

Berichte aus dem Zentrum für Meeres- und Klimaforschung

Reihe Z: Interdisziplinäre Zentrumsberichte



Nr. 10

Synthesis and New Conception of North Sea Research (SYCON)

Working Group 8: Zooplankton

Heino Fock · Wulf Greve · Birke Heeren
Michael Krause · Gesche Winkler

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**Working Group 8:
Zooplankton**

Heino Fock · Wulf Greve · Birke Heeren
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Zentrum für Meeres- und Klimaforschung der Universität Hamburg
2001

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1. Introduction

Zooplankton is the sum of heterotrophic organisms in the pelagial zone which move more passively than actively and thus can be discriminated from the nekton which moves more actively and from the benthos that is stationary or reduced vertical mobility. Ecologically this discrimination creates conceptional boundaries which impede holistic research between functional groups which continually interact trophically and ontogenetically especially in a shelf sea like the North Sea. Not only the throughput of primary production from the phytoplankton through the six size classes of zooplankton (picozooplankton to megazooplankton) to the end-users (bacteria to fish, benthos and gelatinous zooplankton) is determined within the zooplankton; it also is the environment in which the year classes of many benthic species from various phyla and most fish species are being decided upon.

Further exchange between the benthos occurs in animal migrations of e.g. mysidacea and Cumacea with diurnal vertical migrations between the sub-systems. Many zooplankton species diurnally migrate between surface - and some hundred meter deep waters. They thereby may utilise shearing current systems for determining their distribution.

The reduction of the understanding of zooplankton to the transfer of primary production towards higher trophic levels does not embrace the richness of zooplankton ecology. The fact that historically this process has become the dominating paradigm may have caused the lack of success in developing reliable and operative predictive models for the population dynamics of zooplankton.

The zooplankton as the centrepiece, the „pivot“, of the marine ecosystem (Banse 1995) thus remains to be a scientific challenge for the years to come.

1.1 The history of zooplankton research

Um die verschiedene Ertragsfähigkeit der einzelnen Gebiete vergleichen zu können, ist es nöthig, so genau wie irgend möglich festzustellen, was und wieviel an kleineren Planktonorganismen in einem bestimmten Gebiet und zu bestimmter Zeit vorhanden ist. ... Alles (emphasis by H. Fock), ... muss der Art nach bestimmt werden. ...

Karl Brandt 1902

Karl Brandt made this statement at the beginning of a period of intensive quantitative research on marine plankton in the North Sea, at that time already set within the frames of the ICES convention and shared conjoint international investigations. Roughly 100 years have passed since then, and part of the history on the research of zooplankton and the state of the art has been worked up in the review of Fransz et al. (1991a). We say 'part', because the authors made some assumptions under which they conducted their review, which will be discussed later on. They focussed on omnivorous and herbivorous zooplankton, which means they focussed on copepods, which means they focussed on a handful of calanoid and cyclopoid species, only. This already marks a difference between the attitude of Brandt to analyse everything ('Alles') and the emphasis on a specific trophic guild in the most recent review on North Sea zooplankton. This emphasis on a small section within a large field of possible research topics probably indicates a general trend in development of North Sea zooplankton ecology, and is to some degree paralleled by the development for other regions albeit there the dualism of crustacean and gelatinous zooplankton was more pronounced (Seguin 1992). Hence, for the North Sea a branching or diversification in zooplankton investigations took place, of which some branches developed much better than others.

Consequently, zooplankton biology in total suffers from an inconsistent appearance and from all marine disciplines probably has endured the most shadowy existence during the last part of the 20th century. In spite of its recognised importance, it has not gained proportional effort compared to its enormous complexity as other fields of marine ecology such as fisheries research, phytoplankton and benthic ecology. Thus, the field of zooplankton ecology has not succeeded in a comparable way to provide answers for societal demands. A look upon the international standards and protocols for environmental surveillance may serve as an indicator for this feature: These guidelines often give a wide array of benthic and primary production reference data, birds to be monitored and data on total allowable catch for fishes, but no evidence that can be regarded as good or bad in zooplankton. The one exception from this rule can be seen in the inclusion of zooplankton monitoring in the HELCOM monitoring framework.

Why does zooplankton science endure this underrated existence? The key to this problem is the diversity of zooplankton, its wide range of taxonomical, functional, physiological and behavioural aspects as well as the complex interplay with hydrophysics and other biota. For instance zooplankton incorporates protozoans as well as metazoans, covers size classes from mixotrophic small-sized dinoflagellates to giant jellyfish (with all implications for the bodysize-water relationship, viz. Reynoldsnumber), and all taxonomic classes in the sea from simple structured coelenterates to juvenile vertebrates. The variety of species involved implies a similar variety of spatio-temporal scales and processes which are relevant for zooplankton ecology, from micro-structure analysis of turbulence to decadal variability of climate. Furthermore, zooplankton depicts a great diversity in life cycle strategies, with juveniles feeding on other resources than adults, preferring different habitats and environmental requirements.

This diversity of topics attracted a similar diversity of effort, splitting up the resources among very different fields of research. Or, as G. Fransz describes it (in Fransz et al. 1991a), "in a later stage (after 1925, H. F.) the interest in zooplankton diversified", branching into research on long-term time series, phytoplankton-copepod relationships, biochemistry and specific autecology (the famous work of Marshall & Orr 1955 on *Calanus finmarchicus*) and others.

Operating this wide field of research with relatively limited human resources, zooplankton research never reached the threshold of formulating strong holistic concepts on ecosystem dynamics on its own such as were developed in fisheries research and phytoplankton ecology, leading towards a predictable and better understanding of the system. Landry (1998) tagged two such major concepts which were able to influence the course of marine research for decades. The first one was the 'critical depth'-concept of phytoplankton development, first introduced by H. Gran in the 1930's and later by H. Sverdrup in 1953. The second one was the match-mismatch-hypothesis for the survival and recruitment of fish populations, prominently formulated by D. Cushing.

Research plans formulated in the light of these major theories treated zooplankton biology rather as a gap between them than an independent matter of subject¹. In narrowing this gap between these two diametrical milestones, scientific work intruded into zooplankton biology, with strong effects at the direct interfaces to the neighbouring fields of phytoplankton ecology (copepods eating phytoplankton) and fisheries (fish eating copepods), but becoming increasingly vague the more this research entered the heart of the zooplankton, the interactions within this numerous community, with its multitude of carnivorous and omnivorous species

¹ Examples to highlight this attitude are the titles of papers by W. Greve & T.R. Parsons (1977). Photosynthesis and fish production. Helgol. Wiss. Meeresunters. 30, 666-672 and of J.A. Runge (1988). Should we expect a relationship between primary production and fisheries? The role of copepod dynamics as a filter of trophic variability. Biology of Copepods. Boxshall, G.A. 167 (1988), 61-71., although the intentions of these papers actually are not to simplify zooplankton dynamics but to make the topic probably more appealing.

and the possible interactions between them. The lack of an independent major theory for marine zooplankton was partly concealed with concepts borrowed from limnetic ecology, e.g. the top-down vs. bottom-up approach to plankton ecology. However, the present state of the art reveals that a simple transduction of this concept into the marine environment is not meaningful due to the highly diversified and often inverse feeding relationships in marine zooplankton (e.g. Greve 1977). Results in zooplankton-fish relationships are often equivocal and also indicate the importance of atmospheric forcing and climate (Cushing 1995).

Marine zooplankton ecology was not always on the sidelines. At the beginning of the last century, when the first large plankton campaigns were conducted under the auspices of ICES, zooplankton was regarded as an integral part of the pelagic community, gaining equivalent reception compared to the other fields of marine research. This is proven by the above citation of Karl Brandt from 1902, describing a holistic research plan for all of the pelagic ecosystem components from the nutrients to the fishes, and secondly by the fact, that in the beginning phyto- and zooplankton investigations were carried out by the same investigators. A last reminiscence of this all-in-one expertise is probably preserved by the team running the CPR, the SAHFOS Continuous-Plankton-recorder-Survey, Plymouth. Hence, zooplankton is not a gap to be filled, but rather a 'connecting link' (Reeve 1988), for which understanding is essential for the understanding of the whole system as well as its basal and top members.

1.2 An age of new opportunities

At the start of the new century, probably a new era for marine research in general depending on the degree of commitment society spends to scientific topics that do not pay-off directly but in the long run, zooplankton research is able to throw off some chains that hampered its development in the past.

First, new technologies offer a promising variety of tools to address the very different questions yet insufficiently resolved. Research vessels, microscopes and nets marked the three methodological traits that determined scientific resolution in the past. Optico-acoustical devices, small recording units to be mounted on ships-of-opportunity, biochemical probes and computerised analysis and modelling broaden the palette of opportunities for analysis in fields that were yet secretive to science.

Second, re-analysis of existing knowledge by means of new tools such as meta-analysis (Mann 1990; Osenberg et al. 1999) can lead to new insights and concepts and provide ranges and threshold values for certain features relevant to decision making processes to environmental managing authorities.

Third, the opportunities to design experiments at different scales have improved parallel to the improvement of in situ capabilities and microsensors taking off the fetters from the simple 'copepods-eat-diatoms' logic. Stable isotope techniques, radiolabelling and fluorescent and biochemical tagging lead into a new world of diversification of energy flow in marine ecosystems.

Whereas the first aspect actually points at instrumental improvements, the last two aspects also involve the improvement of ecological theory in marine plankton research, for example the theory of predation in plankton and fisheries (Bax 1998). Already Brandt (1902) stresses the importance of predation as a major regulating force describing the results of a weir-experiment off Norway, where 50 fish prey items were eaten to the bone by predatory crustaceans. Further theory concerns the relationship between distribution ranges for populations and species areas as well as latitudinal gradients of diversity (e.g. presented by Sinclair 1988) or discussed as Rapoport's rule (Stevens 1989; Rohde et al. 1993). The role of evolutionary stable strategies for marine populations is discussed as the member-vagrant-hypothesis by Sinclair (1988) or as the life-cycle theory by Verity and Smetacek (Steidinger & Walker 1984).

The further development of theory for zooplankton also means to overcome some misperceptions which often hamper the development of new ideas. This probably begins with the choice of terms, i.e. plankton, which means 'those that are drifted by the sea'. However, we must concede that already Hardy (1956) introduced the concept of maintaining of the geographical position for certain zooplankton species. The mode is to take advantage of the different stratified currents in the sea by means of vertical migration. This strategy has now been intensively studied for the northern North Sea population of *Calanus finmarchicus* during TASC, the *Trans-Atlantic Study on Calanus*, which showed that overwintering individuals hibernate at 600 m depth at the shelf edge and rise up at spring time, sweeping into the North Sea by means of selected currents (e.g. Heath et al. 1997b). Basis work with similar results, however, has been done e.g. by Østvedt (1955), Marshall & Orr (1955), Vinogradov (1968), Krause (1978) and Krause & Radach (1989). Estuarine species as well can maintain their coastal position by occupying the estuarine circulation pattern. So, indeed zooplankton can play a very active part in its environment. Some further kind of misperception arose from the many feeding experiments in laboratory cultures, leading to the view of a diatom-feeding zooplankton community – presently, a rather omnivorous community has to be assumed (Reeve 1988). This discrepancy becomes evident at community level, when, though copepods constitute at times the major component of the plankton community and then also determine the utilisation of primary produced matter up to 70 %, on an annual basis this portion relatively decreases to 5 to 15 %, indicating a major transfer into the microbial loop or to the benthos (after Baars & Fransz 1984; Nielsen & Richardson 1989; Fransz et al. 1991a).

2. collection of the pertinent literature

As a basis, the inventory of present knowledge and critical assessment of the state of knowledge about the North Sea ecosystem strived for in SYCON require a thorough review of the relevant literature. The results of the literature survey on zooplankton are described in the following.

Up to now we have evaluated and classified almost 7800 publications relevant to zooplankton using bibliographical software (EndNote2). Although this is certainly not a complete survey, we interrupt it at this point to make an interim evaluation. Nevertheless, we estimate that we have documented about 75% of the existing publications, about half of which we possess in the form of reprints, copies or monographies. These papers have been studied and assigned key words. A further, large part of the registered publications were chosen according to the registrations from the ***Aquatic Science and Fisheries abstracts*** (ASFA). The ASFA's cover the entire spectrum of marine science and fisheries publications and the registrations include author, title, publication organ as well as the abstracts of the papers. In recent times the publications receive key words here as well. The ASFA's are available as monthly issues and, since 1978, on EDP media and can be viewed in specialised libraries.

About 20-30% of the publications registered by us were noted from literature lists of other publications. The choice of key words here could only be made from the citation and they were thus of a more general character. For example, if the investigated species were not named in the title they were not listed in the register of key words. These publications will be studied and given more detailed key words at a later date.

In the meantime, the key words used by us, including e.g. the names of species or the investigated marine areas, amount to well over one thousand. With these, it is possible to merge the papers using diverse selection criteria and thus to gain overviews of the literature on the respective topics. This is a prerequisite for a comprehensive stocktaking and assessment of the knowledge about the zooplankton in the North Sea.

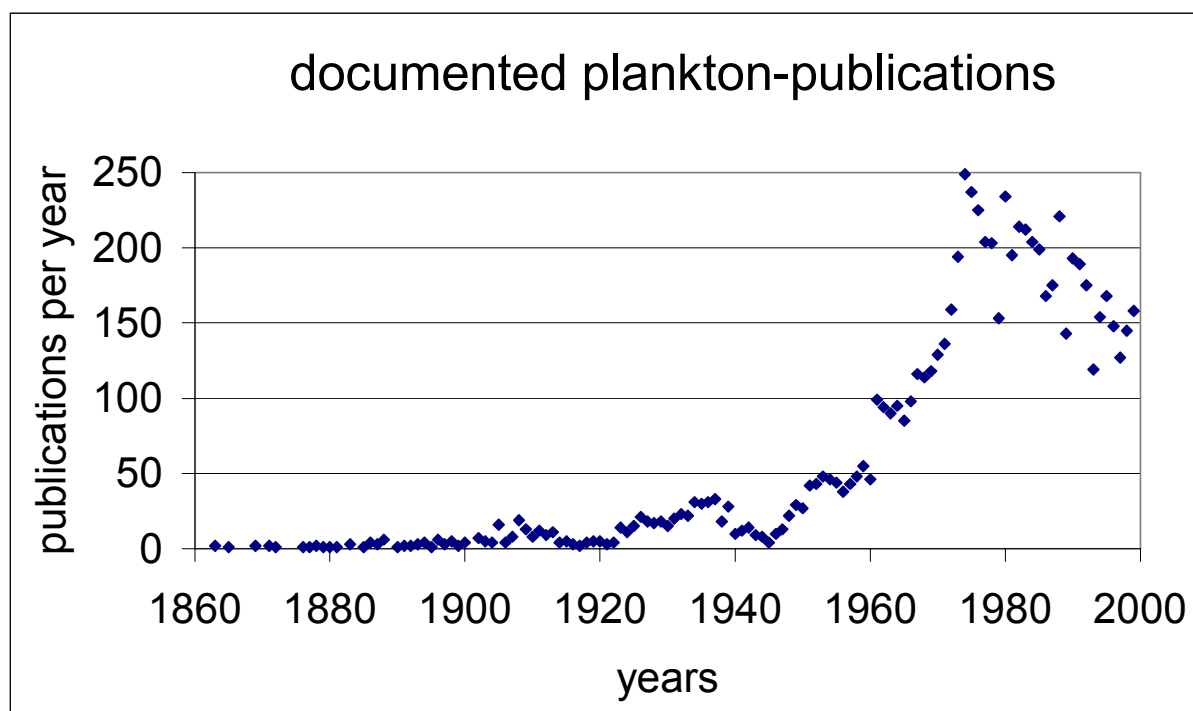


Fig. 1: Time-series of the registered zooplankton-relevant publications per year from 1860 to 1999.

The described literature file – which is still not completed – will be made available in the internet. So, it can be used by interested colleagues for literature searches. On the other hand, we hope in this way to be able to complete the file more quickly through information about still missing citations given us by users of our internet file.

A complete extraction of the literature relevant to plankton from the ***Aquatic Science and Fisheries Abstracts*** did not seem feasible to us. In addition to the fact that the publications registered in ASFA do not reach back far enough, this bibliography does not give all existing publications about a special subject if only because the key words used are not uniform for one focal point. Thus it is often difficult to filter out the needed literature completely. Therefore, ASFA could only be a supplementary means for us to gain a complete review of existing literature.

Fig. 1 shows the time series of plankton relevant publications which we have registered for each year since 1860. According to this, during the entire nineteenth century the number of publications each year remained at a very low level. In the first half of the twentieth century, the two World Wars each apparently prevented an increase in published papers. After the Second World War there was a rapid increase which reached a maximum in the midst of the 1970's (1974). Thereafter, a slight decrease in the number of publication can be noted. Although we still have not registered all publications, we can assume that the curve shown is fairly representative. During the various phases of our literature searches using random criteria, the development in time was always similar. We can conclude from this that the greatest proportion of knowledge at least about physiology and ecology of zooplankton originated in the past thirty to forty years.

In the first and second halves of the nineteenth century, emphasis was mainly placed on the collection, description and taxonomy of planktonic organisms, and this is reflected in the publications of that time. Later, particular organs and other body parts began to be investigated more with respect to structure and function. At the beginning of the twentieth century, attempts were already being made to quantify the occurrence of plankton organisms in various

number of documented plankton-publications according to sea areas			
North Sea	1293	Antarctic Ocean	204
German Bight	156	Pacific Ocean	480
Atlantic Ocean	1168	North Pacific	175
North Atlantic	875	Black Sea	79
eastern North Atlantic	373	Mediterranean Sea	176
western North Atlantic	297	coastal waters	406
northwestern European shelf sea	303	fjords	158
Norwegian Sea	115	estuaries	152
Baltic Sea	202	mesocosm	102
Arctic Ocean	473	freshwater	332

Tab. 1: number of documented plankton-relevant publications, subdivided according to sea-areas.

number of documented publications according to important key words	
key words	number of publications
methods	769
taxonomy, morphology, anatomy	727
model changes	363
abundance, occurrence, distribution	2750
horizontal distribution, geographical distribution	1193
vertical distribution	848
vertical migration	646
vertical flux, vertical transport, sedimentation	292
aggregation, marine snow	47
body length, body weight, body size, dry weight	454
chemism; chemical composition	457
grazing, feeding	1733
carnivorous feeding, predation	597
respiration	445
excretion, defaecation	298
production	1138
reproduction, egg production	450
growth	528
population dynamics	179
food web	453
microbial loop	137
pollution; eutrophication	460

Tab 2: Number of documented plankton-relevant publications, subdivided according to a range of important key-words.

number of documented publications according to coarse plankton groups									
taxon	total	abundance	chemism	feeding	respiration	excretion	growth	production	pop. dyn.
copepoda	2541	873	205	840	161	130	217	562	91
euphausiacea	495	217	75	82	33	21	38	45	13
coelenterata	375	138	23	156	25	19	33	34	14
ctenophora	146	49	12	81	17	9	13	14	9
protozoa	334	117	16	186	22	16	55	53	7
ciliata	192	75	11	117	8	2	36	35	4
meroplanktonic larvae	193	89	2	32	7	3	7	18	2
decapoda larvae	48	25	0	4	4	0	1	2	0
cirripedia larvae	43	19	2	12	1	1	1	2	0
bivalvia larvae	39	29	0	6	1	1	1	6	0
polychaeta larvae	27	21	0	7	0	1	1	6	0
echinodermata larvae	20	14	0	4	1	1	1	1	0
cyphonautes larvae	8	5	0	0	0	0	1	2	0
actinotrocha larvae	7	3	0	0	0	0	0	0	0
chaetognatha	193	108	25	46	16	9	15	19	5
cladocera	202	86	11	88	15	10	15	32	4
fish larvae	157	95	2	60	0	0	7	9	0
mysidacea	116	31	21	32	16	4	7	5	0
salpida	101	46	7	33	6	11	5	5	3
amphipoda	104	54	20	14	18	6	1	8	0
appendicularia	77	37	6	22	3	3	5	9	1
pteropoda	67	49	7	11	6	4	4	3	0
doliolida	30	15	2	9	2	2	1	0	0

Tab. 3: Number of documented plankton-relevant publications, subdivided into coarse zooplankton-taxa in connection with some important key-words.

