total. All of these were identified to genus or species. The remainder constitutes as little as 3 % or as much as 5 %. However, in our CalCOFI collections this remainder includes some hundreds of kinds of fish larvae - perhaps between 300 to 400 kinds.

The CalCOFI surveys documented the decline in abundance of eggs and larvae of the Pacific sardine *Sardinops caerulea,* and the marked increase in abundance of those of the northern anchovy, *Engraulis mordax.* The CalCOFI egg and larval surveys still provide the basic information for estimating anchovy biomass. There is also the interesting problem of trophic level competition involved in the sardine-anchovy population interaction. The sardine-anchovy problem has been well documented (AHLSTROM, 1966, 1967, 1968 ; MURPHY, 1966 ; SMITH, 1972).

The CalCOFI surveys pointed to the magnitude of the Pacific hake, *Merluccius productus,* stock at a time when there was not a fishery on this species. Hake larvae were consistently second in abundance to the anchovy (AHLSTROM, 1965 a). The Russians now have exploited this species off our waters for over a decade and were recently joined by Polish vessels ; but the U.S. fishery for hake still remains negligible. The reported catch in 1974 and 1975 exceeded 200,000 metric tons. Larval data has also provided evidence for the recent decline of this resource.

Rockfish larvae, *Sebastes* spp., as a group, usually rank third in abundance. *Sebastes* larvae can readily be identified to genus, but not to species. The primary reason for this is that there are approximately 60 species of *Sebastes* that occur off California. However, we are gradually filling in a number of the blanks, and several of the larvae of commercially important species are known and routinely identified (MOSER *et al.,* 1977).

The jack mackerel, *Trachurus symmetricus,* affords a classic example of how much information can be obtained about a species from ichthyoplankton surveys. The younger age classes of this species are fished commercially, not the older adults. The fishery is confined to the southern California Bight area. There was no real knowledge of the distribution of this species until the CalCOFI surveys. It was shown to be the most wide ranging of the commercially important wetfishes. The adults can occur up to 600 miles offshore off California and up to 1,100 miles off Washington in the latter region in the eastward flowing limb of the North Pacific Current gyre. Jack mackerel eggs have been identified for some CalCOFI cruises (FARRIS, 1961), and estimates have been made of the jack mackerel population's biomass (AHLSTROM, 1968). Spawning aggregations of jack mackerel are markedly smaller than those of hake and even of sardine or anchovy. One consequence of this is that we never sample as large a concentration of eggs or larvae of jack mackerel as of the other three, but we sample them over a more extensive area. Jack mackerel spawning is usually at its peak in May and larvae are most abundant in June (FARRIS, 1961).

EASTROPAC expedition survey cruises.

We wish now to turn our attention to the EASTROPAC Expedition cruises. Information concerning the kinds and relative abundance of the fish larvae taken on the first and second multivessel EASTROPAC surveys, spaced 6 months apart during 1967, have been published (AHLSTROM, 1971, 1972). EASTROPAC is an acronym for « eastern tropical Pacific ». The EASTROPAC area was a sizable portion of the eastern tropical Pacific, lying between 20° N and 20° S latitude and offshore to 126° W longitude on ETP I, and to 119° W longitude on ETP II. As stated in the introduction to the paper dealing with the kinds and abundance of fish larvae on ETP I, the task was undertaken to demonstrate the value of identifying all elements of the larval fish fauna of tropical regions rather than restricting interest to a few kinds such as scombrids or billfishes.

The first thing that one learns is that most of the larvae one encounters in offshore oceanic areas are either myctophids or sternoptychids. Myctophid larvae make up approximately 50 %

of the larvae obtained on EASTROPAC cruises, and sternoptychids, under which we include gonostomatids, over 25 %. Bathylagid larvae made up about 5 %. Only a few families of perciform fishes have been able to make a living in the open ocean, but these include the important scombrids and istiophorids, as well as gempylids, trichiurids, coryphaenids, bramids, nomeids, tetragonurids, and chiasmodontids. Most candidates for commercial exploitation are in this group.