species	total	abundance	chemism	feeding	respiration	excretion	growth	production	pop. dyn.
<i>Calanus finmarchicus</i>	502	262	52	120	20	20	43	130	19
<i>Calanus helgolandicus</i>	174	67	28	62	12	10	19	38	5
<i>Acartia clausi</i>	226	93	15	77	26	12	20	59	10
<i>Acartia tonsa</i>	193	41	12	95	15	17	23	66	14
<i>Acartia longiremis</i>	40	26	2	8	2	1	2	11	2
<i>Temora longicornis</i>	175	82	13	68	9	10	16	49	5
<i>Centropages typicus</i>	120	49	9	29	15	4	13	42	6
<i>Centropages hamatus</i>	104	53	3	32	7	1	6	30	7
<i>Pseudocalanus elongatus</i>	119	74	10	36	4	1	12	30	5
<i>Paracalanus parvus</i>	95	59	0	26	4	1	7	30	5
<i>Metridia lucens</i>	62	49	3	10	2	0	2	11	1
<i>Metridia longa</i>	53	30	10	9	9	6	5	7	2
<i>Eurytemora affinis</i>	68	20	4	21	1	1	6	26	6
<i>Microcalanus</i> spp.	31	28	2	6	1	0	1	7	1
<i>Oithona similis</i>	97	66	3	26	5	5	6	27	2
<i>Microsetella norvegica</i>	18	15	1	1	0	0	0	5	0
<i>Meganyctiphanes norvegica</i>	107	38	28	18	5	5	10	13	6
<i>Thysanoessa inermis</i>	43	30	8	7	1	1	6	12	5
<i>Evadne nordmanni</i>	19	16	1	4	0	0	0	3	1
<i>Podon leuckarti</i>	7	5	1	2	0	0	0	2	1
<i>Parathemisto abyssorum</i>	6	1	4	0	2	0	1	0	0
<i>Hyperia galba</i>	4	1	1	1	1	0	0	0	0
<i>Spiratella retroversa</i>	34	31	1	1	0	0	0	1	0
<i>Clione limacina</i>	29	23	1	3	2	1	1	0	0
<i>Sagitta elegans</i>	65	39	5	10	9	3	6	3	3
<i>Sagitta setosa</i>	33	23	1	5	1	1	5	2	0
<i>Oikopleura dioica</i>	25	17	2	5	0	0	3	7	1
<i>Fritillaria borealis</i>	10	10	1	0	0	0	0	1	0
<i>Pleurobrachia pileus</i>	30	9	3	15	5	1	0	2	1
<i>Aurelia aurita</i>	43	6	1	24	1	4	7	5	3
<i>Aglantha digitale</i>	23	17	4	1	3	1	1	3	0
<i>Salpa fusiformis</i>	31	20	1	7	0	2	0	0	0

Tab. 4: Number of documented plankton-relevant publikations, subdivided according to some important zooplankton species of the North Sea, connected with a range of key-words.

sea areas and to investigate different environmental factors as causes for the differences in spatial distribution. Since a major characteristic of planktonic organisms is their passive drift with the currents in the sea, the idea arose in the early years that plankton could be used as a tracer for the investigation of marine currents. That means that stock investigations of plankton were carried out on behalf of hydrographic research. As it became evident in the 1920's that there is a close connection between the accumulation of plankton and pelagic fish shoals, plankton inventories received great support also for commercial reasons. This culminated in the construction of the Hardy Plankton Recorder by the British marine biologist Sir A.C. Hardy. With the help of these sampling gears the Continuous Plankton Recorder surveys have been carried out in the North Sea and in the North Atlantic up to the present.

It was not until the past thirty or forty years that ecosystem research began to become more and more prominent. Hereby, the role of individual species or even entire organism groups is investigated with respect to the processes and fluxes of matter in the food web as well as the influence of abiotic and biotic environmental factors on marine ecosystems. Along with species inventories, the experimental determination of process rates, e.g. of feeding, respiration, excretion, growth and reproduction, have gained great significance, not least because these data are needed as dynamic factors for ecosystem modelling. In addition to this, of course up to now new species are still being found and described, particularly in remote marine areas.

Table 1 lists the number of documented publications according to the marine areas concerned. The main emphasis of our search was the North Sea (1293 publications) and the adjacent waters (1453 publications). We also found it pertinent to include publications from the Arctic (473 publications) and the Antarctic (204 publications), the western North Atlantic (297 publications), the Pacific (480 publications), the Mediterranean (176 publications) and the Black Sea (79 publications), since in these regions the same or nearly related species were treated or work was done on topics relevant to the North Sea. Some attention was also given to planktonic work being done in freshwater (332 publications), since it is here that often pioneer work with respect to physiological and ecological questions has been carried out. In addition, there has also been a great amount of experimental work done in the laboratory or in mesocosms. This is reflected in several thousand registered publications.

Table 2 lists the number of registered plankton relevant publications for a few important key words. From the listing it can be concluded that there is already a lot of knowledge about these points which it is necessary to analyse. For example, at least 2750 publications are concerned with the abundance and distribution of zooplankton stocks. There are 646 publications treating the phenomenon vertical migration, alone or together with other aspects. For the key words grazing or feeding there exist at least 1733 publications; for respiration 445, for excretion 298, for total production 1138 and for reproduction alone 450. In 363 publications there were approaches to mathematical modelling of various developments or processes.

Table 3 shows the number of publications classified according to rough categories of zooplankton which are connected by a few important key words. Here it becomes evident that the individual taxa have apparently been investigated with differing intensity. The most publications are concerned with the species rich Copepoda, which are the most important mass organisms in the zooplankton in practically all marine areas. Here, we registered 2541 publications. Second place with 495 papers was taken by the Euphausiacea, which enjoyed a certain degree of interest with respect to fisheries under the name „krill“. 375 publications were registered for the gelatinous Coelenterata (Medusa; Ctenophora). Further gelatinous groups are the Chaetognatha (193 publications), the Appendicularia (77 publications) the Salpida (101 publications) and the Doliolida (30 publications). Investigations on meroplanktonic larvae, to which the Cirripedia-, Echinodermata-, Gastropoda-, Polychaeta-, Decapoda-, Actinotrocha- and Cyphonautes-larvae belong, comprised 193 publications of the literature surveyed by us. These plankton groups, in contrast to the Copepoda or the Euphausiacea, are relatively hard to handle, particularly in experimental investigations, since in the case of meroplankton they are small and fragile and only available for a relatively short time and in the case of gelatinous plankton they have a soft structure which can be easily damaged. The one-

celled zooplankton, the *Protozoa* (ciliates, heterotrophic dinoflagellates etc.) also belong to the relatively seldom investigated groups, with 334 publications found by us.

Table 4 give the total number of publications found for some of the most important North Sea species as well as connections of the species to important key words. It becomes evident that most of the investigations are concerned with the typical copepods of the North Sea. The large *Calanus finmarchicus*, dominating the zooplankton of the central and northern North Sea in summer is, with 502 publications, the most investigated species of all. Further copepods of the oceanically influenced North Sea are *Centropages typicus* with 120 publications, *Metridia lucens* with 62 publications and *Metridia longa* with 53 publications. Contrary to this there are only 14 publications about the small copepod *Microcalanus pusillus*, a species which forms large stocks in the deeper water of the northern North Sea. This might be due to the small size of this organism and its occurrence in deeper water layers. Among the smaller copepods dominating in the more shallow southern North Sea are the species *Acartia clausi* (226 publications) and *Temora longicornis* (175 species). Further copepods occurring particularly in the central and southern North Sea are *Calanus helgolandicus* (174 publications), *Pseudocalanus elongatus* (119 publications), *Centropages hamatus* (104 publications), *Oithona similis* (97 publications) and *Paracalanus parvus* (95 publications). The copepods *Acartia tonsa* (193 publications) and *Eurytemora affinis* (68 publications) are more estuarine forms. Examples for Euphausiaceae in the northern North Sea are *Meganyctiphanes norvegica* (107 publications) and *Thysanoessa inermis* (43 publications). The most important Chaetognaths of the North Sea are *Sagitta elegans* (65 publications) and *Sagitta setosa* (33 publications). Both species are indicators for different water masses, since *Sagitta elegans* prefers the Atlantic-influenced water of the North Sea, while *Sagitta setosa* dominates in the continent-influenced southern North Sea. The pteropods *Spiratella retroversa* (34 publications) and the carnivore *Clione limacina* (29 publications), which have a predator-prey relationship, are also indicative of an Atlantic influence in the northern North Sea. Representatives of the gelatinous zooplankton are the coelenterates *Aglantha digitale* (23 publications) and *Pleurobrachia pileus* (30 publications) as well as the tunicates *Oikopleura dioica* (25 publications) and *Salpa fusiformis* (31 publications). The 202 publications about cladocerans registered by us (Table 3) are predominantly from limnic areas, where *Daphnia spp.* is one of the most important organisms in the zooplankton studied in many different respects. The most important cladocerans of the North Sea, namely *Evadne nordmanni* (19 publications) and *Podon leuckarti* (7 publications) are only represented by a few investigations.

Certainly, the numbers of publications listed here must be extended, since, as already mentioned above, the registration work on the publications has not yet been concluded and the fine classification according to key words is not sufficient for a number of publications. Nevertheless, at this stage of our literature collection we can already state that the often articulated demand in expert circles for investigations of key species, i.e. of species which play a major role in fluxes of matter in the ecosystem, should begin with a thorough evaluation of existing literature. Here, particularly with respect to the important copepods of the North Sea, there exists a vast literature. For the species other than copepods it can be assumed that there are gaps in knowledge, but these can only be made evident after a profound study of the literature. Unfortunately, a thorough analysis of the literature in this respect could not be carried out within the scope of the SYCON project.

The publications can be roughly sorted into two large categories: the first consists of field investigations, usually aboard research vessels where observations and measurements can be made *in situ*. The second consists of experimental investigations carried out in mesocosms or in the laboratory. With these it is attempted to study a broad spectrum of questions which cannot or can only with great difficulty be tackled at sea. These include e.g. the determination of process data for feeding, respiration, excretion, egg production and growth.

Stock inventories: Up to now, we have collected approximately 1300 publications about stock inventories in the North Sea and adjacent marine areas. Generally it can be said of these that they are typically quite limited in time and space. Furthermore, they were carried out within the course of the past century using a great variety of collection devices (vertical nets, towed nets, water bottles, pumps etc.). The nets used had various forms and mesh widths and were often thus not suitable for collecting smaller species of the mesozooplankton or the younger stages of larger species

in a quantitative manner. The numerical data on the stock sizes are also extremely diverse in the literature, e.g. number per haul, per sample, per cubic meter or per square meter. This all allows for qualitative statements with regard to zooplankton distribution, but for absolute data about stock strength and its variability there is a lack of comparability. The knowledge gained from this is very fragmentary. For example, it is hardly possible to gain information about long-term variabilities or long-term trends, since the data were not gained with standardised methods.

In order to investigate area wide plankton distributions, British scientists under Sir A.C. Hardy tried to develop a standardised sampling method by constructing the Hardy Plankton Recorder. With this, it has been possible to monitor large scale distribution patterns of the species in time and in space up to the present over the entire North Sea and North Atlantic. However, there are a number of questions regarding the accuracy of this technique and its results must be considered critically (see chapter 3.1.1.).

Investigations of processes: The many publications about experiments deal, as mentioned above, primarily with the investigations of rates for processes such as feeding, respiration, excretion, egg production and growth. From the collected literature it is evident that there have been a great number of individual observations and measurements (see Tables 3 and 4). Accurate values for these rates are urgently needed as dynamic factors in mathematical models of processes and fluxes of matter. A first step to obtain them is the analysis and evaluation of data already given in the literature. This should be carried out as follows:

1. The relevant data for each of the investigated species and taxa must be filtered out of the literature and transformed into uniform dimensions.
2. The quality of these data must be tested. That means that it must be tested statistically whether they are comparable for the same experimental conditions.
3. It must be tested whether the data show trends under varying environmental conditions in the experiments (e.g. temperature, food supply).
4. Attempts must finally be made to draw general conclusions from the available data material, i.e. to formulate bulk parameters. This could lead, for example, to the result that the process rates for the crustacean plankton must not be related to species and their developmental stages but more easily to orders of magnitude of body size, which would mean a considerable simplification for mathematical modelling.

Only after such evaluation of existing literature deficits and gaps in knowledge will become recognisable, which can then be alleviated through new experiments and investigations. If, however, such an analysis of existing data shows that the individual measurement data are not comparable, then it is high time to work out standardised experimental designs for the individual parameters which can be employed in a world-wide manner.

In principle, it is not advisable to restrict such literature surveys only to the most recent publications and trends under the assumption that these have been adequately tested. Many new and old experimental results on specific complexes contradict each other in our opinion, and these contradictions do not seem to have been clarified sufficiently up to now. Some examples for that are given in the following:

- Up to now *Calanus finmarchicus* was considered to be the most important grazer of diatom stocks in the Arctic-boreal latitudes of the North Atlantic and in the northern North Sea. Although – as is the case for most pelagic copepods – a certain seasonal shift in its feeding basis is allowed for, spawning always extends into the spring diatom bloom. Various authors report even that the diatom bloom is needed as an initial trigger for the females to spawn. After the breakdown of the diatoms, at latest in July/August, the older, satiated developmental stages migrate into the deep water, where a ‘diapause’ occurs until the following spring. Not until the next spring diatom bloom do the organisms reappear in the surface layers in order to reprodu-

ce. Newer experimental results show, however, that in diatom cultures the reproduction rate of *Calanus finmarchicus* decreased and its mortality increased, while in dinoflagellate or other flagellate cultures the survival rate of eggs and the larval development was optimal. What is, then the main food which supports reproduction in *Calanus finmarchicus* (as well as in other zooplankton organisms)? This needs to be clarified.

- In many scientific publications attempts have been made to explain the phenomenon of diurnal and seasonal vertical migration of zooplankton and to identify causes and mechanisms. A satisfactory explanation still has not been found. The most widespread opinion is that the vertical shifts in the stocks occur due to a light-triggered alternation between active and passive phases of the organisms. During their active phases the animals swim upwards, against their negative buoyancy, and sink accordingly during their passive phases due to their relative density down into lower layers. More recent considerations based on limnological observations see the diurnal migrations a strategy which has been selected for in prey organisms through the feeding pressure of predators. At daybreak the animals disappear into deeper, darker water layers and can thus escape visual detection by predators. Still other observations contradict such theories. Then there are times in which the populations of different species do not migrate at all but remain in the mixed layer or in which they begin their vertical migrations a long time before the beginning of dawn. A small increase in salinity can cause a drastic reduction in diurnal migration amplitudes. Predators such as myctophids and many fish larvae migrate synchronously with the prey organisms.

On the basis of the evaluation of the data from FLEX'76 we could observe no migration whatsoever of zooplankton during the spring bloom. Not until about ten days after the breakdown of the algae bloom did stock-building organisms such as *Calanus finmarchicus*, *Pseudocalanus elongatus* and *Microcalanus pusillus* begin with pronounced diurnal vertical migrations, whereby the stocks remained at depth during daylight and came into the mixed layer at night. During a secondary (smaller) phytoplankton bloom thereafter, the migration amplitudes of all investigated copepods decreased again. Is then a scarcity of food the trigger for such migrations? The advantage would be that the remaining algal stocks could recover during daylight while the herbivorous zooplankton could reduce its metabolic rate at depth, which would be an economical way for the pelagic system to work. However, active, energy-consuming vertical migrations still do not seem plausible. It would be important to search for endogenous mechanisms and chemical processes which – perhaps with the help of density changes in the organisms – allow for vertical shifts in the stocks in such a way that the animals must not „climb the stairs“ but can rather „take the lift“. Research is needed on this point.

- Based on experimental investigations, many authors believe that faecal pellets of copepods sediment with extremely high sinking rates. The rates given in the literature range between 15 and 950 m/day. Hence, faecal pellets are attributed to have a considerable part in the downward transportation of matter, considering the fact that the daily defaecation rate of copepods can amount to almost 15% of their body weight under good feeding conditions. That means that during the productive seasons organic matter corresponding to 15% of the biomass of the copepod stocks would daily be sedimenting out of the euphotic zone into deeper water, which would imply a drastic nutrient depletion of the illuminated layer, particularly in the presence of a summer thermocline. The retention of the faecal pellets in the mixed layer would have the advantage for the pelagic system that here through remineralisation nutrients would be released again which could promote an extension of the algae bloom. This, in turn, would mean a longer food supply for the herbivorous zooplankton. In connection with the evaluation of the water bottle samples collected during FLEX '76, our working group consistently found a pronounced accumulation of copepod faeces in 0-30 m depth, that is, in the mixed layer. Even after *Calanus finmarchicus*, the most important producer of these organic particles, had begun its diurnal vertical migrations and was disappearing on a regular basis from this layer, this faeces maximum still did not disappear, which is an indication of a low sedimentation rate. More recent publications are somewhat more cautious about attributing high sedimentation rates for faecal pellets, but in our opinion the contradictory observations have still not been clarified sufficiently.

These examples show that well directed research is still needed in order to clarify aspects which are often discussed with contradictory opinions, suppositions and hypotheses in the literature.

3. Discussion of the knowledge about zooplankton

In the following chapters a detailed survey is given on the present state zooplanktology of the North Sea. An attempt is made to depict the state-of-the-art in the different areas of knowledge and at the same time to discuss contradictory opinions and hypotheses as well as to point out the gaps in knowledge.

3.1 Stocktaking and detailed assessment

3.1.1 Stock data

The marine zooplankton comprises a broad spectrum of species ranging from protozoans to vertebrates and including representatives from all animal phyla. Zooplankton includes microscopic ciliates measuring only a few micrometers as well as large medusae measuring more than a meter in diameter. The only thing they all have in common is their dependence on the currents. They are drifting organisms which occur in all parts of the open water. The total number of species of zooplankton in the North Sea is > 300 (de Wolf & Zijlstra 1988). A number of general publications on the North Sea and specialised reviews of the zooplankton have appeared, e.g. Salomons et al. (1988), Lozán et al. (1990), Fransz et al. (1991), van Beusekom & Diel-Christiansen (1994), Krause et al. (1995).

Methods

Generally, microzooplankton (20 – 200 μm) is sampled with water bottles. The protozoans (e.g. heterotrophic flagellates and dinoflagellates, ciliates) will be handled like phytoplankton by taking a subsample from the water bottle for carrying out taxonomic identification and counting after settlement of the fixed plankton in the chamber of a reverse microscope. The metazoans of the microzooplankton (e.g. copepod nauplii, meroplankton) are filtered from the water in the bottle through a fine gauze (e.g. 40 μm). The mesozooplankton (0.2-20 mm), which is composed mainly of older developmental stages of the copepods (copepodites and adults) as well as larger meroplanktonic organisms, is generally sampled using nets. The relative large mesh sizes (approximately 150-500 μm) necessary in order to avoid a pressure head at the net opening or clogging effects often prevent a quantitative sampling of smaller species or of the younger developmental stages of larger species. Makroplankton (2-20 cm) such as euphausiids, chaetognaths, fish larvae and medusae as well as the much larger megaplankton (e.g. large medusae) are sampled using special nets with the appropriate mesh sizes (approximately 500-1000 μm). For gelatinous zooplankton such as medusae, ctenophores and salps, special sampling technique is necessary to avoid damage to the individuals which would prevent identification. None of the individual traditional sampling gear types is capable of catching the entire zooplankton spektrum quantitatively. At most an overlap of the groups can be attained. Because of the tremendous effort involved in simultaneous sampling of the entire zooplankton spektrum using the necessary assortment of gear types and the great number of samples, assessments of entire zooplankton stocks are relatively seldom. Usually publications only deal with a part of the zooplankton.

A large number of publications (approximately 1300) exist on stock assessments of zooplankton in the North Sea and adjacent waters. Generally, however, these are characterised by strong limitations in space and time. The reasons for this are, among others, limitations in the capacity of research vessels and the very time-consuming effort necessary for taxonomic evaluation of the samples under the microscope.

In addition, the stock assessments which have been carried out over the past one hundred years have used a wide range of different sampling gears such as vertical nets, towed nets, water bott-

les, pumps etc. The nets used had different forms and mesh sizes (50-1000 μm). The units given in the literature for the stock sizes are also highly variable, e.g. number per haul, per sample, per cubic meter or per square meter. This allows for quantitative statements regarding zooplankton distribution, but comparability of the stock sizes found and their variability is difficult. To be sure, there have been periodic attempts to derive seasonal and annual variabilities and successions of plankton communities at sites or for regions using comparable collection methods. However, the data gained in this way cannot really be linked together in order to compare stock sizes or to derive long-term trends for the whole North Sea. Knowledge in these areas is thus fragmentary, because the investigations were usually not area wide nor were standardised collection methods used.

In order to investigate the large scale plankton distribution, British scientists led by Sir A.C. Hardy attempted to develop a standardised collection method by construction of the Hardy Plankton Recorder as early as the 1930's. The Continuous-Plankton-Recorder-Surveys (CPR-Surveys) are still being carried out with this method today over the entire North Sea and North Atlantic. The data gained are used to create maps of distribution patterns of species of the mesozooplankton as well as for diatoms, dinoflagellates and chlorophyll (colour index). Furthermore, annual fluctuations and long-term trends are investigated and related to various environmental parameters such as currents and climate change and mathematical modelling is carried out. The Continuous Plankton Recorder Surveys represent the only standardised collection method which has been used area wide for more than fifty years. There are, however, various aspects to be criticised with this method.

The sampling gear consists of a pointed, streamlined housing with fins and a solid depressor. When towed, the current drives a propeller which winds up a gauze band (mesh size 270 μm) by means of a gearing. The water, which enters through a 4 cm^2 opening, is sieved through the gauze which is continuously filtering out the plankton. The gauze band is divided into individual, numbered segments and is continually rolled up, so that fresh gauze is always in front of the water stream. After collection the gauze becomes covered with a second gauze band. Both bands, which closely sandwich the collected plankton, then enter a chamber filled with formaldehyde. The gauze transport can be set between 0.5 and 5 cm per nautical mile. Usually the collected plankton material is divided into 10 nautical mile blocks for which 3 m^3 of water are filtered, if the catching efficiency of the recorder is 100%. For evaluation of the collected material, the marine areas which are covered by the Hardy Recorder (North Sea, North Atlantic) are divided into grid boxes as standard areas, and the collected stock data per box are averaged over selected time intervals.

For many years such devices have been employed on ships of opportunity travelling set routes, filtering at depths between 8 and 10 m at speeds which amounted to ca. 8 knots at the beginning of the surveys and attaining more than 20 knots today. Meanwhile we have registered 438 publications dealing with the results of these Continuous Plankton Recorder surveys (CPR's). Along with conclusions about the large scale distributions of organisms and their seasonal variabilities, the publications have increasingly considered long-term variabilities and trends as a function of water quality and climate conditions. In spite of the prestige of this time-honored method of investigation, there are some critical remarks which must be made concerning it:

1. The only plankton stocks sampled by the Hardy Recorder are those in depths of 8 to 10 m; it is thus a two dimensional survey. Depending on physical and biological factors, however, plankton populations can be concentrated in thin water layers and thus do not have their vertical stock maxima always in the regularly sampled water depth. Figure 2 shows an example for the vertical distribution of dominant populations of the zooplankton. The sampled material was collected at midnight with the Longhurst Hardy Plankton Recorder (a further development of the Hardy Recorder, suitable for specified plankton sampling in the whole water column) at a permanent station at the shelf edge in the southern Norwegian Sea (0-900 m depth). The vertical profiles of the individual taxa (ind. m^{-3}) are shown together with a temperature curve, thus showing the close association with the water stratification. During the samplings at midday the near surface populations formed maxima of the same magnitude, however at depths which were more or less below 10 m. That means that many species which carry out diurnal and/or

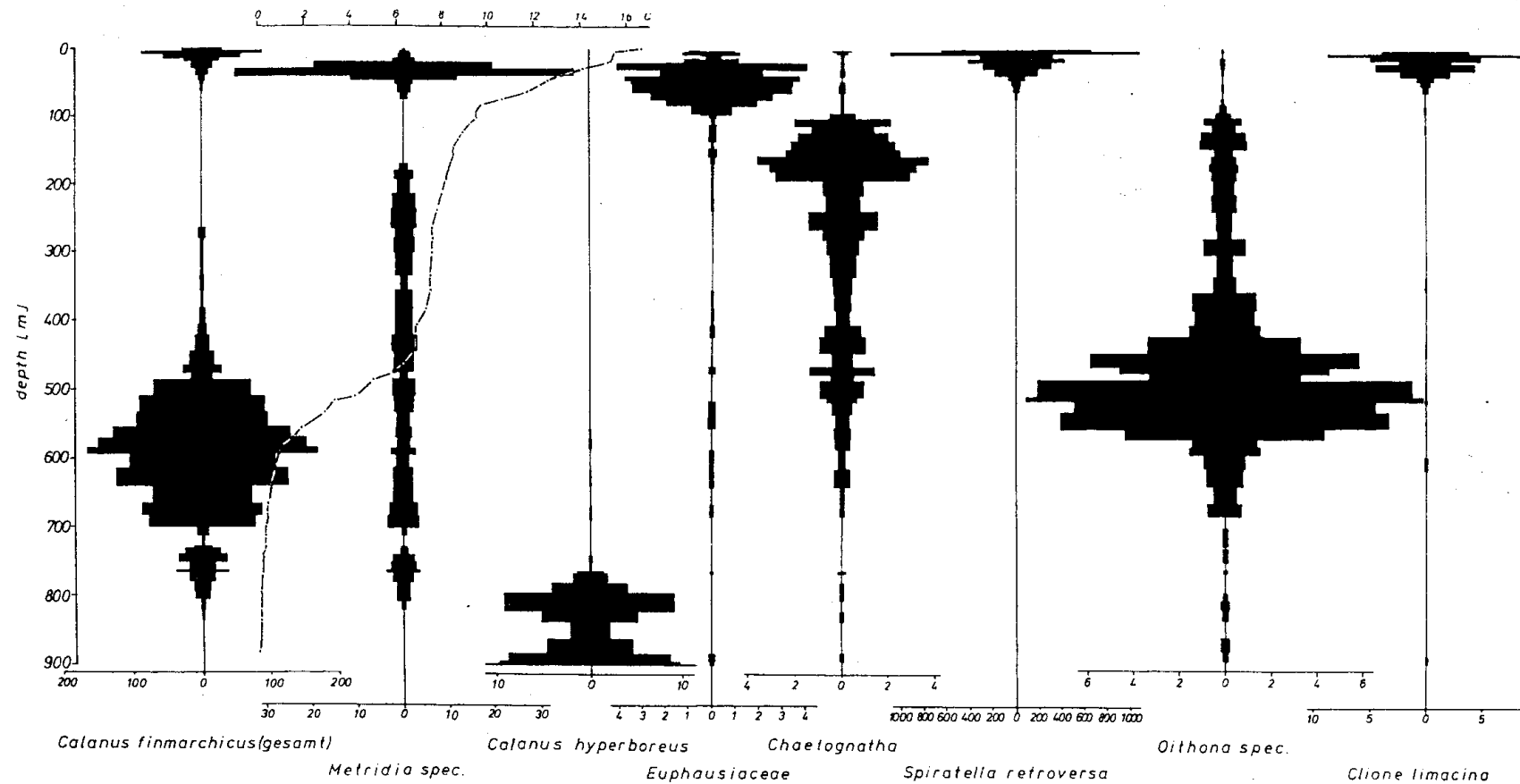


Fig. 2: Vertical profiles of several taxonomic groups of the mesozooplankton on a station at the shelf edge of the southern Norwegian Sea (Pos.: 62° 59'N; 03° 44'E), overlaid with the corresponding temperature curve (data from Krause 1978).

seasonal vertical migrations and only come to the surface during particular time of day or the year will not or only sporadically be collected by the Hardy Recorder, although they can be present in the water column in large stocks. Species such as *Microcalanus pusillus*, which live mainly in the deeper areas of the North Sea, will not be represented in the CPR surveys at all. But also the organisms of the uppermost water layers like *Anomalocera patersoni* or *Labidocera wollastoni* will not be sampled with that sampling system.

2. Mesozooplankton is defined for the size orders from 200 to approximately 2000 μm . Small species or the younger developmental stages of larger species from this part of the plankton spectrum are not or not quantitatively caught due to the relatively large mesh size of 270 μm , considering the fact that these organisms are often relatively narrow and can thus squeeze through the mesh lengthwise.
3. Comparisons with other sampling gears such as water bottles or finer meshed nets show that there are generally lower numbers of individuals caught by the Hardy Recorder. This impression we got also by our own preliminary comparisons (Dippner & Krause, in prep.) between copepod samplings using a multi-closing net (mesh width 200 μm) during the basin wide surveys carried out during the ZISCH project and the numbers of individuals from the CPR surveys averaged over more than twenty years (Colebrook & Robinson 1965). For this, we averaged our results from the near surface hauls of the multi-closing net in the individual CPR-Boxes and compared them with the monthly mean values of the CPR data (Fig. 3). The upper diagram is limited to the winter stock data, while the lower diagram also includes data from the ZISCH survey in late spring. It can be seen that the multi-closing net collected an average of about 13 times as many individuals as caught by the Hardy Recorder. If it can be assumed that this sampling error is constant, then it would be possible to still make relative statements about the geographical distribution of organisms based on the CPR surveys, but the biomass estimates derived from them, for example, would always lead to considerable underestimations of the existing stocks. Recently published papers seem to confirm the poor sampling efficiency of the Hardy Recorder. So, the publication of Clark et al. (2001) is to be mentioned, where long-term changes in relative and absolute zooplankton abundance were compared between the Dove Marine Laboratory and Continuous Plankton Recorder time series in the central-western North Sea. The collected individual numbers seem to differ by a factor of 10. The authors attributed this primarily to active and passive avoidance mechanisms of the organisms occurring during CPR sampling. John et al. (2001) made a comparison between zooplankton data collected by the Continuous Plankton Recorder survey and by vertically towed WP-2 nets in the English Channel. The data of abundance differed by a factor of between 2 and 35.
4. The Hardy Recorder is towed by merchant ships along constant routes. Since, for commercial reasons, no requirements can be made with respect to speed limitations, the sampling gears are not towed at constant speeds. On the contrary, these vary depending on the ship type. The range of variability of the ships' speeds is at least ten knots. Sampling gears, particularly high speed samplers, should always be towed at a constant speed to ensure comparability of the results. It can be assumed that the average cruising speed of the ships of opportunity has steadily increased during the past sixty years. The question therefore arises whether the catching efficiency of the Hardy Recorder has changed in a reverse proportion to this. In this respect, The continual decrease in numbers of zooplankton individuals in neritic and oceanic waters found by CPR surveys during the fifties, sixties and seventies (the stocks have still not really recovered up now) might be due to a decrease in the catching efficiency as a result of increasing ships' speeds. A satisfactory publication on the catching efficiency of the Hardy Recorder at different ships' speeds was not found by us in the literature up to now. A statistical analysis of the CPR stock inventory data in connection with the corresponding ships' speeds during the hauls would clarify this question. In addition, the possibilities and limitations of the CPR data should be identified and featured more clearly in order that the demands placed upon them remain realistic.

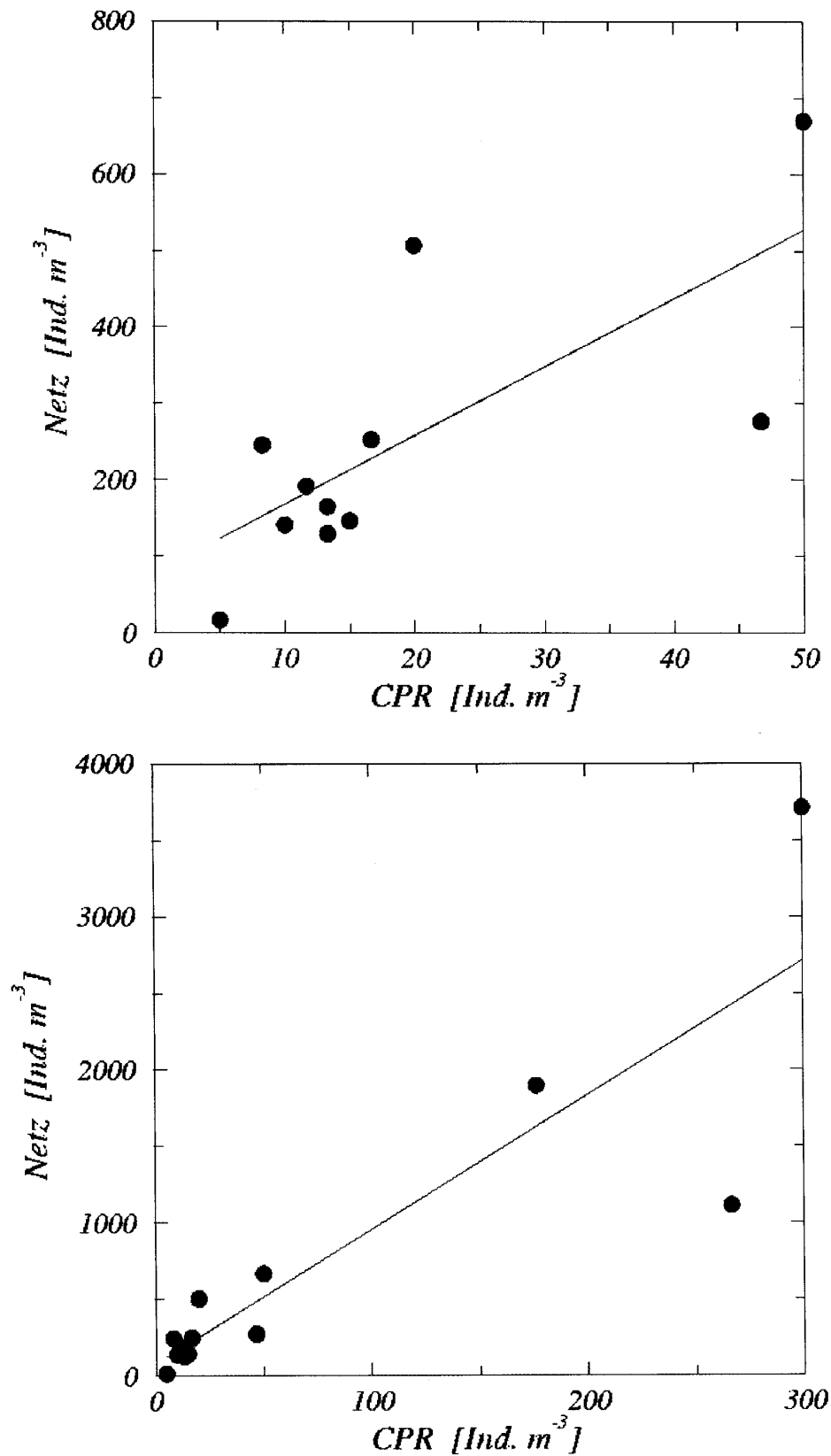


Fig. 3: Comparison of the individual numbers of the copepods from the CPR-Surveys (averaged between 1948 and 1960) drawn from Colebrook & Robinson (1965) and from the near-surface-catches of the ZISCH-Project. These data have been averaged per CPR-Box. Above: Comparison of winter data. Below: Comparison of winter and spring data (Dippner & Krause in prep.).

These remarks show that up to now there exists no satisfactorily exact data set with which it is possible to make firm statements about the long-term changes in the zooplankton stocks of the North Sea. What is needed are large scale quasi-synoptic surveys, if possible with undulating devices that sample the whole water column in a three dimensional manner.

Modern, standardised and automated methods for large scale three dimensional stock inventories of the zooplankton are urgently needed so that distribution patterns can be surveyed with sufficiently fine spatial and temporal resolution, similar to that available to physical oceanographers for the parameters of interest to them (e.g. temperature, salinity). This would be of immense value for the interdisciplinary evaluation of data in future research projects. In the literature there are a number of publications which are concerned with the development of such instruments – primarily based on acoustical or optical techniques. Unfortunately, up to now none of these has been able to supply stock inventory data of comparable quality to that produced by expert microscopic examination of zooplankton samples.

At the moment the new methods can only substitute traditional zooplankton studies that suffice with coarse information. As several workers stated the Optical Plankton Counter (OPC) is successfully used to count particle concentrations and measure size equivalents. Taxonomic identification needs to be done separately. In cases of few dominant species that occupy different size categories OPC counts can be related to key species by accompanying net hauls. Acoustic measurements are still struggling to convert signals into biomass or concentrations. The advantage is a large sampling volume, but the better the resolution the smaller the volume sampled. Genetic methods are well suited for screening purposes but not for surveys. In surveys, unexpected species might be encountered. These would not show up by the use of genetic markers, since no marker specific to them would have been used in sample treatment (see chapter 5.2.).

Provinces of the North Sea

The different regions of the North Sea are primarily defined according to physical conditions. For example, the annual fluctuations in sea surface temperature increase from an average of 5° C near the Shetland Islands in the North to more than 15°C off the mouth of the River Elbe. Through freshwater influxes from the rivers and their seasonal fluctuations there is a decrease in salinity but also particularly strong salinity fluctuations near the coasts. Particularly in the southern North Sea this causes extreme seasonal changes in the environment to which the organisms living here must adapt. As a consequence, for example, the number of copepod species decreases from around 25 in the oceanic region to about 7-12 stock-building species in the coastal areas of the southern North Sea (Colebrook et al. 1961).

Physically differing water masses are to be found in the various regions of the North Sea. For example, the influx of oceanic water masses from the Atlantic between the Orkney Islands and the Norwegian Trench transports a broad tongue of relatively saline water towards the Dogger Bank. Corresponding to the narrow opening through the English Channel, a comparatively narrow zone of saline water extends into the Southern Bight. In both areas the salinity reaches more than 35 psu ("Atlantic Water"). In the coastal areas near freshwater discharges the salinity is below 34 psu. On the western and southwestern coasts of the North Sea this water is designated as "Coastal Water" and off the Norwegian coast it is called "Baltic Water". In the rest of the North Sea the water masses have salinities between 34 and 35 psu ("North Sea Water"). This water is formed by the mixing of both other water types (Böhneke 1922). The dispersal of these water masses is subject to seasonal variability. For example in summer, the Atlantic Water retreats partially from the North Sea; from November on it occupies a broad zone again. Contrary to this, the Baltic Water and the Coastal Water increase in area during summertime. The outflow of water masses occurs only over the Norwegian Trench. The general circulation pattern in the North Sea is a large, basin-wide cyclonic gyre controlled predominantly by the inflows and outflows and the complexity of the bottom topography. Inflow and outflow are strongly influenced by the wind (e.g. Aure & Saetre 1981; Backhaus 1990). The general pattern of circulation has been well documented in a number of reviews and atlases (Dooley 1974; Lee & Ramster 1976; Otto et al. 1990). The zooplankton communities exhibit characteristic assemblages in the various water masses.

Drawing a line between the mouth of the Humber along the Dogger Bank to Skagen, roughly two areas with completely different hydrography and matter flux can be discerned, the northern and the southern North Sea (e.g. Tett and Mills 1991). With increasing resolution of surveys, a third spatial component became evident: the central North Sea. The separation into the three zones corresponds well with the 50, 100 and 200 m depth contour lines (de Wilde et al. 1992), underlining the importance of hydrography for the performance of pelagic ecosystems.

Fine scale investigations revealed the structure of the border between the central and the southern North Sea (van Haren and Joordens 1990). In this particular area a persistent chlorophyll a maximum was observed. As a mechanism, vertical advection of nutrient enriched water over a field with high mud content and thus remineralisation potential was assumed. This vertical advection is partly propelled by a tidal mixing front. Seemingly, a comparable investigation of the border between central and northern North Sea is lacking.

Abundance data

Field investigations covering larger areas of the North Sea and adjacent sea areas were already carried out in the years 1902 to 1908 under the auspices of ICES (actually this was the first ICES activity) and published in the 'Bulletin Trimestriel'. These results represent the baseline knowledge available for the North Sea. This promising development was disrupted by WW I. The oldest and one of the longest consistent data sets over periods of years is a series of observations off the west coast of Scotland extending to the Faroe-Shetland Channel. The observations extend from 1920 to the middle of the 60's. Here, primary emphasis was on the fluctuations in the species composition as a function of the currents and water transports. Fraser (1969) supplied a comprehensive overview of these results. British scientists were the first to present large scale horizontal distribution patterns obtained by standardised and mechanised methodology. The leading scientist in this field was Sir Alistair Hardy, who instituted the Continuous Plankton Recorder (CPR) Survey in 1931. As a result an invaluable data base was built up.² Due to WW II disruption again, changes in methodology and logistics the CPR-data set presently used to investigate present trends and distribution patterns originated in 1948 (Colebrook in Fransz et al. 1991a).