A surprising fact about the EASTROPAC collections was that more larvae per standard haul were obtained in the tropics than in the CalCOFI area.

Another surprising fact was that two kinds of larvae dominated most collections. The most abundant larvae in both EASTROPAC I and EASTROPAC II was that of the myctophid, *Diogenichthys laternatus*. This species contributed 26.6 % of the total fish larvae on ETP I and 38.1 % of the larvae on ETP II, and this despite the fact that it did not occur in offshore collections made in the central water mass of the South Pacific. This can readily be seen in its distribution on ETP I (AHLSTROM, 1971). *D. laternatus* is one of the smaller species of myctophids, measuring only 20 to 30 mm SL as adults, hence its biomass undoubtedly is not nearly as large as its larval abundance would indicate.

The other abundant category is that of the sternoptychid *Vinciguerria* spp. Two species are involved here, *Vinciguerria lucetia*, the dominant form, which is replaced offshore and in central water masses by *Vinciguerria nimbaria*. Larvae of these two species combined made up 19.7 % of the larvae obtained on ETP I and 18.0 % of the larvae on ETP II.

These two categories of larvae are about as dominant in the eastern tropical Pacific as are larvae of anchovy and hake in the California Current region.

The two multivessel eastern tropical Pacific cruises (ETP I and ETP II), when used in conjunction with four monitoring cruises, gave bimonthly coverage of a sizable area in the eastern tropical Pacific during a 1-year period (AHLSTROM, 1972). This monitoring area was located between longitudes 119° to 98° W and latitudes 20° N to 3° S. Essentially the same kinds of fish larvae were taken on each of the six coverages and for most species the range in relative abundance during the annual cycle was 3x or less. This finding has two implications. For most tropical species, spawning occurs throughout the year. We question whether individual fish spawn over such an extended period, rather different segments of the population probably reach maturity at different periods - presumably in relation to the time they were originally spawned. The other implication is that only comparatively little more was learned about the fish resources from six monitoring cruises than could have been deduced for the monitoring area from any one of the monitoring cruises. We have repeated the word monitoring cruises, which were basically offshore oceanic cruises, inasmuch as more marked seasonal differences were found in coastal areas for a moderate number of species as between ETP I and ETP II.

Characters used in identification of early life history stages.

Although the taxonomy of fishes has largely been based on characters of the adults, it has become increasingly obvious that characters of the juveniles, larvae, and eggs are important and sometimes essential in identifying and establishing relationships among taxa. Life history series are established by one of two techniques. The investigator can start with fertilized eggs from identified parents and rear these through the various early life history stages, embryonic and larval through to juvenile. This, of course, is the preferred technique. For the majority of fishes taken in plankton collections as eggs or larvae, it is necessary to establish life history series by tying larval series to juveniles or adults, primarily through meristic characters, but also using a variety of characters - osteological, morphometric, pigment patterns, etc.

The ichthyoplanktonologist has to be thoroughly acquainted with the adult taxonomy of the fishes he may encounter in his hauls. Inasmuch as meristic characters are his primary tools, he needs to know these in as much detail as is practical for each group of fishes. These include counts of all fins, vertebral counts divided into precaudal and caudal groups, branchiostegal ray counts, gill raker counts. For some fishes, it may be necessary to know the arrangement of dorsal and anal fin pterygiophores in relation to neural and haemal spines, the

number and arrangement of predorsal bones, and the exact composition of the caudal fin complex (POTTHOFF, 1974, 1975 ; AHLSTROM, BUTLER and SUMIDA, 1976), etc.

We hardly need point out that such detailed meristics are seldom available for any group of fishes and that the taxonomist working on larval stages has to set about getting his own sets of data. Fortunately, through the use of two techniques, clearing and staining of specimens and the use of radiographs, it is possible to not only obtain exact counts of meristic characters, but also osteological features, such as arrangements of pterygiophores, details of the caudal fin supporting bones, etc.