The only standardised, basin-wide sampling of mesozooplankton stocks over a longer period of time which has been attempted up to now is represented by the CPR surveys. Therefore, many scientists believe that on a basinwide scale the CPR (Continuous Plankton Recorder) data series from the Sir Alistair Hardy Foundation of Ocean Science is of outstanding importance for the knowledge on distributions and trends of North Sea zooplankton (e.g. CPR Survey Team 1992). Despite its restraints (discussed e.g. in Radach 1984) the CPR is the presently only available zooplankton data set to meet with climatological data sets on a comparable scale. For example, the CPR series provided the data base for the NOWESP (The North West European Shelf Project) analysis (e.g. Bot et al. 1996; Visser et al. 1996). CPR-series also serves as a spatio-temporal data set of lower resolution.

Local monitoring stations also contribute to knowledge on temporal trends. However, their temporal extensions are shorter than for the CPR. Continuous high frequency measurements (weekly or higher) are relatively rare. One example is from the Helgoland Roads time series for phyto- and zooplankton (some results published in Greve and Reiners 1995), for which an extensive report on phytoplankton dynamics has been recently published (Hickel et al. 1997). Further zooplankton monitoring activities are listed in the respective reports of the ICES Working Group on Zooplankton Ecology (ICES 1998; ICES 1999).

The FLEX data set additionally serves as a data set with high spatio-temporal resolution, so that temporal trend, advection and patchiness in the sea can be investigated. A series of publications

² It should be noted that Germany does not support the Sir Alistair Hardy Foundation which presently runs the CPR Survey. As a consequence, German scientists have no access to this unique data set.

dealing with the special spatio-temporal character of the FLEX data set has been published (Steele and Henderson 1977; Steele and Henderson 1979; Steele and Henderson 1992b). The analysis of an yet unpublished spatio-temporal data set from the German Bight led to evolution of the concept of population waves (Greve and Reiners 1988).

A further data source are national independent surveys and synoptical monitoring. Zooplankton monitoring activities are listed in the respective report of the ICES Working Group on Zooplankton Ecology (ICES 1998; ICES 1999). Most of the independent studies are regionally delimited. The Belgian RENORA project covered the southern coastal North Sea (Belgrano et al. 1995) spending much effort on meroplankton dynamics. A couple of cruises undertaken from the NIOZ (the Netherlands) followed the gradient from the central North Sea to the North. This gradient analysis involved several types of measurements including grazing experiments (Fransz et al. 1998; Kuipers & Witte 1999). Within German surveys a series of cruises in the whole and in the Southern North Sea were conducted, allowing for seasonal and regional differentiation (e.g. Krause & Martens 1990; Krause et al. 1995). The cruises are tabulated in the SYKON data base.

In addition, in the North Sea numerous regional or point stock inventories have been carried out which, contrary to the CPR surveys, have the advantage of covering a larger part of the water column. Examples for the western and central North Sea are Wimpenny (1933, 1937), Bainbridge & Forsyth (1972) and Bainbridge et al. (1978), for the central and northern North Sea Fraser (1939, 1949, 1952, 1972), Glover (1957), Williams & Lindley (1980), Fransz et al. (1984), for Skagerrak and Norwegian Trench Wiborg (1954, 1955), Eriksson (1973a +b, 1974, 1976), Richardson (1985), for the eastern North Sea including the coastal waters Jespersen (1928), Blanner (1982), for the German Bight Lücke (1912), Künne (1952), Martens (1978, 1980, 1981), Gerdes (1985), Steiff (1988), Hesse et al. (1989), Uhlig (1990, 1995), Greve (1991), Martens & Brockmann (1993), for the southern North Sea and the Wadden Sea Fransz (1978, 1983a+b); Fransz et al. (1992), Le Fèvre-Lehoërff et al. (1983) and for the English Channel e.g. Russell (1935, 1936) und Lindley (1997).

Generally, it is to be said that most of the inventories which have been carried out in the North Sea during the past more than one hundred years are fragmentary, since they usually were neither conducted on an area-wide basis nor according to standardised sampling methods. That means that the various data on stock abundances from the literature are only comparable to a certain degree. So, it was possible to make qualitative statements about horizontal and vertical distributions and composition of the assemblages in the various sea areas. It was also frequently attempted to derive information about seasonal and annual variabilities and successions by point or regional samplings with comparable methods. These, however, are not sufficient for a comprehensive, comparative assessment of the stock abundances nor for the investigation of long-term trends.

Species distribution

Copepoda: These species which belong to the crustacean plankton are stock-building for the mesozooplankton in almost all marine areas. One of the most important and best investigated large copepods of the North Sea is *Calanus* sp. Distribution patterns for species of the genus *Calanus* on the European shelf were indicated e.g. by Rees (1949, 1957), Matthews (1969), Jashnov (1970) Colebrook (1986a) and re-analysed by Planque & Fromentin (1996). In the 50's and 60's it was disputed whether or not *Calanus finmarchicus* and *C. helgolandicus* belong to one species. So, because of intermediate forms found in the boundary areas between the two species, Aurich (1966) still assumed that the two forms were not genetically strictly isolated but rather geographical races connected by a flexible species, *Calanus finmarchicus sensu lato*. It appeared that *Calanus finmarchicus* was linked to colder environments, which means that it is a boreal form occupying northern North Sea, whereas the closely related *C. helgolandicus* is more a warm temperate species belonging to the Lusitanian water, which originates from Gibraltar and from the Bay of Biscay living in the southern regions of the North Sea. Furthermore, *C. helgolandicus* is seemingly linked to neritic habitats, whereas *C. finmarchicus* also inhabits oceanic areas. Nevertheless, Matthews (1969) and Hirche (1984) found the main distributional centres of *C. helgolandicus* in the Atlantic to the west and southwest of the British Isles. Its relative frequent occurrence in the southern North Sea in

summer might be explained by a mass invasion through the English Channel from its main areas of production.

Glover (1957) has already shown in his stock inventories with the Hardy Plankton Indicator, a precursor for the Hardy Recorder, how the boreal *Calanus finmarchicus* drifted into the North Sea with saline Atlantic Water between the Shetlands and the Norwegian Trench. Backhaus et al. (1994) and Harms et al. (2000) tried to model the northeast Atlantic circulation and the spring invasion of *Calanus finmarchicus* into the North Sea. However, this large copepod has its winter refuge at the shelf edge at great depth. The Figure 4 shows the vertical distribution pattern of *Calanus finmarchicus* together with the corresponding temperature curves in the water column during 19 oblique hauls which were carried out in August 1969 at a permanent station at the shelf edge of the southern Norwegian Sea with the Longhurst-Hardy Plankton Recorder. In spite of the fact that the hauls reached differing depths, two pronounced concentration maxima are recognisable in each case which correspond in their depths with the thermoclines. The reproductive stock, which consisted of all developmental stages, was found in an accumulation center limited to a few meters within the seasonally warmed mixed layer. This stock carried out diurnal vertical migrations within the upper 70 m. In the transition zone between the Atlantic Water and the Arctic Bottom Water, approximately between 400 m and 700 m, the second accumulation center with the overwintering stock could be found, which consisted mainly of the copepodite stages V and IV as well as some young females. Diurnal vertical migrations were also recognisable here (Krause 1978; Krause & Radach 1989).

Besides distribution trends for *Calanus* in the different areas were given by Fromentin and Planque (1996). The CPR survey team provided data on the trend of zooplankton and selected species for the different CPR boxes (CPR Survey Team 1992). Changes were discussed in relation to environmental factors salinity and temperature as well as westerly weather and south wind anomalies (Colebrook 1978; Gamble 1993). Next to the change at the end of the 70's a change during 1987-1988 for the dinoflagellate *Ceratium* spp. occurred, which was regarded as a major effect in the northern North Sea (Dickson et al. 1992). The seasonal distribution for German Bight plankton also changed at that time (Greve pers. comm.).

Besides *Calanus* further attention was spent on the smaller copepods, e.g. *Pseudocalanus elongatus*, *Paracalanus parvus*, *Temora longicornis*, *Centropages typicus*, *Centropages hamatus* and the different *Acartia* species. Although these species can occur overall in the North Sea, they dominate the mesozooplankton in the southern North Sea to the Dogger Bank. They have developed special adaptations suitable for shallow waters which are different from those of *Calanus finmarchicus*, which migrates to deeper regions of the sea in unfavourable seasons being here subjected to a 'diapause'. However, these adaptive strategies are not fully understood yet.

During the past century a number of authors concerned themselves with the occurrence and distribution of the copepods of the North Sea. Early work on copepod stocks in the North Sea and Baltic Sea was published by Kraefft (1910). Lücke (1912) reported on the species composition and stock sizes of the entire zooplankton, including copepods, in the German Bight. Tesch (1915) investigated the occurrence of the copepods and their developmental stages in the southern North Sea. Graham & Harding (1938) found connections between the hydrological conditions, phytoplankton composition and the fluctuating occurrence of small and large copepods in the English Channel.

In March, August, September and October, Wimpenny (1933) recorded *Temora longicornis* as being the numerically dominant copepod off the British coast, only being exceeded in abundance during May by *C. finmarchicus*. At that time, however, he found large stocks of *T. longicornis* in the central North Sea. The alternating dominance of these two copepod species in the coastal area is explained by the 'Fulton drift' which transports *C. finmarchicus* along with oceanic water into the region, whereas *T. longicornis* which is neritic dominates when the Atlantic influence becomes minimal. To Hardy (1924) these two species were of great importance as fish food in the fishing grounds of this area, making up about 96% of the stomach contents of herring.

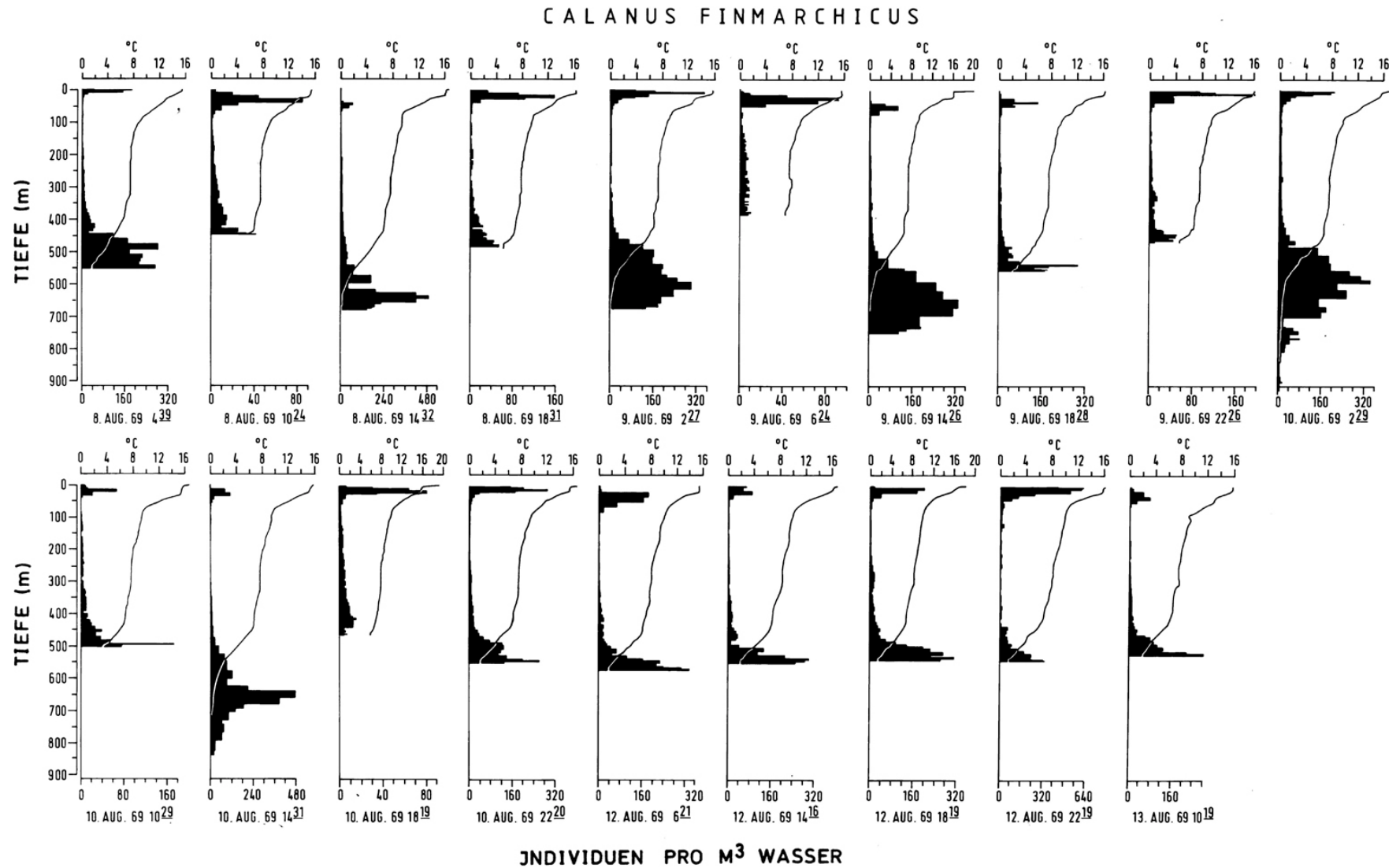


Fig. 4: Vertical profiles of *Calanus finmarchicus* from 19 LHPR-hauls (reaching to different depths) on a fixed station at the shelf edge of the southern Norwegian Sea (Pos.: 62° 59'N; 03° 44'E), overlaid with the corresponding temperature curves (Krause 1978, Krause & Radach 1989).

Wiborg (1940) investigated stocks and production of the copepods in Oslo Fjord. Marshall (1949) reported on the biology of the small copepods in the Scottish Loch Striven. Kiørboe & Johansen (1986) studied stocks and egg production of the large and small copepods in the Buchan Region (northern North Sea) in order to get information about the trophic conditions for herring larvae. Krause & Radach (1980; 1989) and Krause & Trahms (1982; 1983) followed the spring development of the *Calanus finmarchicus* stocks as well as small copepods such as *Pseudocalanus elongatus*, *Pseudocalanus parvus*, *Microcalanus pusillus* und *Oithona similis* from water bottle series in the Fladen Ground (northern North Sea) during FLEX '76. From this data series Fig. 5 shows the depth integrated time series of all developmental stages of the small cyclopoid copepod *Oithona similis* and the large calanoid copepod *Calanus finmarchicus*. Greve & Reinert (1986) and Greve (1988) found significant increases in the stocks of the small copepods as a result of their evaluation of data from Helgoland Roads in the German Bight.

Investigations of the stocks over large areas were only possible through the CPR surveys. Rae & Fraser (1941) evaluated the copepods of the CPR samples from the southern North Sea. Rae & Rees (1947) extended these investigations to include the entire North Sea. Rees (1949; 1957) and Matthews (1969) also used the CPR data to study the geographical distribution of *Calanus finmarchicus* and *Calanus helgolandicus*. These investigations were then continued by Fromentin & Planque (1996) and Planque & Fromentin (1996). Over many years, Colebrook systematically evaluated the CPR surveys, investigating primarily the stocks of the copepods and their seasonal cycles in the different standard areas (e.g. Colebrook et al. 1961; Colebrook 1966; 1978). Later, after a great deal of data material had become available, he began to consider annual and long-term fluctuations of the copepod stocks (e.g. Colebrook 1972a+b; 1982a+b). These evaluations of the CPR surveys have been continued up to now, for example by Broekhuizen & McKenzie (1995), which also report on the stocks of *Calanus spp.* and the smaller copepods and their fluctuations in the North Sea. Aside from the CPR surveys there are only a very few data sets which describe the copepod stocks of the entire North Sea. One of these was collected during the ZISCH project and describes the winter distribution of the mesozooplankton in 1987 (Krause et al. 1995).

Euphausiacea: This taxonomic group of macroplanktonic crustaceans can seasonally build up considerable biomass (up to 90%) in the central and northern North Sea (e.g. Lindley & Williams 1980). Detailed studies of the CPR-data by Lindley (1980; 1982a) indicate that for the North Sea 4 species must be considered important. The most common species is *Meganyctiphanes norvegica* occurring in Norwegian waters and northeast of Scotland. *Thysanoessa inermis* has its main focus in the northwestern North Sea extending as far south as the Dogger Bank. Furthermore *T. raschi* and *Nyctiphanes couchi* must be noted with minor abundances. The abundance of euphausiids in the North Sea is correlated with depth, the highest abundances are recorded over the Norwegian trench and the northern North Sea. The line from the mouth of the Humber to Skagen seems to be a southern limit (e.g. Krause et al. 1995).

Mysidacea: These crustaceans, which like the Euphausiacea also belong to the Malacostraca, can be found in masses in coastal areas protected by seaweeds and seagrasses. Some live on hard, sandy or muddy bottoms. Most of them stay close to the bottom during the day and rise to the surface at night (Riedl 1983). Newell & Newell (1963) also emphasise that Mysidacea are seasonally abundant in inshore and estuarine waters. A few important species in the coastal regions of the North Sea are *Siriella armata*, *Schistomysis spiritus*, *Praunus flexuosus*, *Anchialina agilis* und *Lepidomysis gracilis*. There are hardly any publications dealing with stock investigations of Mysidacea in the North Sea.

Amphipoda: These crustaceans, which also belong to the Malacostraca, are usually benthic. Only one family, the Hyperiidae, are fully planktonic, although in shallow sea areas many bottom-dwelling amphipods may appear in plankton collections – particularly in samples taken at night. Important Hyperiidae in the North Sea are *Hyperia galba* and *Parathemisto spp.* (Newell & Newell 1963).

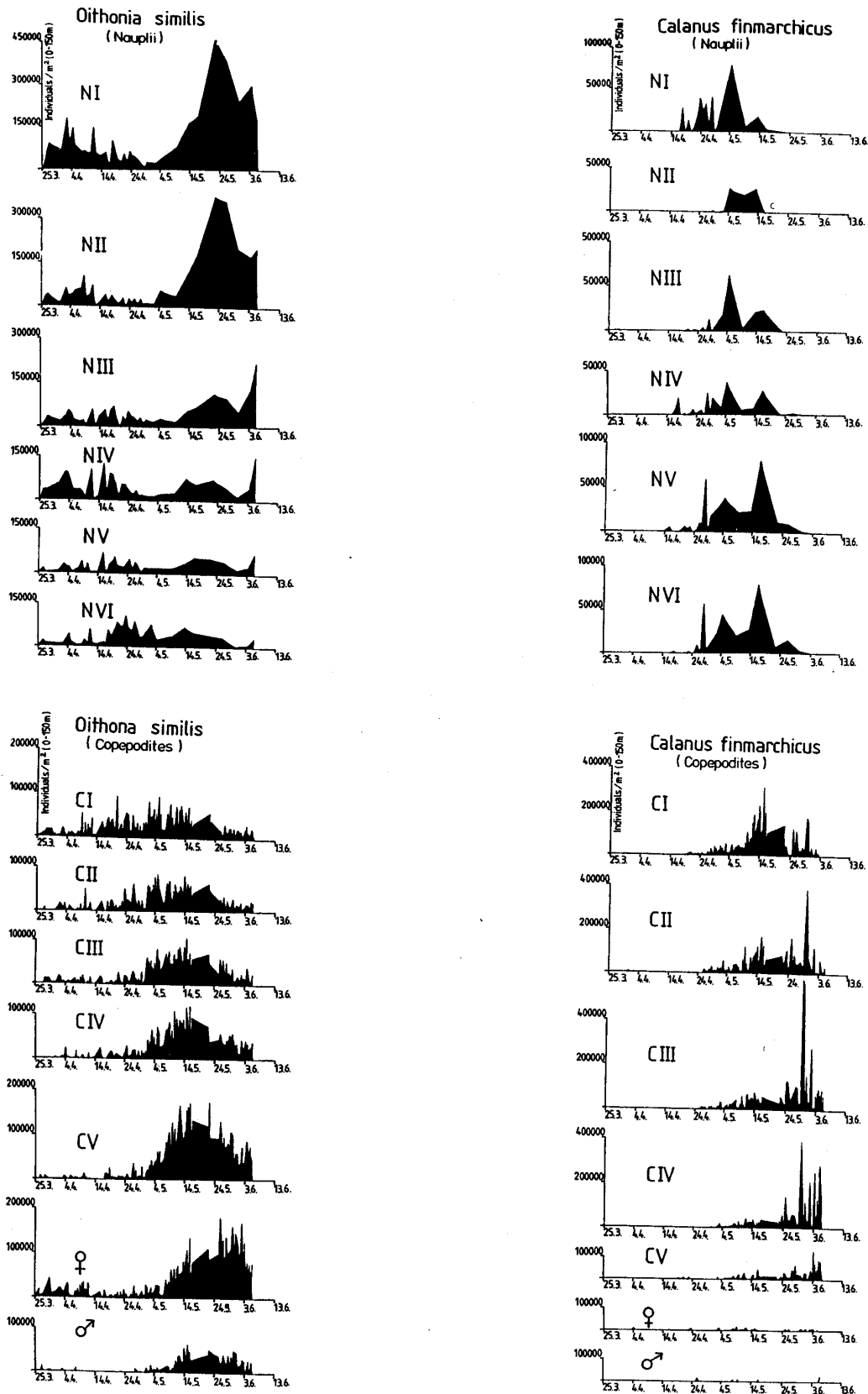


Fig. 5: Depth-integrated time series of all developmental stages of *Oithona similis* and *Calanus finmarchicus* during FLEX'76 (Krause & Trahms 1983).