We have been giving concentrated courses on the identification of fish eggs and larvae during the past 6 years, and one of the by-products of this has been the challenge to assemble characters of both adults and larvae that will permit the worker to assign specimens to order or suborder, as the first step in indentification. Such characters are presented for eight orders and two suborders in tables 2 to 4. This is by no means a comprehensive listing of such characters, as we have not included such counts as branchiostegal rays and gill rakers, or dealt with some of the characters afforded by teeth. Pigmentation is too variable among species within each order to be a useful character in these summary tables, but pigment patterns provide essential characters for identification to the genus or species level. Meristic characters are given more emphasis than morphometric characters because complete counts for most structures are obtained in the larval stage, whereas body shape, while sometimes helpful, can change markedly between the larval and later life stages.

The fins that are of prime use in identification to the ordinal or subordinal level are the caudal and ventral (pelvic) fins. All fins are useful in identification to genera and species within families.

The pectoral fins, although the first to form as larval fins, are often the last to form rays ; pectoral rays form only at metamorphosis in several orders. We consider time of formation of P rays to be an important ordinal character.

The ventral fins are as important with regard to their placement on the body (i.e., whether abdominal, thoracic, or jugular) as for their meristics. The stabilization of the ventral fin counts to one spine and five rays found in most perciform fishes and many scorpaeniform fishes is also an important character.

Whether the dorsal and anal fins are made up of rays only, or have both spines and rays are important characters for identification to the ordinal level. Also important is whether the terminal ray in the dorsal and anal fins is bifurcate to its base. One of the interesting larval characters related to the dorsal fin is the development of one to several elongated anterior rays in the dorsal in those fishes having only rays in their fins (for example, trachipteroid, many pleuronectiform fishes, etc.) or one to several elongated spines in the first dorsal of fishes having spines and rays (for example, melamphaids, scombroids, serranids, etc.). The elongated rays can be quite long and are sometimes highly ornamented. When these occur they constitute excellent characters for placing larvae in families or subfamilies.

We have found the caudal fin and its supporting bones to have the most decisively useful set of characters for identifying larvae to order, suborder and often to family.

The larval fish taxonomist is very aware of the caudal fin for another reason ; the formation of the caudal fin has an effect upon measurements of larval length. The anlage of the caudal fin forms under the notochord, a short distance before its tip. The principal caudal rays and their supporting bones for both lobes are laid down ventrally and then brought into their terminal position by the upward flexing of the posterior portion of the notochord. The act of flexion of the notochord may even shorten body length somewhat. On some kinds of larvae, the posterior tip of the notochord can extend for a millimeter or so beyond the outer margin of the hypural bones even after these become terminal in position, further changing the body length determination. Hence, larval development falls naturally into three substages based on C fin formation : preflexion, flexion and postflexion. The measurement of body length made before flexion, from tip of snout to end of notochord, is termed notochord length (NL) to distinguish it from standard length (SL), the measurement made after the caudal fin has become terminal. The latter is the measurement from the tip of the snout to the posterior margin of the hypural bones,

	Clupeiformes	Argentinoidei	Stomiatoidei	Anguilliformes	Gadiformes
Predominantly pelagic eggs	Yes (sometimes demersal)	Yes	Yes	Yes	Yes
Egg shape	Round Oval (Engraulidae)	Round	Round	Round	Round
Chorion	Smooth	Usually ornamented (Pustulate)	Usually smooth, (hexagonal (facets - *Maurolicus*) sometimes double (example : *Stomias, Chauliodus*)	Smooth	Usually smooth, hexagonal pattern (macrurids)
Yolk	Segmented	Segmented	Segmented	Segmented	Homogeneous
Perivitelline space	Various, wide to narrow	Narrow	Various, wide to narrow	Wide	Narrow
Oil globules	1 or 0	1 to numerous	0 or 1	0, 1 or more	0, 1