Marshall (1948) found *Parathemisto* sp. being mainly confined to the middle latitudes and the Dogger Bank during spring and summer, but had a wide distribution during autumn and winter. In late winter Krause et al. (1995) found amphipods (no taxonomic separation was carried out) in small numbers everywhere in the North Sea except in the German Bight and along the Danish west coast, in the Norwegian Trench and in the region of the Moray Firth. But relatively high concentrations (>100 ind. m^{-2}) were found in an area extending from the east coast of England out over the Dogger Bank in a pattern corresponding with the distribution of the Central North Sea Water. Based on the CPR-data McHardy (1970) in his thesis at the University of Edinburgh has investigated distribution and abundance of hyperiid amphipods in near-surface waters of the north Atlantic Ocean and North Sea. Also Vane (1951) evaluating CPR-data was employed with distribution and ecology of some north Atlantic planktonic Amphipoda in his thesis. Generally stated, there are only very few publications dealing with hyperiid stocks in the North Sea.

Isopoda: These Malacostraca are partly bottom-dwellers, whereby, however, usually the larval stages are planktonic. Planktonic species in the North Sea are *Gnathia maxillaris* and *G. oxyuraea*, *Eurydice grimaldii*, *Idotea balthica*, *I. emarginata* and *I. linearis* (Newell & Newell 1963). Isopods, however, do not form large stocks. Investigations of them are very scarce.

Cumacea: These Malacostraca are bottom-dwellers which may, on occasions, get whirled up and so collected with true plankton (Newell & Newell 1963). Van der Baan & Holthuis (1972) gave a short note on the occurrence of Cumacea in the surface plankton collected at 'Texel' lightship in the southern North Sea. Kurian & Radhadevi (1985) worked up CPR-data and gave a survey about Cumacea in the whole North Sea.

Cladocera: In addition to Henderson & Marshall (1944) and Marshall (1948), especially Gieskes (1970, 1971 a+b) used the CPR data for North Sea wide stock investigations of these crustaceans, which belong to the Phyllopoda.

Marshall recorded that the densest populations of *Evadne* sp. were found in the northwestern area of the North Sea and around and within the German Bight and the mouth of the Skagerrak. *Podon* sp. was rarely taken in such high numbers as *Evadne* sp., but in general there appeared to be some correlation between the distribution of the two genera. Gieskes stated that in the North Sea exist *Podon intermedius*, *Podon leuckarti*, *Podon polyphemoides*, *Evadne nordmanni* and *Evadne spinifera*. *Evadne nordmanni* was found in large numbers in shelf waters, especially in the North Sea as well as in the eastern Atlantic. *Podon intermedius* was also common in the North Sea and the eastern North Atlantic. *Podon leuckarti* proved to be typically neritic. *Evadne spinifera* was found only in the southern extremity of the sampled area. This suggests that it prefers warmer regions of the temperate zone. *Podon polyphemoides* is a truly estuarine euryhaline species.

Reproduction of these animals is mainly parthenogenetic, so that a very rapid increase in population size is possible when environmental conditions are optimal. Under favourable circumstances, large populations occur both in coastal waters and in the open ocean (Wiborg 1955; Gieskes 1971b). The species are never abundant as long as the water column is not stratified. This dependence on stratification suggests, that Cladocera need near-surface conditions for their successful propagation, both in neritic and oceanic regions. Thus, the time at which they occur in maximum numbers is in the summer months. Overwintering is achieved by means of resting eggs. Gieskes (1970) gives a detailed account of the life history of these animals.

In addition, a number of publications about stock investigations exist which cover a part of the North Sea of which were only carried out at individual points and where the Cladocera appear as a component of the mesozooplankton. For example, Jorgensen (1933) investigated the horizontal and vertical distributions as well as the life cycles of *Evadne nordmanni* and *Podon* spp. over ten years off the coast of Northumberland. Glover (1957) investigated the stocks of cladocerans between the Shetland Islands and the Norwegian Trench with the Hardy Plankton Indicator and found relatively large populations in the summer months. Eriksson (1973b, 1974) studied annual development of numbers of individuals of cladocerans off the western Swedish coast. Hay et al. (1991) determined the biomass and seasonal fluctuations of cladocerans in the northern North Sea. Niel-

sen (1991) found correspondences in the vertical migrations of *Ceratium* spp. and cladocerans (*Evadne nordmanni*, *Podon* spp.) at a permanent station in the Kattegatt. In parallel laboratory experiments he showed that the cladocerans consumed an appreciable proportion of the daily production of *Ceratium* spp.

Ostracoda: This group of small bivalved crustaceans found in the North Sea belong to two main families, the Cypridinidae and the Concheocidae. *Philomedes globosus* is widespread in the North Sea and Icelandic waters. *P. lilljeborgi* and *P. interpunctata* are found mainly in the northern North Sea. *Conchoecia elegans* is known throughout the North Sea. And *C. borealis* and *C. obtusata* are found in the northern North Sea (Newell & Newell 1963). All these species occur, however, in very small populations. Based on the CPR-data Williams (1975) presented an atlas of the Ostracoda in the North Atlantic and the North Sea during 1963. With this exception, there are hardly any publications about stock abundances of ostracods.

Pteropoda: This is a group of gastropods which belong to the holoplankton. The most important species of the North Sea are the thecosomatous Pteropod *Spiratella* (= *Limacina*) *retroversa* and the gymnosomatous Pteropod *Clione limacina*. *S. retroversa* is herbivorous, while *C. limacina* feeds primarily on *S. retroversa*. Both species thus occur together in a predator-prey relationship (Mileikovsky 1970).

According to Tesch (1946), *S. retroversa* lives in the Atlantic transition zone between the Arctic and subtropical regions. In the North Sea, this species is considered an indicator for Atlantic Water (Rae 1949). Paulsen (1910) already assumed that the stock of *S. retroversa* probably is being constantly replenished from the Atlantic and is capable of living in mixed waters. This theory is supported by Vagn Hansen (1960). Wiborg (1955) localised the main stock of the species in the central part of the southern Norwegian Sea. Vagn Hansen (1960) found the largest stocks between 10°W and East Greenland and between 55°N and 62°N. Morton (1954) produced a comprehensive publication about the biology of *Spiratella retroversa*.

Clione limacina was considered by Russell (1935) to be an indicator for Arctic Water. Wiborg (1955) found it distributed over the whole of the Norwegian Sea, while Gran (1902) characterized it as typical of the East Icelandic Current.

The CPR surveys show relatively large stocks of *S. retroversa* in the northwestern North Sea as well as in the Skagerrak between May and October. In summer stocks of this species were also found northeast of the Dogger Bank. The line from the mouth of the Humber to Skagen seems to be a southern limit. *Clione limacina*, which occurs in smaller numbers, was found primarily in the northern North Sea and in the Orkney-Shetland region (Henderson & Marshall 1944; Marshall 1948). Wimpenny (1933) found the largest stocks of both species in the western North Sea (Flam-borough Line) in August/September. According to the CPR-Surveys Vane (1961) recorded that *S. retroversa* and *C. limacina* showed distributions intermediate between the oceanic and neritic forms. Both species appear to be important in relation to the degree of penetration of mixed coastal and Atlantic water into the North Sea. Redfield (1939) found in the Gulf of Maine a comparable relationship between *Spiratella* and the inflow of oceanic water. Vane (1961) stated that a strong similarity is shown in the Recorder collections between the distributions of *Clione*, *Spiratella*, *Candacia armata* and *Metridia lucens*.

Chaetognatha: These relatively large carnivores belonging to the gelatinous zooplankton are often used as indicator species for different water bodies (e.g. Fraser 1937, 1939, 1952; Russell 1935, 1939; Furnestin 1938). *Sagitta maxima* and *Eukrohnia hamata* are found in the cold oceanic water (and in the deep layers of the Norwegian Trench). *Sagitta serratodonta* indicates warm oceanic water and *Sagitta elegans* mixed oceanic and coastal water. In the shallow North Sea, mainly *Sagitta elegans* and *Sagitta setosa* were found. The waters of the northwestern North Sea and off the British coasts which are influenced by the Atlantic inflow are characterized by *Sagitta elegans*, whereas pure North Sea water of the southeastern areas is characterized by *Sagitta setosa* (Russell 1939). Wimpenny (1937) investigated abundances and distributions as well as life cycles and feeding of *Sagitta setosa* and *Sagitta elegans* in the southwestern North Sea. Tungate (1975)

studied abundances of chaetognaths as well as their influence as carnivores on plaice fry in the southern North Sea. Hay et al. (1991) estimated the biomass of chaetognaths in the northern and central North Sea. Kopacz (1994) investigated abundances and seasonal fluctuations of the chaetognaths in the area around the Island of Sylt. LeFevre-Lehoerff et al. (1995) investigated the stocks of the mesozooplankton – including *Sagitta setosa* – as a function of hydrography, winds and climate change.

Henderson & Marshall (1944) and Marshall (1948) also investigated the distribution of chaetognaths in the North Sea in connection with their evaluation of CPR-surveys. Later, Bainbridge (1963) continued this work on the CPR-data with respect to this taxonomic group. Bary (1963) assigned the species stock data from the CPR-surveys – including *Sagitta setosa* and *Sagitta elegans* – to specific water masses of the North Sea and the North Atlantic.

Coelenterata: North Sea wide stock data on medusae and ctenophores are hardly to be found in the literature. Even the CPR-surveys hardly give any information about this important group of carnivorous macrozooplankton. The reason for this could already be found in Henderson & Marshall (1944), who tried to quantify these gelatinous organisms from the CPR-samples of the southern North Sea and mentioned that the "medusae are badly damaged by the recorder".

Nonetheless there are a number of stock investigations which, however, are predominantly localised at one point or in a small marine area: Wimpenny (1933) mentions in his survey of the mesozooplankton of the western and central North Sea the trachymedusa *Aglantha digitale*, which only occurred in small numbers in his catches (maximum: October). Werner (1961) investigated the morphology and life cycles as well as temperature dependence with regard to the distribution and the seasonal appearance of the hydromedusa *Bougainvillia superciliaris*. Smedstad (1972) reported on the abundances and life cycle of *Aglantha digitale rosea* in Oslo Fjord. Van der Baan (1980) investigated the seasonal occurrence of Scyphomedusae in surface waters near "Texel" light vessel and van der Veer & Sadée (1984) reported on the seasonal occurrence of *Pleurobrachia pileus* in the western Dutch Wadden Sea. Kopacz (1994a+b) wrote about the gelatinous zooplankton (Scyphomedusae, Hydromedusae, Ctenophora) and Chaetognatha in the area around the Island of Sylt. Hay et al. (1991) gave estimates of population sizes for *Aglantha digitale* in the northern and central North Sea and Moeller (1980) carried out random sampling of a summer stock of scyphomedusae in the North Sea and the Baltic Sea. Hay & Adams (1975) and Hay & Hislop (1980) also investigated the distribution and abundance of Scyphomedusae in the North Sea. During the winter ZISCH survey, only the stocks of *Aglantha digitale* were worth mentioning with respect to numbers of individuals. Relatively high concentrations (100 - >1000 individuals m⁻²) occurred in the region extending from the British coast out over the Dogger Bank into the central North Sea, tracing the flow of the Central North Sea Water. Throughout the rest of the North Sea during the survey this species was caught regularly in small numbers (Krause et al. 1995).

The well-known British zooplanktologists J.H. Fraser and F.S. Russell apparently only became particularly interested in medusae at a relatively late stage in their professional work. Russell (1953, 1970) studied the medusae of the British Isles. Fraser (1970) reported on the ecology of the ctenophore *Pleurobrachia pileus* in Scottish waters and Fraser (1972) on the distribution of medusae likewise in the Scottish area.

As an outcome of the international Young-Fish-Survey bycatch is also registered. One bycatch form are medusae. According to this scyphomedusa seem to be inhomogeneously distributed in the North Sea. The western and central North Sea depict higher densities compared to the German Bight and the adjacent Wadden Sea areas (Hay et al. 1990; Kopacz 1994a+b). Nevertheless, the unpublished KUSTOS data sets from the German Bight in summer of 1994 show extremely individual numbers for young as well as small hydromedusae (up to 13 000 ind. m⁻³) and ctenophores (up to 60 ind. m⁻³).

Numerous authors carried out stock inventories for medusae in order to gain information about their role as predators in the ecosystem. For example Tungate (1975) investigated the abundance and distribution of chaetognaths and the ctenophore *Pleurobrachia pileus* in the southern North

Sea and established the significance of this group as a predator of plaice eggs and larvae. Fransz et al. (1978) also demonstrated correlations between the abundance and growth of the fish larvae and the occurrence of medusae and ctenophores in Dutch coastal waters. van der Veer & Oorthuyzen (1985) investigated abundance and growth as well as food requirements of the scyphomedusa *Aurelia aurita* in the Dutch western Wadden Sea. Also, Daan (1989) worked at a fixed station in Dutch coastal waters. He found that naupliar declines in July/August coincided with maximum densities of the hydromedusa *Phialidium hemisphaericum*, which dominated the macroplankton both in abundance and in biomass and reached a maximum density of 467 specimens m^{-3} or 7 mg C m^{-3} . Kuipers et al. (1990) studied a spring outburst of *Pleurobrachia pileus* in Dutch coastal waters and examined its feeding pressure on the copepods. Hay et al. (1990) investigated the scyphomedusae, their estimated biomass and their influence on the gadoid fish larvae.

Tunicata: These more or less gelatinous holoplanktic organisms belong to the Appendicularia and the Thaliacea. According to Newell & Newell (1963) four species of the Appendicularia are common everywhere in the North Sea: *Oikopleura dioica*, *O. labradoriensis*, *O. fusiformis* and *Fritillaria borealis*. The Thaliacea include the Salpida and Doliolida. *Salpa fusiformis*, *Salpa asymmetrica* and *Doliolum gegenbauri* occur mainly in the northern North Sea. *Doliolum nationalis* is occurring in the southern North Sea, when favourable wind prevails (Newell & Newell 1963).

Already Savage (1937) has shown how important *Oikopleura* spp. can be in the diet of herring, especially in the northern North Sea. Henderson & Marshall (1944) note that these gelatinous organisms are very much damaged in the CPR-catches and therefore cannot be identified by species. Marshall (1948), evaluating the first CPR-surveys, found the main months of abundance for *Oikopleura* spp. extending from April to September. First increases in the population were apparent in the Southern Bight and over the Dogger Bank in April and May. Based on the CPR-investigations, the occurrence of planktonic tunicates was reported, especially *Salpa fusiformis* and *Doliolum gegenbauri*. Other publications worth mentioning are Barnes (1958), Hunt (1966), Glover & Robinson (1967, 1968) and Roskell (1983, 1984, 1986 a+b).

In addition, there are a number of stock investigations which are not based on the CPR-surveys. Russell (1935) designated *Salpa democratica* and *Doliolum gegenbauri*, among others, as indicator species for the "Southwestern Water" which enters the North Sea through the English Channel. Lindley et al. (1990) found connections between the occurrence of doliolids in the German Bight and exceptional inflow into the North Sea. Gerdes (1985) estimated the proportion of Appendicularia (*Oikopleura dioica*) in the holoplankton of the German Bight to be 1.6% in April and 13.1% in August, sinking again to 1.6% in October. In the inner part of the German Bight this species did not occur. However, the greatest numbers of individuals were found in the western part, in the direct inflow area of North Sea water. In winter in the German Bight, *Oikopleura dioica* made up 0.9% of the total zooplankton abundance (Hesse et al. 1989), and, according to Martens & Brockmann (1993) occurs mainly in a mixture of "Wadden Sea Water" and "German Bight Water". During the ZISCH winter survey Krause et al. (1995) found the largest populations of *Oikopleura* spp. (>1000 ind m^{-2}) north of the Dogger Bank in the central North Sea.

Meroplanktic larvae: Contrary to the holoplankton, the meroplankton is characterised by the fact that it only spends a part of its life cycle in the plankton, later settling to the benthos or, as in the case of fish, becoming more independent of the currents as nekton. Most benthic organisms produce planktonic larvae. These include the different worm groups as well as the bivalves, gastropods, bryozoans, barnacles, gooseneck barnacles and higher arthropods.

Generally, large stocks of bottom invertebrate larvae are expected primarily near the coasts, since in shallow water, particularly where there is hard substrate, a diverse benthic fauna can develop. Nevertheless, Hickel (1975) found in the Wadden Sea at the Island of Sylt that in spite of large numbers of meroplanktonic larvae present, small calanoid copepods like *Temora longicornis*, *Pseudocalanus elongatus*, *Acartia clausi* and *Centropages hamatus* dominated with an average of 85% of the zooplankton biomass. Only from June to September were other zooplankton groups, mainly polychaeta larvae, of quantitative significance. Martens (1980) observed high densities of meroplanktonic larvae, which sometimes even exceeded the biomass of the copepods, in the Wad-

den Sea at the Island of Sylt. Likewise, Fransz (1983) found in the Dutch Wadden Sea that the biomass of the small copepods dominated mainly in the northern Wadden Sea. In the western Dutch Wadden Sea, however, they were matched by merozooplankton like polychaeta larvae. Later investigations such as those by George (1996) confirm these findings. In the German Bight, the influence of merozooplankton is similar to that in the Wadden Sea although to a lesser degree. That means that although small copepods dominate the zooplankton at all seasons, in spring and in summer the larvae of the benthos gain importance (e.g. Gerdes 1985). Hesse et al. (1989) investigated the stocks of phytoplankton, zooplankton and marine fungi in the German Bight as a function of the hydrodynamic conditions and elucidated the importance of salinity fronts for the distribution of planktonic organisms. Fronts function as boundaries for different plankton communities. In the mixed water near the coasts, polychaete and cirripede larvae dominated; in the more saline North Sea Water, copepods dominated. The still unpublished data from the KUSTOS project reveal that in the German Bight in winter of 1996 approximately 96%, in the spring of 1995 69% and in the summer of 1994 only 64% of the total numbers of individuals in the zooplankton were copepods. The rest consisted of meroplanktonic larvae as well as – in summer 1994 – of gelatinous plankton such as coelenterates and chaetognaths.

Eriksson (1973) investigated off the west coast of Sweden holo- and meroplankton. On an average Copepoda comprised 69%, meroplanktonic larvae 19%, Cladocera 6%, Chaetognatha 3% and Copelata 2% of the total individual numbers. Blanner (1982) did the same in the Limfjord. Here the meroplankton greatly dominated the spring bloom, but during the rest of the year its relative importance was greatly surpassed by the holoplankton, particularly by the copepods. Off the coast of Northumberland, Wilson (1982) investigated annual cycles of stocks of meroplanktonic larvae, concentrating on horizontal and vertical distributions.