	Pleuronecti-formes	Myctophiformes	Beryciformes	Perciformes	Scorpaeniformes
Predominantly pelagic eggs	Yes (seldom demersal)	Yes	Yes	Various, many pelagic, many demersal	Seldom pelagic, (predominantly demersal or ovoviviparous)
Egg shape	Round	Round	Round	Round (mostly), spindle-shaped	Round
Chorion	Usually smooth, hexagonal pattern on *Pleuronichthys*	Usually smooth, hexagonal pattern (Synodontidae)	Smooth	Usually smooth	Smooth
Yolk	Homogeneous	Segmented or homogeneous	Homogeneous	Homogeneous can be secondarily segmented)	Homogeneous
Perivitelline space	Usually narrow (wide in 1 genus)	Narrow	Narrow	Narrow	Narrow
Oil globules	0, 1 or many	0, 1	1	0, 1 or more	1 or many

TABL. 2. — *Characters of pelagic eggs that aid in identification to order or suborder.*

	Clupeiformes	Argentinoidei	Stomiatoidei	Anguilliformes	Gadiformes
Larvae					
Predominant body shape	Elongate, slender	Elongate, slender	Elongate, slender	Leptocephalus	Various, elongate to deep-bodied
Snout to anus length	65-95 %SL	70-90 %SL	30-95 %SL (usually long)	40-95 %SL	Usually < 50 % SL
Character of gut	Straight	Straight	Straight	Straight or looped	Usually coiled
Trailing gut	Not trailing	Not trailing	Often trailing, sometimes markedly	Seldom trailing, (markedly trailing on some congrids)	Not trailing
Number of vertebrae	ca. 40 to 60	ca. 40 to 85	ca. 30 to 100+	68 to 400+ (most 100 to 250)	ca. 40 to many (Macruridae)
Larval stage characters					
Larval eyes	ca. Round	Round or narrowed, sometimes stalked	Round to markedly narrowed (stalked in *Idiacanthus*)	Round or moderately narrowed (telescopic : 2 families) choroid tissue under eye (sev. families)	ca. Round
Larval head spination	None	None	None	Usually none	Usually none
Early forming fin rays or spines (often ornate)	No	No	Occasionally (P in *Ichthyococcus*)	No	V fins (sometimes)
Transformation stage	Marked D, A & V fins move, anchovy snout forms	Marked	Marked, photophore formation can be prolonged	Marked	Gradual
Early juvenile stage (prejuvenile of Hubbs, 1958)	No	No	No	No	No

TABL. 3. — *Characters of pelagic early life history stages*

	Pleuronecti-formes	Myctophiformes	Beryciformes	Perciformes	Scorpaeniformes
Larvae Predominant body shape	Various markedly compressed	Various often elongate	Slender to stubby	Various usually stubby	Various usually stubby
Snout to anus length	Usually < 40 %SL	ca. 40-70 %SL	ca. 30-60 %SL	Various, 20-60 % SL	ca. 35-60 % SL
Character of gut	Coiled	Straight, variously shaped	Coiled	Various, usually coiled	Coiled
Trailing gut	Not trailing, but gut can be distended from body	Seldom trailing, reverse can apply gut gradually increases in relative length on larvae	Not trailing	Not trailing	Not trailing
Number of vertebrae	25 to 65	Myctophids 28 to 45, others 29 to 121	Usually 23 to 33	ca. 20 to 100+, often 24 to 28	ca. 25 to 65
Larval stage characters Larval eyes	Round	Round to markedly narrowed ; often choroid tissue under eye, infreq. stalked	ca. Round	Usually round, can be narrowed with choroid tissue	ca. Round
Larval head spination	Frequently-various, useful in ident.	Various - none to markedly heavy	Various - none to markedly heavy	Various - none to markedly heavy	Usually - useful in ident.
Early forming fin rays or spines (often ornate)	Often : 1 to 12 ant. D rays Sometimes : 2 or 3 V rays	Occasionally P fin rays	Often V & ant. D	Sometimes 1 or more 1st D sp. and V sp. & rays	No, but P fin can be quite large
Transformation stage	Marked (1 eye shifts to right or left)	Various, often marked, sometimes delayed sometimes prolonged	Usually gradual	Usually gradual	Gradual
Early juvenile stage (prejuvenile of Hubbs, 1958)	No, but larval stage can be markedly prolonged	In some forms (ex. Macristiella stage)	Sometimes marked (ex. Holocentrids)	Sometimes (in var. families)	Pelagic juvenile stage (ex. some scorpaenids)

that aid in identification to order or suborder.