Almost all of the North Sea wide investigations of meroplankton were carried out on the basis of the CPR-surveys. Henderson & Marshall (1944) evaluated the CPR-surveys from 1932-1937 in the southern North Sea. The main centers of echinodermata larvae were off the Dutch-German coast and the northeast border of the Dogger Bank (extending to the Danish coast). The most important area for lamellibranch larvae was also the Dogger Bank. Marshall (1948) extended the evaluation of the meroplankton for the years 1938 and 1939 to the entire North Sea. The main productive period of the lamellibranch larvae in 1938 extended from May to July, the most important areas lying to the northwest (particularly in the Orkney-Shetland region) and in a region extending over the Dogger Bank (especially the northeast end) and the Great Fisher Bank. In both years by far the greatest production of echinodermata larvae took place from May to August in the southern Bight, the German Bight and off the Skagerrak. In northwestern waters much smaller populations were produced rather later in the year. Also, Rees (1951) analysed the CPR-surveys with respect to lamellibranch larvae, determining the greatest abundances over and to the northeast of the Dogger Bank, extending to the Danish coast. Rees (1952) and Lindley (1987) investigated the geographical distribution and seasonal fluctuations of decapod larvae in the North Atlantic and the North Sea, the latter finding correlations in the distributions with the water temperature.

During the winter ZISCH survey, Krause et al. (1995) found lamellibranch and Ophiuroidea larvae partly directly off the British and continental coasts but primarily over and to the northeast of the Dogger Bank. The largest concentrations of these larvae were associated with the Scottish Coastal Water and the Central North Sea Water. In early years a comparison has been made of records of the planktonic larvae of lamellibranchs with such knowledge as was available on the adult distribution on the bottom (Davis 1923, 1925; Stephen 1933, 1934). For the Ophiuroidea and lamellibranch larvae, the patterns found during ZISCH seemed to correspond to the North Sea wide distribution of the adults observed by Davis and Stephen. Likewise, both trochophora larvae and late polychaeta larvae were most abundant over the Dogger Bank, spreading with the Central North Sea Water to the northeast. Cyphonautes and Cirripedia larvae had large population maxima in the Skagerrak, which probably can be explained by the rocky coast of southern Norway and Sweden.

Protozooplankton: Species distributions and biomass for tintinnids (ciliata) in the North Sea and adjacent seas were already described by Gran (1915). Zeitzschel (1965, 1966), Lindley (1975) and Reid & John (1978, 1983) investigated stocks of ciliates based on CPR-surveys in the North Sea

and the North Atlantic. Due to the relatively large mesh size of the Hardy Recorder (270 μm) and the small size of these organisms, the quantitative representativity of such samples seems rather doubtful. Pingree et al. (1982) investigated the vertical distributions of protozoans and copepods in the Skagerrak as a function of water stratification. In the German Bight, Steiff (1988) investigated abundances, seasonal fluctuations and production of ciliates (tintinnids) and copepods. Uhlig (1982, 1990, 1995) investigated abundances as well as seasonal and long-term fluctuations of the heterotrophic dinoflagellate *Noctiluca miliaris*/*N. scintillans*. The 30 l water bottle series analysed by Krause & Kattner (1989) from the POSER project in the Rosfjord (Skagerrak) showed, in addition to copepods, considerable stocks of tintinnids (*Leptotintinnus pellucidus*). During the one month long investigation, the stock sizes of the copepods and the tintinnids were highly variable, depending on the wind-induced exchange processes of the water masses in the fjord. It is well known that in the Skagerrak area the protozooplankton belongs to one of the most frequent herbivorous groups, consisting to a great degree of tintinnids (Pingree et al. 1982). This reflects a situation in which the small size of algal cells of certain populations occurring in masses enables the protozooplankton to enter into competition with copepods for food resources (Chester 1978). Beers & Stewart (1967), Parsons and LeBrasseur (1970) and Berk et al. (1977) ascertained that, in general, microzooplankton feed on smaller sized particles which are not utilized efficiently by larger consumers. Thus the microzooplankton, as a trophic intermediate link, make the considerable production of ultraplankton available to higher order consumers. Cordeiro et al. (1997) investigated the spatial distributions of tintinnids in the North Sea in the spring of 1986. There is only very little quantitative, North Sea wide information on the stocks of protozooplankton.

3.1.2. Seasonal cycles

As a shelf sea in temperate latitudes, the North Sea is characterised by a pronounced seasonal cycle due to the differential solar energy input during the course of the year. This results in a strong seasonality of phytoplankton and zooplankton stocks. The CPR-Surveys, which have been conducted area-wide, at all seasons and over a long time period, are predestinated for investigations of the seasonal and long-term fluctuations of various species in the Standard Areas. Indeed, most of the publications evaluating CPR-material report on the seasonality of the stocks.

Based on the CPR-data a comprehensive analysis of the seasonal cycles of phytoplankton and copepods in the North Atlantic and the North Sea were given by Colebrook. So, Colebrook (1979) presented "means of transformed counts [$y = \log_{10}(x+1)$] of the numbers of copepods in samples of 3m^3 , based on all the samples taken in each month, averaged over all the years of sampling (1948 to 1976), in each of a set of standard areas". These presentations were then compared with the corresponding mean annual cycles of phytoplankton development, which were also determined from the CPR-data. With this, Colebrook could derive the timing and the amplitudes of the seasonal stock fluctuations of individual species as well as the entire phytoplankton and zooplankton stocks in the individual standard areas.

The Figure 6 shows as an example a clear geographical pattern of *Centropages hamatus* with the highest amplitudes in the coastal zones of the North Sea corresponding to the neritic habits of this copepod (from Colebrook in Fransz et al. 1991a). These results speak for the working methods of the CPR-surveys. The stocks of total copepods presented by Colebrook in Fransz et al. (1991a), however, appeared to reach merely maximal magnitudes of 1000 ind. m^{-3} (1 sample = 3 m^3 of filtered sea water) in the CPR-surveys of the North Sea, and this only in the outer German Bight. For this sea area, however, during the KUSTOS-project in spring of 1994 mean values of $20\,400 \text{ copepod ind. m}^{-3}$ were cited, gained with a vertically towed WP-2 net.

In addition, there are numerous publications on regional and point studies with regard to the seasonality of zooplankton organisms, most of which have the advantage of covering a greater part of the water column. To name a few examples: Lücke (1912) investigated zooplankton variability at the light vessel "Borkumriff". Van der Baan et al. (1972) studied the seasonal occurrence of decapod larvae and van der Baan (1980) of the scyphomedusae in the waters near "Texel" light vessel. Baretta (1980) published results on the seasonality of the smaller copepods and van Veer & Sadée (1984) about seasonal occurrence of the ctenophore *Pleurobrachia pileus* in the Dutch Wadden

Centropages hamatus

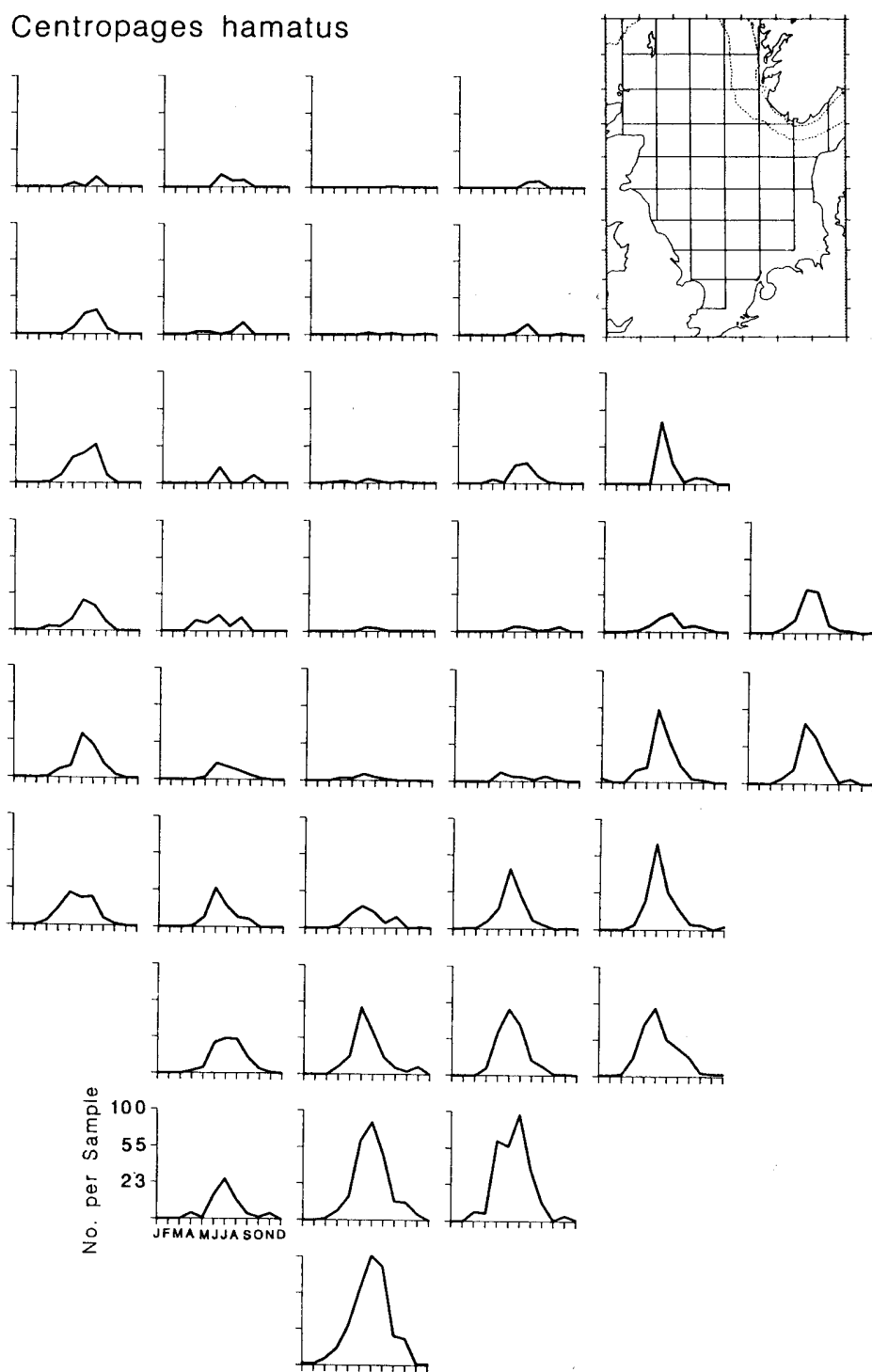


Fig. 6: The seasonal distribution of the neritic copepod *Centropages hamatus* in the North Sea (Colebrook in Fransz et al. 1991).

Sea. Martens (1980) investigated the stock fluctuations of the small copepods, cladocerans, medusae, appendicularians and the meroplanktonic larvae in the North Sylt Wadden Sea. He made estimates of the biomass by counting the numbers of individuals of the different taxa and using factors to convert these numbers to carbon values ($C\ l^{-1}$). Martens (1981) investigated the seasonality of phytoplankton and various *Acartia* species in the same marine area. Marshall et al. (1934) reported on the seasonality of *Calanus finmarchicus* in Loch Striven (Scotland), whereby here no differentiation was yet made between *Calanus finmarchicus* and *Calanus helgolandicus*. Hirche (1984) recorded the seasonal distribution of both species (*Calanus finmarchicus* and *Calanus helgolandicus*) in a Swedish fjord. Blanner (1982) investigated composition and seasonal variation of zooplankton in the Limfjord (Denmark). Wiborg (1954) reported on the seasonal stock fluctuations of copepods and other taxa of the mesozooplankton off the Norwegian coast.

Furthermore, regionally differentiated seasonal cycles were analysed for copepods (e.g. Bot et al. 1996) and total zooplankton (Tett et al. 1994). and for *Calanus* spp. (Planque 1997 et al.) in particular. In turn, for a single location seasonal cycles are more often more detailed. For instance, not only copepods are targeted (e.g. appendicularians off Plymouth, Acuna et al. 1995). A whole community approach was chosen by Greve & Reiners (1995) for the German Bight. On an ecosystem level seasonal cycle descriptions were provided for the Kiel Bay (Smetacek et al. 1984), but which cannot be extrapolated to the situation in the German Bight or even the North Sea.

Except for species triggered by light (Miller et al. 1991), changes in the annual cycle of decapod larvae (Lindley et al. 1993) and gelatinous species (Heyen et al. 1998) were related to changes in warmer winter temperatures providing suitable conditions for earlier growth and in calm weather conditions providing favourable conditions for copepods to utilise early plankton blooms (Colebrook 1978; Dickson et al. 1992).

In total, there is thus a large number of publications which deal with seasonal stock variability of zooplankton in the North Sea and adjacent waters. It is hard to summarise these results, since the data were gained with completely different methods. Nevertheless, it is worth trying to derive a way to use these individual results to get a picture of the seasonality of zooplankton in the North Sea. One possibility might be to convert the absolute numbers of individuals or values for biomass into relative values (e.g. percentages) in order to achieve a better comparability.

3.1.3. Long-term fluctuations

Since Cushing & Dickson (1976) started their comprehensive paper on climate and marine ecosystems with the introductory remark: 'For a long time events in the sea have appeared to be periodic', knowledge on cyclic behaviour of biological oceanographical records has rapidly increased due to the increasing availability of long-term data sets. These cycles can overlay linear climatic trends.

For the plankton the increasing availability of data sets of more than 20 years length has led to various analyses of periodic behaviour of biological time series. Periodic events, other than the seasonal cycles, were recorded having period lengths between >2 and 11 years. The longest, well documented plankton cycle is presumably the Russel-cycle in the English Channel (Cushing & Dickson 1976) with app. 40 years duration per cycle.

Colebrook tried to find evidence for the causes of the year to year fluctuations in phytoplankton and zooplankton stocks, and his statistical analyses brought him at first to the conclusion that, together with the currents, the levels of the overwintering stocks and the temperature are controlling the rate of population increase in the following year. That means that form and structure of the time series may be influenced from year to year by an "inherent persistence" modulated by temperature (Colebrook 1981, 1982a+b, 1984, 1985, 1986a). Nevertheless, a second option was a possible relationship between the annual fluctuations in the abundance of the zooplankton and long-term changes in climate, based on variations in the frequency of westerly weather from year-to-year (Colebrook 1978; Colebrook & Taylor 1984).

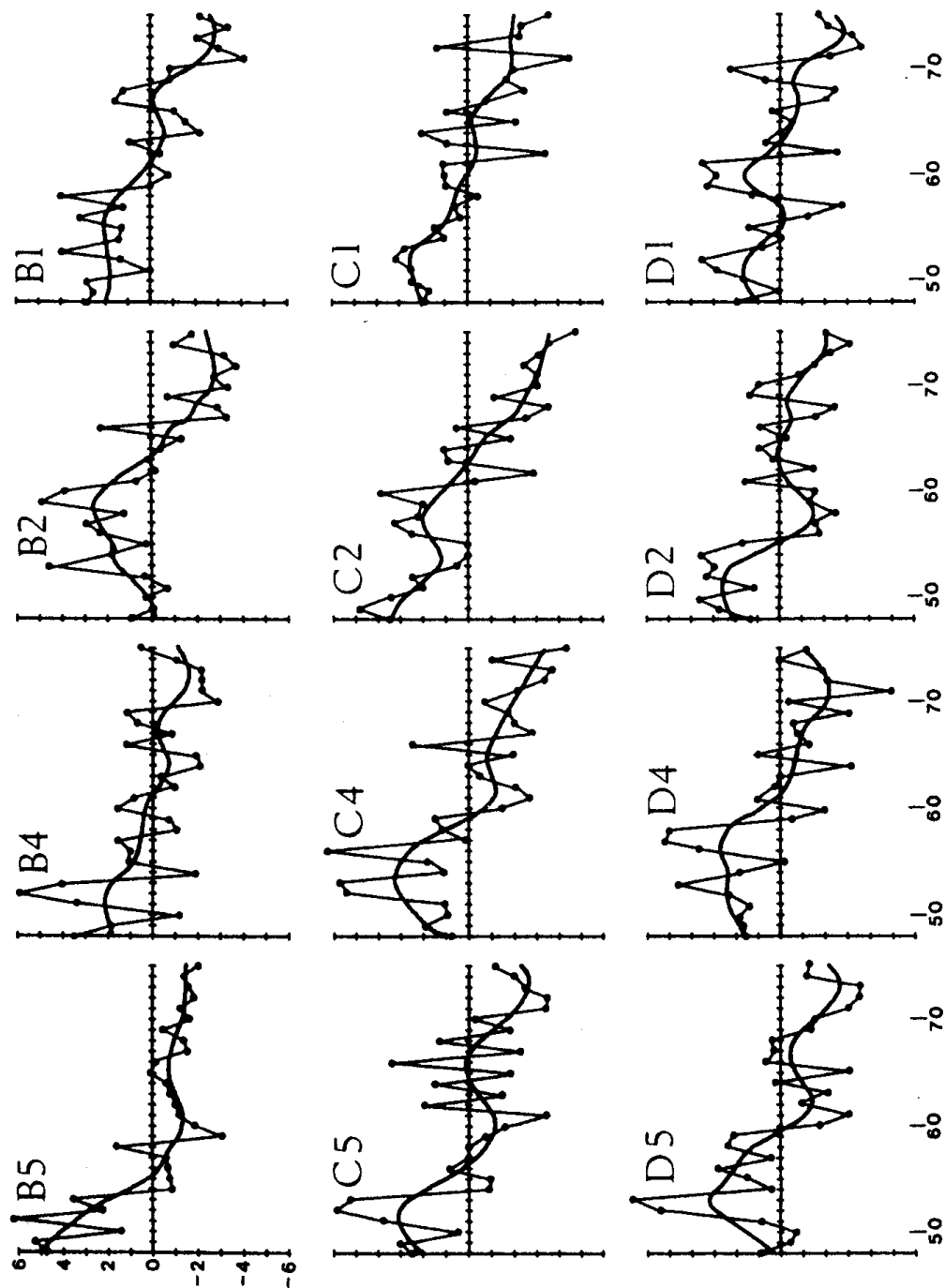


Fig. 7: Examples of the decreasing abundances of the copepods from the CPR-collections in different standard areas around the British Isles between 1948 and 1975. The principal component analyses has been used to describe the major year-to-year changes in the abundance of the zooplankton (Colebrook 1978).

Colebrook (1978) presented an approximately linear trend which was the dominant feature of the year-to-year changes in the abundance of the most taxa investigated by means of the CPR-surveys. That means, over the first three decades of the CPR-surveys – so in the 1950s, 1960s and 1970s - there has been a clear systematic pattern in the year-to-year changes in the plankton in the form of the quasi-linear downward trend (Fig. 7). The areas range from the shallow waters of the southern North Sea to open ocean areas (from the Faeroes to the Bay of Biscay). It is shown by 14 out of 24 species of phytoplankton and 16 out of 24 species of zooplankton (Colebrook 1978; 1982b). The extent of the trend varies from area to area and from species to species. The most pronounced decline in abundance was shown by the copepod *Pseudocalanus elongatus* in the North Sea, where its numbers were down to about 15% of those of 30 years ago. Most of the other species showed reductions of between a quarter to a half over the same period (Colebrook et al. 1984). Reid (1984) stated that the zooplankton of the North Sea has declined to a level that is approximately a third of its value of 30 years ago. The authors supposed to see for the first time signs of a consistent increase in abundance, from about 1980 onwards. However, this assumption does not appear to be confirmed in the CPR-data up to now.

Although Glover (1957) at first thought that, together with the reduction in stocks, a widely distributed change from neritic zooplankton (e.g. *Pseudocalanus sp.*, *Paracalanus sp.*, *Acartia sp.*) to oceanic species (e.g. *Clione sp.*, *Spiratella sp.*, *Calanus sp.*) had taken place, Cushing (1982) showed with long-term series that both the neritic and oceanic species showed the same reduction in stocks.

Evaluation of the CPR-data further showed that not only the annual means of the stock size changed but also their seasonal cycles. For *Pseudocalanus elongatus* in the southwestern North Sea and for *Spiratella retroversa* in the central North Sea the duration of the season became considerably shorter (Colebrook 1972 a+b). For *Temora longicornis* in the southern North Sea, there was a time lag of more than six weeks after 22 years and for *Acartia sp.* more than a month. Although no homogeneous pattern is evident, Glover et al. (1972) is of the opinion that in the Northwest Atlantic and in the North Sea the duration of the seasonal cycle has become shorter by about 1.5 days per year on the average over the past decades. The productive season has thus become reduced to somewhat more than five months, compared to approximately seven months thirty years ago. Cushing (1982) interpreted this that meanwhile one or two generations of zooplankton have been lost during an annual cycle.

Based on the CPR surveys, Cushing (1990) reported: In the western North Sea between the fifties and seventies, phytoplankton and zooplankton declined by a factor of 5, to recover in the eighties. The event was linked to strong northerly winds and gales by which the time of onset of production in spring was delayed. The decline in quantity between fifties and the late seventies was accompanied by a shortened productive season. Cushing referred to the investigations of Dickson et al. (1988a+b), who examined these changes. They constructed a chart of the air pressure difference between the fifties and seventies in the northern hemisphere and showed an increment of pressure over a broad area to the west of the British Isles. The establishment and subsequent intensification of a pressure-anomaly ridge over the eastern Atlantic between 1950s and 1970s supported an increased northerly airflow along the European littoral from the North Sea to northwest Africa. In effect, the seasonal build-up of the Azores-Bermuda High was earlier and more intense. This caused a long-term increase in northerly wind component and storminess over the eastern North Atlantic and European seaboard between 1950 and 1980. It was associated both with a decline of phytoplankton and zooplankton biomass in sea areas around the British Isles (and with an increase in upwelling intensity along the Iberian west coast). The onset of primary production was delayed, and phytoplankton stocks were declined in abundance. Consequently, the stocks of the herbivores (e.g. *Pseudocalanus elongatus*), and their growing season was shortened. Ultimately, this also has a negative effect on the herring stocks in the North Sea.

Hereby, Dickson et al. (1988a) referred to the investigations of Sverdrup (1953), who defined the „critical depth“ for the phytoplankton. The formation of organic substance through photosynthesis by phytoplankton sinks with increasing depth because of light attenuation. The depth at which photosynthesis is compensated by respiration is the critical depth. Growth resulting in a stock increase

cannot occur here. In the layers below, plants are no longer viable. Thus, the depth of a mixed surface layer must be less than the critical depth, if the phytoplankton population of the mixed layer shall increase. Storms increase the mixed layer, however, thus retarding algal growth.

Garrod & Colebrook (1978) found significant correlations between the water temperature in the surface layer of the North Atlantic and the annual stock sizes of zooplankton in the CPR catches. That means that the stocks decreased in the same way as the water temperature. These fluctuations in the water temperature as well as the salinity were attributed to the fluctuations in the position of the Gulf Stream (Taylor & Stephens 1980a+b), which were a result of atmospheric pressure anomalies. Taylor et al. (1992) and Taylor (1995) showed for the years 1966 to 1990 (or 1993) surprising agreement in the fluctuations of the north wall of the Gulf Stream compared with the logarithm of the number of copepods in areas of the CPR-surveys.

One should, however, keep in mind that the results mentioned above, which were obtained using CPR surveys, are area wide but based on an only two dimensional stock assessment of phyto- and zooplankton in 8 to 10 m depth. Wind stress can lead to a changed vertical distribution of any type of suspended matter. Thus, recent studies of Incze et al. (2001) showed that copepodite stages of *Temora spp.*, *Oithona spp.*, *Pseudocalanus spp.*, and *Calanus finmarchicus*, and all of their naupliar stages (except for *Temora spp.*) were found deeper in the water column when turbulent dissipation rates in the surface mixed layer increased in response to increasing wind stress. Taxa that initially occurred at the bottom of the surface mixed layer at 10 to 15 m depth (dissipation rate $\leq 10^{-8} \text{ W kg}^{-1}$) before the wind event located in the pycnocline at 20 to 25 m depth when dissipation rates at 10 m increased up to $10^{-6} \text{ W kg}^{-1}$. After passage of the wind event and with relaxation of dissipation rates in the surface layer, all stages returned to prior depths above the pycnocline. These results of Incze et al. (2001) indicate that turbulence from a moderate wind event can influence the vertical distribution of copepods in the surface mixed layer. That means in other words, the pressure-anomaly ridge over the eastern Atlantic found by Cushing and Dickson, which supported an increased northerly airflow must not inevitably have caused a decline of phyto- and zooplankton stocks in all investigated sea areas, but could have shifted the bulk of the organisms into deeper water layers. Through that, the Hardy-Recorder catching the plankton in 8-10 m of depth might not be able to meet them any more.

Nevertheless, further zooplankton stock investigations, which were not based on the CPR surveys but which confirm the long-term fluctuations at least for a part of the time period in question were carried out. So, Roff et al. (1988) found a declining trend of mesozooplankton abundance from 1971 to 1980 followed by a certain increase derived from investigations off the Northumberland coast. At a fixed station, 8 km off the coast the WP-2-Net was employed for vertical hauls over 53 m of the water column. All groups of meso- and macrozooplankton were analyzed by Roff et al. during a 15 year period. In addition, between 1961 and 1992, surveys of stocks were carried out by Astthorsson & Gislason 1995 in the area surrounding Iceland on 9 transects and 61 fixed stations. Vertical hauls were conducted with the standard Hensen net or the WP-2 net over the upper 50 m of the water column. A comparison of the long-term fluctuations from these investigations with the CPR-surveys also resulted in good agreement. George & Harris (1985) found even in the freshwater of Lake Windermere (U.K.) similar relationships between the plankton stocks and the northern front of the Gulf Stream like Taylor et al. (1992) and Taylor (1995) later on.

Turrell (1992) found relationships between the inflow of Atlantic water into the North Sea and the transport of Gulf Stream water. „The most likely cause of decreased Atlantic inflow was the coincidence of a minimum in Gulf Stream transport, resulting from a decline in the formation of 18° mode water in the Sargasso Sea, with the lowest occurrence of westerly winds that has occurred over the British Isles this century”. Corten (1999) investigated long-time variations in Atlantic plankton species in the North Sea in order to find support for the hypothesis of a reduced inflow of Atlantic water into the North Sea during the 1960s and 1970s. He also used the data material from the CPR-surveys between 1948 and 1996. *Candacia armata*, *Metridia lucens* and *Tomopteris spp.*, indicator species for Atlantic water, showed temporal variations which the author related to changes in Atlantic inflow. However, closer examination of the time series presented by Corten show that the three taxa considered from the CPR material only occurred in extremely low numbers of indivi-

duals. Other taxa which also indicate an origin in the Atlantic such as *Limacina* (= *Spiratella*) *retroversa*, *Clione limacina* or *Calanus finmarchicus* and were present in much greater numbers did not show these stock fluctuations.

Fromentin & Planque (1996) stated that west wind stress intensity and temperature are strongly related to the North Atlantic Oscillation (NAO). And fluctuations in abundance of *Calanus finmarchicus* and *C. helgolandicus* mainly result from a combination of several factors, driven by the NAO, namely west wind stress effects on spring primary production, temperature and competition between the two *Calanus* species. They found that since 1962 (previously both species had not been differentiated taxonomically) the long-term trends of the two *Calanus* species are opposite. According to the authors, *C. finmarchicus* shows a clear downward trend in abundance, while *C. helgolandicus* presents an upward one.

As above mentioned for the period 1970 to 1990 trends first showed a downward tendency until approximately 1980; after then an increase occurred both for total mesozooplankton (CPR-Survey Team 1992; Evans & Edwards 1993) and for selected copepod species (e.g. *Pseudocalanus elongatus* in Colebrook 1986b; for *Calanus finmarchicus* in Fromentin & Planque 1996), whereas for certain species opposite trends were recognised (e.g. for the larvacean *Fritillaria borealis* in Evans & Edwards 1993). This change was also visible in changes in community structure (Austen et al. 1991), also being visible in benthic community structure (Austen et al. 1991). A change in systems dynamics at that time was postulated by Lindeboom and co-workers (1995) with a shift from a 'benthic' to a 'pelagic' ecosystem.

Another change was recognised in 1989, when southerly waters entered the southern North Sea, indicated by invasions of doliolids (e.g. *Doliolum nationalis*) and siphonophores (e.g. *Muggiaea atlantica*) (Lindley et al. 1990; Greve 1994). Fluctuations in abundance were successfully related to climatic features (Aebischer et al. 1990; Dickson et al. 1992), whereas connections to fish abundance, and by this top-down control, were less evident (Rothschild 1998). Fluctuations in flow regime at the northern North Sea borders, esp. for *C. finmarchicus*, were related to import of Atlantic waters via the Fair Isle current (Stephens et al. 1998), which again was related to climate indicators such as NAOI. The relationship between NAOI and *C. finmarchicus* dynamics was shown by Planque and Fromentin (Fromentin & Planque 1996; Planque & Fromentin 1996).

Besides new species in the North Sea plankton at that the end of the 80's, changes in abundance were then also recognised, no longer following the pattern of climatic fluctuation as represented by the NAOI. This downward trend for zooplankton was observed in the southern North Sea for abundance and in the Bay of Biscay for copepod diversity (ICES 1998). As an hypothesis for the recurrent downward trend in the 90's increased wind induced turbulent mixing was suggested (ICES 1999).

Nevertheless, as mentioned above, closer examination of the time series presented by Corten (1999) for the CPR data from 1948 to 1996 reveals that, except for the relatively rare species *Candacia armata*, *Metridia lucens* and *Tomopteris* spp., hardly any of the taxa named seem to show a return to the stock sizes on the level of the 1950's, as had been expected by Colebrook and others at the beginning of the 1980's. On the contrary, species occurring in masses such as *Calanus* sp., *Para-* and *Pseudocalanus* sp., *Acartia* spp. and *Oithona* spp. but also phytoplankton species such as *Rhizosolenia alata* f. *inermis* and *Thalassiothrix longissima* show west of Scotland as well as in the northwestern North Sea up into the 1990's either an indifferent or even a decreasing trend. Planque & Batten (2000) even recorded that in 1997 in the catches of the CPR-Surveys the abundance and biomass of *Calanus finmarchicus* have been the lowest ever recorded in the north-eastern Atlantic. The authors stated that this recent phase of persistent decline appears to be uncoupled with the NAO signal.

This again raises the question as to the effectivity of the CPR-surveys. Of course, the example from Colebrook's investigations (Fig. 6) shows impressively the seasonal distribution pattern of *Centropages hamatus* as well as the regionally differing stock sizes of this neritic species in the North Sea. The publications cited above also demonstrate that the long-term fluctuations found in the

CPR-data are apparently caused by climatic processes, although a confusingly large and partly contradicting number of climate phenomena are cited as causal: e.g. westerly weather and west wind stress, northerly windstress and storminess, variabilities of the position of the north wall of the Gulf Stream, and reduced inflow of Atlantic water into the North Sea. Further, there are several examples in which the long-term fluctuations found in the CPR-surveys could be reproduced by other methods. Examples for this are the above mentioned publications by George & Harris (1985) in Lake Windermere, by Roff et al. (1988) off the coast of Northumberland and Astthorsson & Gis-lason (1995) around Iceland.

On the other hand, evaluations of long-term stock investigations with nets in the Norwegian Sea and the Barents Sea showed no clear interannual relationship between water temperature and copepod abundance (Tande et al. 2000). Beare et al. (2000) summarized zooplankton data of the Icelandic spring survey for the years 1960 – 1996, along with time-series information on sea surface temperature. Long-term displaced volume of zooplankton remained fairly stable although there were pronounced short-term fluctuations. Nevertheless, the proportion of specimens in each sample belonging to species with affinities to water of Atlantic type has fallen dramatically over the Iceland shelf since the 1960s, whereas the proportion of species with Arctic affinities has increased. This seems to contradict the permanent decrease in the boreal species *C. finmarchicus* and increase in the temperate species *C. helgolandicus* found by Fromentin & Planque (1996) in the northeast Atlantic.

Since the sampling in the CPR surveys is only two dimensional, the whole water column is not covered. Also, a comparison of long-term averaged CPR-data with the stock data for mesozooplankton from the surface net catches during ZISCH reveals a large discrepancy, whereby the CPR-data do not show nearly as high numbers of individuals as do the net samples from ZISCH. An estimate of the biomass is thus not possible with the CPR data. On the other hand, it is certainly possible to use them to detect qualitative signals for seasonal cycles of near surface species as well as – to a certain degree – for long-term fluctuations. Nevertheless, the strong decrease in zooplankton stocks in the entire area of investigation indicated by the CPR-surveys during the 1950's, 1960's and 1970's remains questionable. Then, even today the investigated stocks still do not seem to have reached the level of the 1950's again. The question arises as to whether the increasing cruising speeds of the ships of opportunity could have led to a reduction in catching efficiency of the recorder. There is no comparison with data sets which have been gained with other methods over the entire period of time. An attempt should be made to compile data from the period in question which can be compared with the CPR-data in order to verify or falsify the postulated reduction in zooplankton over the past fifty years.

3.1.4. Zooplankton biomass

In the past, various methods have been used in order to estimate the biomass of the zooplankton and its development in time and space. These include the determination of the displacement volume or of the wet or dry weight as well as measurements of the carbon content. By means of conversion factors from the literature it is possible, for example, to convert wet weight to dry weight or carbon content. Often, however, there are problems in obtaining biomass with this type of conversion, because the sample material might be contaminated with algae, detritus or anorganic particles. Experience has shown, for example, that summer net samples from the German Bight (mesh size 200µm) sometimes only contain 10% zooplankton. Therefore, it is often necessary to determine the biomass of individual components in the zooplankton. In such cases, the samples are taxonomically analysed, i.e. classified according to species and developmental stage, and the obtained numbers of individuals are then converted to dry weight or carbon content by means of conversion factors. Such conversion factors have been published by a number of authors (e.g. Bogorov 1934; Orr 1934; Laevastu 1957; Hagmeier 1961; Hillebrandt 1972; Frasz & van Arkel 1980; Williams & Lindley 1980; Dagg & Turner 1982; Carlotti et al. 1993; Christou & Veriopoulos 1993 etc.). Either the mean dry body weights of individual species and their developmental stages are directly determined and used as conversion factors, or an estimate is made based on the mean lengths of the organisms which are then converted to dry weight based on length-to-weight ratios.

In this case as well there are questions regarding the comparability of the individual methods with each other and with the actual biomass situation in the field.

The publications on stock investigations using the CPR-survey data only rarely give information about biomass estimates. Reid (1984) reported that using data from the CPR-survey an Index of zooplankton biomass (Glover et al. 1974) has been calculated for the period 1948 to 1982 in the North Sea. Nevertheless, he also considered that this index cannot be an estimate of the total biomass, because the CPR which is towed at 10 m depth does not sample the whole water column and young stages or soft bodied plankton are poorly sampled.

Robertson (1968) tried to contribute towards the development of a method for converting the numerical abundance of calanoid copepods obtained by the survey into estimates of biomass. Specifically, the method was developed for stages V and VI of the common calanoids from the recorder survey in the North Sea in 1961. Hereby, factors were determined with the objective of accounting for the younger stages which slip through the gauze of the recorder. Then, it was clear to Robertson that for the small copepod species only individuals in stage V or VI are large enough to be regularly retained by the recorder silk. In his investigations he was able to confirm the assumption of Saville (1958) that for most species of zooplankton, approximately 0.287 mm is the 50% escape breadth through silk of 60 meshes/inch. In view of this knowledge, it is surprising that based on the CPR-surveys so many stock investigations have nevertheless been attempted with the usually even smaller phytoplankton.

Kirkegaard & Lassen (1980) used the CPR-data between 1958 and 1975, in order to estimate the biomass of *Pseudocalanus* sp. CVI splitted in six standard areas of the North Sea. The seasonal maximum was found to be 0.05 – 0.5 g/m². Lindley (1982b) estimated the biomass of Euphausiacea in the North Sea and North Atlantic based on CPR-data. He found, for example, mean annual Euphausiacea stocks of 8.8 mg dw m⁻³ in the Norwegian Sea and of 5.3 mg dw m⁻³ in the north-eastern North Sea.

There are, however, a number of publications in which biomass estimates in the North Sea have been attempted using other sampling methods. For example, Hickel (1975) found a mean copepod biomass of 7.4 mg C m⁻³ in the Wadden Sea off the Island of Sylt. In the western Dutch Wadden Sea and the near shore North Sea the biomass of the metazoan herbivores reached peak densities of 50 – 100 mg C m⁻³ (Fransz 1983). Daan (1989) found on a fixed station in Dutch coastal waters biomasses of the copepods up to 165 mg C m⁻³ and of the carnivorous hydromedusa *Phialidium hemisphaericum* up to 7 mg C m⁻³.

Banse (1962) reported for depth integrated net zooplankton of the Fladen Ground in July and September a mean dry weight of 6.5 g dw m⁻². Krause & Radach (1980) registered with water bottles continuously increasing copepod biomass during an observation of the spring zooplankton development in the Fladen Ground (over 2 ½ months), and towards the end of the fixed station (beginning of June) *Calanus finmarchicus* alone achieved a mean biomass of 20 g dw m⁻² in the 100 m water column. Fransz & van Arkel (1980) found in the 100 m water column over Fladen Ground 40.72 mg dw m⁻³ zooplankton biomass in June. Likewise during FLEX'76 Williams & Lindley (1980) found in the Fladen Ground an ash-free dry weight of 2-8 g m⁻² at the end of May. Fransz & Tijssen (1983) determined the ash-free dry weight of *Calanus finmarchicus* during a drift in the Fladen Ground, also in summer, with two different nets. With the Horizontal High Speed Net they found 0.23 -, 1.28 – and 2.15 g adw m⁻² and with a vertical Net 5.58 -, 7.55 – and 19.04 g adw m⁻². Kiørboe & Johansen (1986) found copepod biomasses of 5 - 15 mg C m⁻³ and 2.8 - 8 mg C m⁻³ in September in the northwestern North Sea on two transects over the entire water column. Nielsen & Richardson (1989) made depth integrated determinations of copepod biomass at various stations in the North Sea in February/March of 1988. The total copepod biomass (all stages) increased from about 2.5 mg C m⁻³ at the northern stations to 8.8 mg C m⁻³ just south of the Dogger Bank.

In the northern North Sea Adams & Baird (e.g. 1968a+b, 1969, 1970, 1971, 1973) carried out area wide samplings of chlorophyll a and zooplankton on a fixed station grid in the 1960's and 1970's.

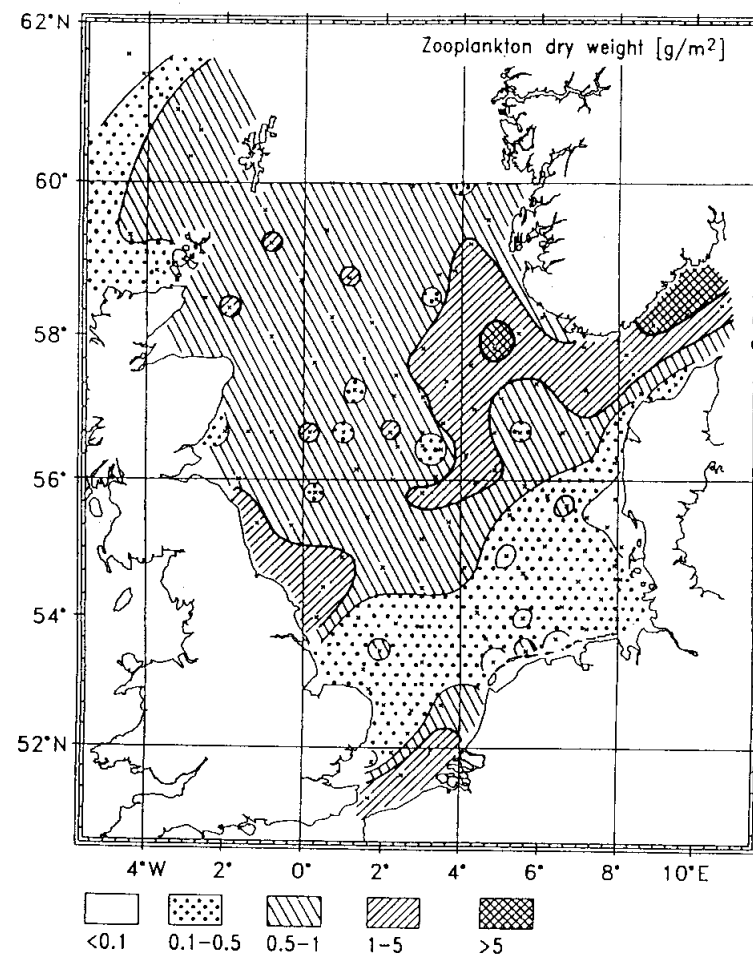
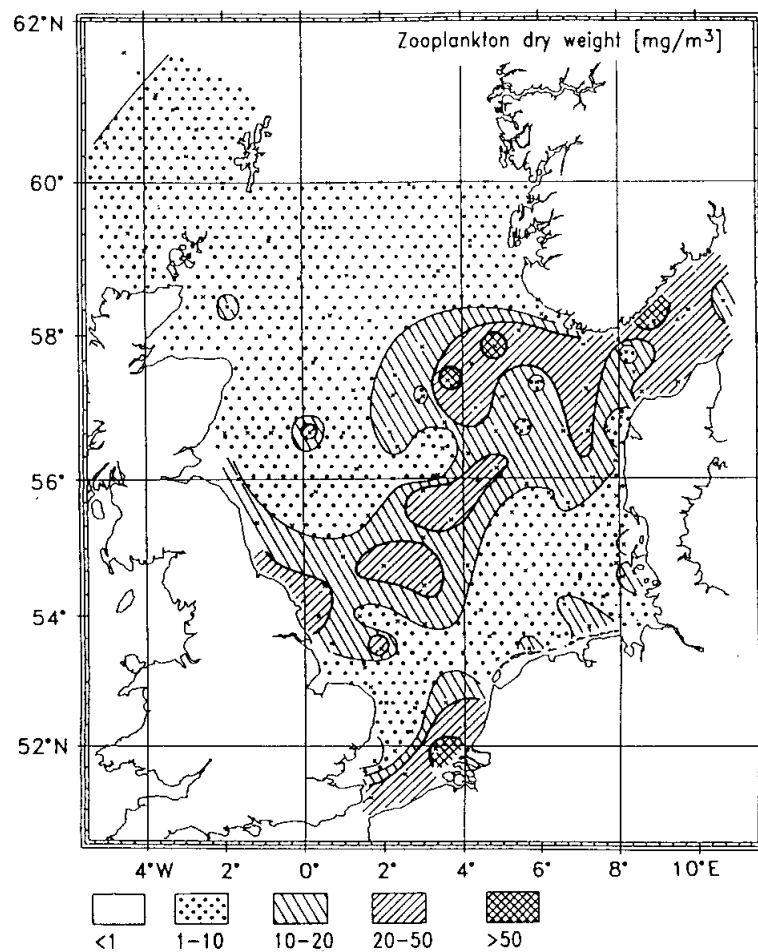


Fig. 8: Horizontal distribution pattern of zooplankton dry weight over the whole North Sea during the winter ZISCH stock mapping. Left side: mg dw m^{-3} ; right side: g dw m^{-2} (from Krause & Knickmeyer 1992; Krause et al. 1995).