	Clupeiformes	Argentinoidei	Stomiatoidei	Anguilliformes	Gadiformes
Type of fin elements	Rays	Rays	Rays	Rays	Rays
Pectoral rays* Sequence of formation	Late	Late	Late	Late	Sometimes late
Ventral rays Sequence of formation	Late	Rel. late	Rel. late	Absent	Often early
Position on body	Abdominal	Abdominal	Abdominal	Absent	Thoracic or jug.
Formula	Var. usually 7-10	Var. usually 8-12	Var. usually 5-8 (*Bathophilus* 4-26)	Absent	Various 2-8
Dorsal fin(s)	1 fin	1 fin	1 fin	1 fin	1 to 3 fins
Anal fin	1 fin, 0 sp.	1 fin, 0 sp.	1 fin, 0 sp.	1 fin, 0 sp.	1 or 2 fins, 0 sp.
D & A terminal ray-bifurcate	+	+	+	No	No
Adipose fin	No	Usually	Often	No	No
Caudal fin type	Homocercal	Homocercal	Homocercal	Reduced homo. prob.	Gadoid type ; few rays on hypurals, br. rays dorsally
Principal C. rays	19	19	19	Reduced number, usually 5 to 11	Various numbers of branched rays
Maximum no. hypurals (including parhypural)	4 + 3	4 + 3	4 + 3	?	3 + 3 (usually 1 + 2)
Maximum no. epurals	3	3	3	?	2
No. ural centra (see text)	3, 2, 1 (occasionally 4)	3, 2 or 1	2 or 1	2	2
Neural sp. on vertebra adj. to ural (pu2 of Monod, 1968)	Normal	Normal	Normal	Normal	Normal

TABL. 4. — *Characters of fins that aid in*

	Pleuronecti-formes	Myctophiformes	Beryciformes	Perciformes	Scorpaeniformes
Type of fin elements	Rays	Rays	Spines & rays	Spines & rays	Spines & rays
Pectoral rays* Sequence of formation	Late	Various ; often early	Not late	Not late	Not late
Ventral fins Sequence of formation	Sometimes early	Early to late	Often early	Various ; sometimes early	Intermediate
Position on body	Thoracic to jugular	Abdominal	Various Thor.-abd.-jug.	Usually thoracic, sometimes abd. or jug.	Thoracic
Formula	6/6, 5/5, 0/4 or various	Various, usually 8-10	Not 1,5 various, often 1,6, 1,7	1,5 or fewer	1,5 or fewer
Dorsal fin(s)	1 fin	1 fin	1 or 2 fins	1 or 2 fins	1 or 2 fins
Anal fin	1 fin, 0 sp.	1 fin, 0 sp.	1 fin, 1 to 4 sp. usually	1 fin, 1 to 3 sp. usually	1 fin, 0 to 3 sp.
D & A terminal ray-bifurcate	No	+	+	+, sometimes -	+, sometimes —
Adipose fin	No	Usually present	No	No	No
Caudal fin type	Mod. homocercal	Homocercal	Homocercal	Homocercal (sometimes mod.)	Mod. homocercal
Principal C. rays	Var. no. br. rays Var. no. total rays	19	19	17 (sometimes fewer)	Variable, less than 17
Maximum no. hypurals (including parhypural)	3 + 3	4 + 3	4 + 3	3 + 3	3 + 3
Maximum no. epurals	2	3	3	3	3
No. ural centra (see text)	1	2 or 1	2 or 1	1	1
Neural sp. on vertebra adj. to ural (pu2 of Monod, 1968)	Normal	Reduced or lacking	Reduced or lacking	Lacking (some exceptions)	Various, normal reduced or lacking

(*) (Larval pectoral fins always early forming).

identification of larvae to order or suborder.

measured at the junction of the two lobes of the caudal fin. The difference (loss) in body length determinations, as between NL and SL, usually amount to 0.5 - 1.0 mm, but can be as much as 2 mm.

The homocercal caudal fin is without doubt the most conservative meristic structure developed on teleost fishes. This applies particularly to the standardization of principal caudal rays at 19 total (10 in upper lobe, 9 in lower lobe), a count applicable to 5 of the orders and suborders included in our several tables. An almost equally conservative stabilization is that of 17 principal rays (9 in upper lobe, 8 in lower lobe) found in numerous families of perciform fishes.

The homocercal caudal fin always develops in approximately the same way. As already mentioned, the principal rays and their supporting bones are laid down under the notochord, hence are hypaxial in origin. They become terminal through flexion of the posterior portion of the notochord. The principal rays of the upper lobe are supported exclusively by superior hypural bones, the principal rays of the lower lobe are supported by inferior hypural bones (we include the parhypural among the inferior hypural bones). When the rays are laid down, the first ones to ossify are always at the junction of the two lobes, hence the anteriormost ray of the upper lobe forms simultaneously with the posteriormost ray of the lower lobe. Addition of rays to the upper lobe occurs progressively posteriad, addition of rays to the lower lobe occurs progressively anteriad, rays in the two lobes are usually added 1 for 1. The complete group of principal rays are usually laid down during flexion.

Secondary or procurrent caudal rays are formed gradually and are often the last to complete formation among the various fins. The dorsal complement of secondary C rays form epaxial to the vertebral skeleton, are laid down progressively anteriad, and are supported by epurals and often by 1 to several neural spines as well. The ventral component also forms progressively anteriad, beginning adjacent to the terminal ray of the lower lobe ; these secondary C rays are supported exclusively by haemal spines.

Before leaving the characters that aid in identifying early life history stages, we wish to emphasize one set of characters that are uniquely larval. These have to do with the recapitulations during larval development of some structural features possessed ancestrally. Ontogeny does recapitulate phylogeny in some characters, the majority of which are associated with the development of the caudal fin and its supporting bones. The fusions among ural bones that are most readily seen during larval development are those between ural centra and those between hypural bones. As an example, the urostyle ossifies initially as two centra in myctophids, a posterior centrum associated with the superior hypurals and an anterior centrum associated with the inferior hypurals. These two centra fuse into a single centrum before the end of the larval period in most myctophids, but they can be retained as separate centra into the early juvenile stage of some species (MOSER and AHLSTROM, 1970). All adult myctophids have only a single ural centrum. Many myctophids retain the unreduced complement of 4 + 3 hypurals as adults, whereas others start with this complement and then reduce the number by fusion between adjacent hypurals during larval development. The ultimate reduction of hypurals in myctophids results in the fusion of all superior hypurals into a single plate and all inferior hypurals into a single plate, a condition found in *Centrobranchus choerocephalus* and *Notolychnus valdiviae* (MOSER and AHLSTROM, 1970). BERRY (1964) documented another type of recapitulation found in the family Notosudidae-larvae developed teeth on the maxillary, but then lost these as the premaxillary developed and excluded the maxillary from the gape. Adult myctophiform fishes never have teeth on the maxillary.

Role of larval stages in systematic investigations.

As we have pointed out in the previous section, there are many larval characters that can aid significantly in differentiating taxa and in defining evolutionary lineages within a family or order. Until recently, most systematic ichthyologists have paid scant attention to larval characters ; partly, we believe, because they were not aware of their potential. Several recent contributions

make extensive use of larval characters in critical reviews of families, i.e., R.K. JOHNSON (1974) in his comprehensive revision of the Scopelarchidae and BERTELSEN, KREFFT and MARSHALL (1976) in their equally comprehensive revision of the family Notosudidae. In several of our recent papers, we have emphasized the value of larval characters in the taxonomy and phylogeny of fishes of the family Myctophidae (MOSER and AHLSTROM, 1970, 1972 and 1974). In a study we are now making on life histories of flatfishes, we find that larval characters are among the more useful in showing relationships among genera and families in this group as well.

Larvae in a number of families of the order Myctophiformes have differentiated to a remarkable degree, allowing ready identification to species and clear insights into evolutionary relationships. The family which has been most studied is the Myctophidae, known commonly as the lanternfishes. With about 250 species and 30 genera, this is the most widespread and speciose family of midwater fishes. In any oceanic plankton tow you can expect to find that about half of the total fish larvae are lanternfishes. Thus, the taxonomy of lanternfish larvae is of great importance.

We have been studying myctophid larvae on a world-wide basis and can now identify 28 of the 30 genera and about half the species in the family. Lanternfish larvae have characters of morphology and pigment that allow ready identification to subfamily, genus, and species. A brief review of these characters will show that lanternfishes are perhaps the most taxonomically tractable of all groups of fish larvae.

Lanternfish larvae fall naturally into two groups on the basis of eye shape, those with narrow elliptical eyes and those with round eyes. These groups correspond nearly perfectly with the two subfamilies established on the basis of adult morphology, meristics, and photophore pattern. Larvae of the subfamily Myctophinae have elliptical eyes, borne on stalks in some species, and those of the Lampanyctinae have rounded eyes.

Within the two subfamilies, larval evolution has proceeded in different directions. In the Myctophinae there is great morphological diversity, body form varying from thin and elongate to stubby and rounded and even some species having deep blade-shaped bodies with voluminous finfolds. Melanophore pattern is highly diverse but a recurrent pattern in many genera is the presence of lateral series of pigment spots along the gut. Photophores, other than the middle branchiostegal pair (Br_2), appear in larval stages of only three genera of the subfamily.

In the subfamily Lampanyctinae, larval body form is conservative. There are no highly attenuate or blade-shaped forms although stubby and rotund species are found in some genera. A recurrent kind of pigmentation in this subfamily is the presence of series of melanophores along the dorsal and/or ventral midline. Also, typical of lampanyctine larvae is the development of photophores, often in early larval stages. These appear in at least 10 of the 19 genera. Generally it is the same group of photophores which develop, although they form in an order unique for each genus. Knowledge of these melanophore and photophore characters is essential for the identification of lampanyctine larvae.

In a series of papers on larval myctophids, we have shown that each species may be identified by a unique character or set of characters, that each genus has an unmistakable morph, and that subgeneric relationships often are more apparent in the larvae than in adults. This can be demonstrated by looking at the genus *Hygophum* of the subfamily Myctophinae. All species of *Hygophum* have a characteristic paired series of melanistic dashes on the underside of the throat, develop only the Br_2 photophore pair late in the larval period, have moderate sized pectoral fins of the same basic shape, and form the dorsal fin late in the larval period. These characters allow a specimen of *Hygophum* to be identified from any plankton sample from any region of the world ocean.

There are striking larval characters which separate the different species into three distinct subgeneric groups. *Hygophum reinhardti* and its close relative, *H. atratum*, are attenuate forms with elongate intestines, linear series of melanophores on the gut and body and stalked narrow eyes, each subtended by a conical mass of choroid tissue.

The second group of species, typified by *H. proximum*, has a moderate body form, a sigmoid gut and wider elliptical unstalked eyes that have prominent choroid tissue. The species can be separated readily by pigment pattern and subtle morphological differences.

In the third group of species, typified by *H. macrochir*, the body is deeper, the gut has a narrow anterior part and a wide posterior section, and the eyes are wider and lack choroid tissue. The species of this group can be separated on the basis of relative body depth and pigmentation. The relationships between the species of *Hygophum* are not apparent from studying the adults and, in fact, the only revision of the genus sheds no light on this important subject. The genus *Hygophum*, therefore, affords an excellent example of how detailed analysis of larval characters not only provides means of identifying species, but also allows insights into subgeneric relationships within an otherwise confusing group.

Just as larval characters have been useful in defining relationships at the subgeneric level, we have used them extensively in working out phylogenetic affinities among genera. Unfortunately, time does not permit a discussion of this. Finally, it should be mentioned that we have been able to postulate a mechanism for the evolution of photophore pattern in myctophids based on the ontogenetic sequence of photophore development in larvae (MOSER and AHLSTROM, 1972).

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