The mean dry weights determined for the zooplankton of the summer months during some of the years are summarised in the following table:

year	mg dw m ⁻³	year	mg dw m ⁻³
1961	250	1968	350
1962	250	1969	250
1965	520	1970	550
1966	560	1971	210
1967	300		

On a fixed station grid in the North Sea, Hay et al. (1991) found mean copepod biomasses in the winter of 1987/1988 of 1.8 g dw m⁻² (October), 0.8 g dw m⁻² (Nov./Dec.), 0.54 g dw m⁻² (January) and 0.64 g dw m⁻² (Feb./March). Frasz et al. (1984) determined the ash-free dry weight of total zooplankton biomass in 1981 in the Oyster Ground (central North Sea). They found in May 1.7 g adw m⁻², in July 5.8 g adw m⁻², and in September 2.9 g adw m⁻². The biomass of the copepods alone amounted to 1.3 g adw m⁻², 2.3 g adw m⁻² and 1.5 g adw m⁻², respectively. At a fixed station in the Kattegatt in August 1989, Nielsen (1991) found biomasses between 1.05 and 1.82 g dw m⁻² and in September between 1.72 and 2.69 g dw m⁻² (Copepoda and Cladocera). Kiørboe & Nielsen (1994) found in the summer months in the Kattegatt biomasses of copepods up to 1 g C m⁻². Also in summer, Nielsen & Sabatini (1996) found up to 3 g C⁻² copepod biomass in the northern North sea and up to 0.8 g C m⁻² in the southern North Sea.

Regarding the northern and central North Sea, in early spring – already before the phytoplankton spring bloom – Euphausiacea constitute up to 90% of the zooplankton biomass (Williams & Lindley 1980). In April/May a shift from the Euphausiacea to the calanoid copepod *Calanus finmarchicus* takes place. During and after the phytoplankton bloom the proportion of *C. finmarchicus* is steadily increasing to about 90% in June (Williams & Lindley 1980; Frasz & van Arkel 1980). Later on this large copepod partly disappears from the near surface layers and probably even out from the shelf sea in order to enter a 'diapause' in the deep sea. Consequently, then small copepods like *Pseudocalanus elongatus*, *Paracalanus parvus*, *Centropages typicus* and *Oithona* spp. dominate the zooplankton biomass (e.g. Wiborg 1954; Davis 1987). In fall and winter the *Spiratella* (= *Limacina*) *retroversa* can contribute substantially to the overall zooplankton biomass in the northwestern North Sea. The chaetognatha contributed max 7% of the total biomass, the trachymedusae *Aglantha digitale* up to 5% and the amphipod *Parathemisto* spp. did not exceed 1.3%.

In the southern North Sea the biomass of large copepods (e.g. *Calanus helgolandicus*) does not play such a large role as *Calanus finmarchicus* in the northern North Sea. Important species there are rather the small copepods *Temora longicornis*, *Pseudocalanus elongatus*, *Acartia clausi* und *Centropages hamatus*. In the Oyster Ground area copepods contributed almost 70% of the zooplankton biomass in May, 35% in July and 48% in September. At times, blooms of meroplankton may outweigh the copepod biomass (Frasz et al. 1984) The gelatinous carnivores (medusae, Chaetognatha) represented 15.9 and 25% of the biomass in May, July and September, the appendicularian *Oikopleura dioica* about 11%.

Based on the stock-mapping of the ZISCH-cruises from 2 May – 13 June 1986 (127 stations; 369 samples) and from 26 Januar - 9 March 1987 (139 stations; 437 samples) the biomasses of meso-zooplankton over the whole North Sea were estimated by means of multi-closing net hauls (mesh size: 200 µm). For this, before the taxonomic analysis, the wet weight of the samples was determined. The results of the measurements were related to the flowmeter data, giving wet-weight m⁻³. Finally, these data were converted to dry weights by means of a conversion factor given by Cushing et al. (1958). Since after fixation of samples with formaline a reduction of biomass between 20 and 40% is observed (e.g. Landry 1978; Durbin & Durbin 1978; Daro & van Gijsegem 1982) these estimates can only be regarded as a rough approximation to the true conditions.

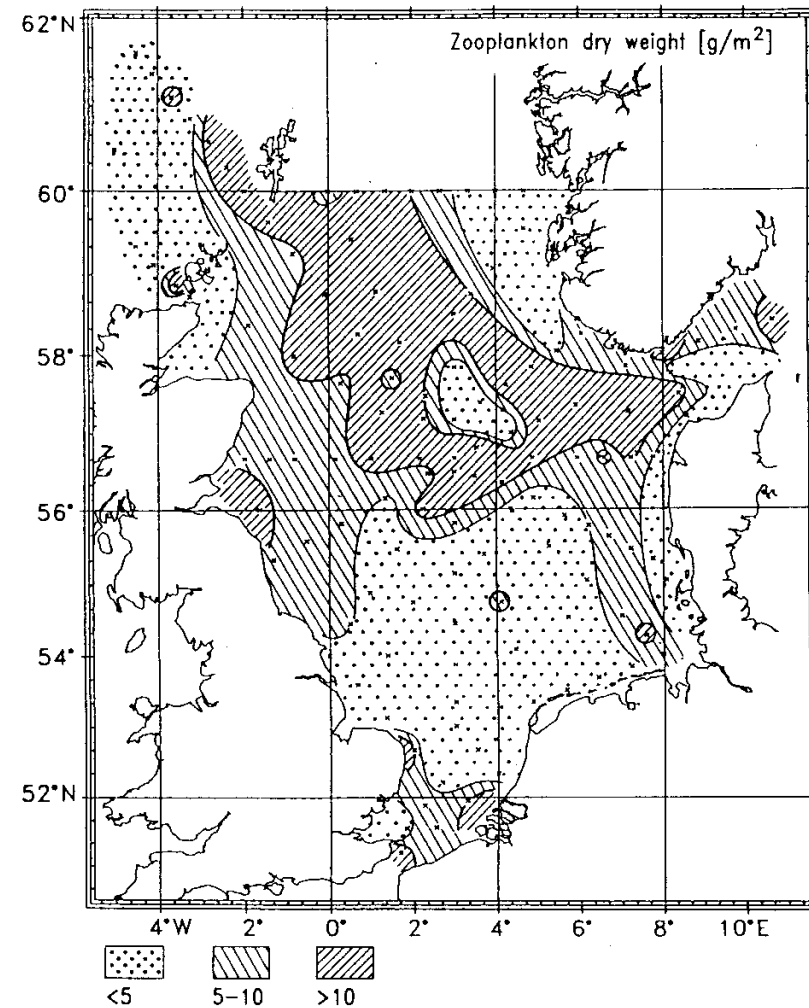
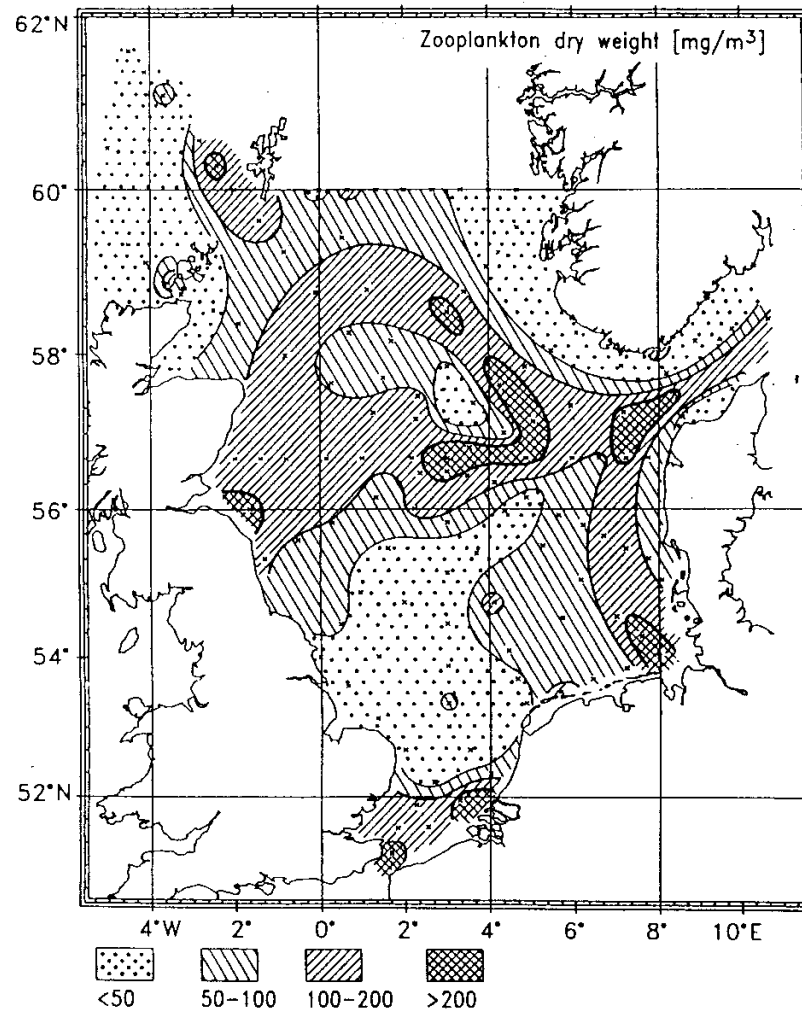


Fig. 9: Horizontal distribution pattern of zooplankton dry weight over the whole North Sea during the spring ZISCH stock mapping. Left side: mg dw m^{-3} ; right side: g dw m^{-2} (from Krause & Knickmeyer 1992; Krause et al. 1995).

With the above mentioned insufficiencies in mind, the data were used for a first quasi synoptical distribution of mesozooplankton-biomass in the North Sea. The Figures 8 and 9 show for the two ZISCH surveys the horizontal distribution patterns of zooplankton biomass. On the right side the biomasses are calculated for the whole water column (g dw m^{-2}); on the left side the mean densities are given (mg dw m^{-3}).

During the winter stock mapping (Fig. 8) larger biomasses ($> 1 \text{ g dw m}^{-2}$) were recorded along the English coast, off the mouth of the River Rhine as well as in the Skagerrak region. In the latter, areas were found with $> 5 \text{ g dw m}^{-2}$. In contrast, biomass $< 0.5 \text{ g dw m}^{-2}$ were found over extensive regions of the southern North Sea, and $< 0.1 \text{ g dw m}^{-2}$ in some areas along the Danish coast. Converting to mean values per m^3 of sea water in order to eliminate the influence of water depth, a different pattern of zooplankton distribution emerged. High concentrations of biomass ($10 - 50 \text{ mg dw m}^{-3}$) occurred in a small region off the mouth of the River Rhine, and in a broad band extending northeastwards from the English coast (from the Scottish border to the Humber), across the Dogger Bank into the Skagerrak. Particularly high concentrations occurred in a region extending from the Skagerrak to the southwest of Norway.

In contrast to the winter situation, the zooplankton stock map for late spring (Fig. 9) revealed large stocks ($> 10 \text{ g dw m}^{-2}$) at the shelf edge between the Shetlands and the Norwegian Trench, which were being advected into the northern North Sea via the two eastern Atlantic Water inflows as far as the mouth of the Skagerrak. These stocks of high biomass mainly consisted of populations of *Calanus finmarchicus*. To the south they were restricted in their spread by the Dogger Bank. In the shallow southern North Sea, smaller zooplankton stocks ($< 5 \text{ g dw m}^{-2}$) were usually found; exceptions being the Hoofden (Southern Bight) and a strip off the Danish coast, where stocks of $5 - 10 \text{ g dw m}^{-2}$ were observed. Here in particular, small copepods were dominant. After conversion to mean biomass per m^3 , a map of the zooplankton stocks still showed high concentrations in the central and northern North Sea ($100 - 200 \text{ mg dw m}^{-3}$), forming a cyclonic distribution pattern, bounded to the south by the Dogger Bank. The stocks off the Danish coast and in the Hoofden assume greater significance when expressed as density (Krause et al. 1995).

During the KUSTOS Project, stockmapping was carried out for zooplankton on a fine station grid in the German Bight in summer of 1994, spring of 1995 and winter of 1996. In Fig. 10 results for copepod biomass are presented. Dry weights were calculated for species and their developmental stages (ind. m^{-3} or ind. m^{-2}) using the corresponding conversion factors. For summer, maximum copepod biomasses of 10 g dw m^{-2} were found. The highest biomass was generally furthest offshore, i.e. in the more saline North Sea water. Near the shore the copepod stocks decreased continuously. This was also the case for the bulk of the other mesozooplankton, so that the lowest biomasses were found off the North Frisian coast (Krause et al. In prep.).

It can thus be stated that the relevant literature supplies a large amount of information on zooplankton biomass in various regions of the North Sea. Here, as well, the data need to be examined with respect to comparability and the possibility of creating integrated data sets.

3.1.5. Contaminants in zooplankton stocks

During the ZISCH- and PRISMA-Projects besides stock mapping also the concentrations of contaminants like cyclic organochlorines or heavy metals in the zooplankton were investigated.

In the framework of the ZISCH-Projekt during the declining spring plankton bloom Knickmeyer & Steinhart (1989) determined the concentrations of five cyclic organochlorines ($\Sigma 24$ PCB congeners, α -HCH, γ -HCH, HCB, p, p'-DDE) in zooplankton samples of the whole North Sea. For instance, the geographical differences in concentrations of Σ PCB showed higher concentrations at the British and continental coasts, the Dogger Bank and the region near Bergen. Maximum concentrations of all the contaminants were found at stations near the continental coast. On the other hand, the highest loads of these pollutants appeared to be incorporated in the large zooplankton stocks

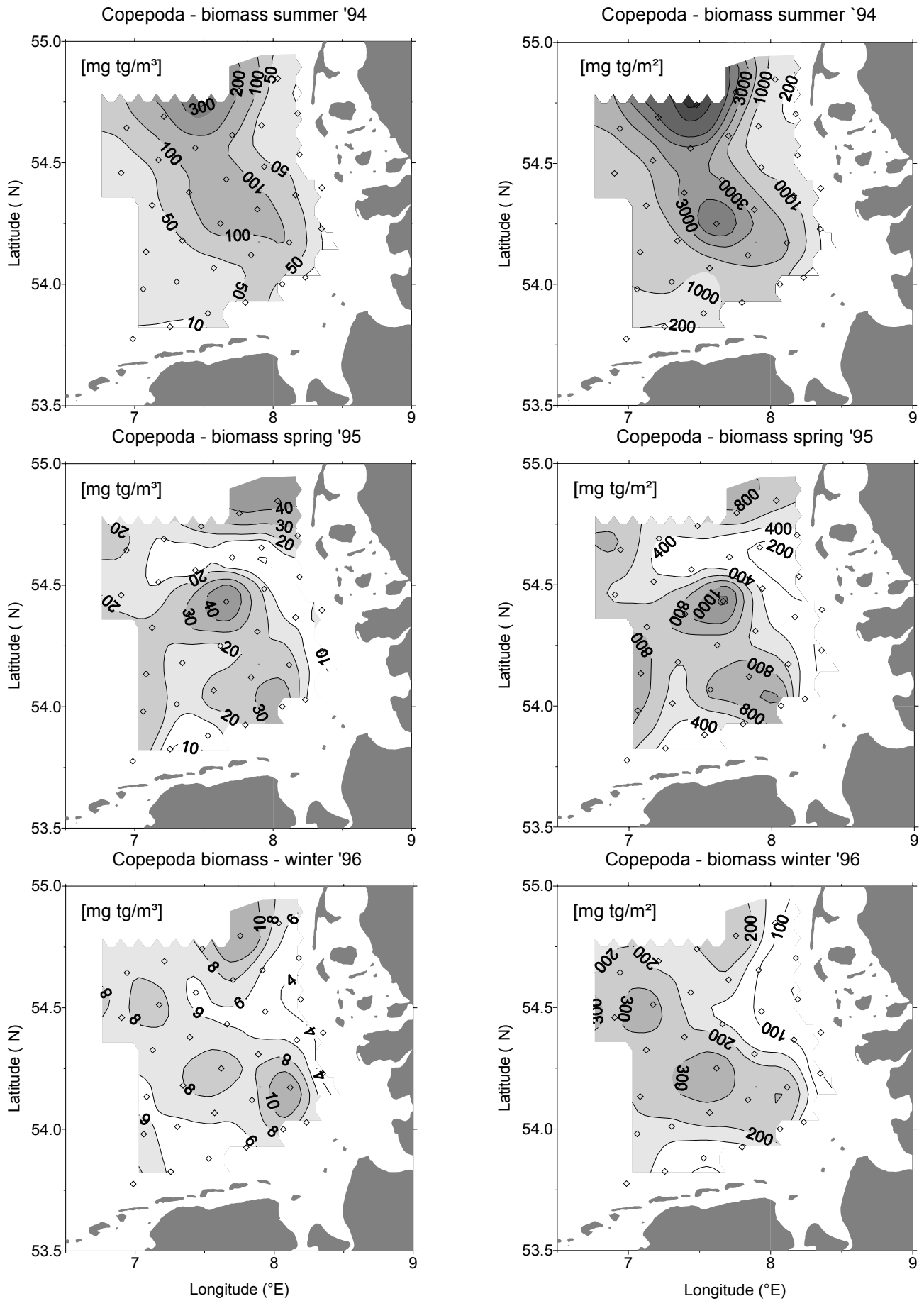


Fig. 10: Horizontal distribution pattern of copepod dry weight over the German Bight during the KUSTOS stock mapping in summer'94; spring'95 and winter'96. Left side: mg dw m⁻³; right side ma dw m⁻² (Krause et al. In prep.).

of the northern and central North Sea, north of 56°N (Krause & Knickmeyer 1992). An example for this is given for the distribution of Σ PCB in Fig. 11.

During the PRISMA-Project, on several cruises trace metals (Cd, Cu, Zn, Pb, Ni) were determined in different zooplankton taxa to assess their role in the biogeochemical cycle in the North Sea and published by Zauke et al. (1996). For this, immediately after sampling individuals were selected from the material in a clean bench, rinsed in ultrapure water and collected in measurable quantities in acid-washed flasks. Primarily, the copepodite stages V and VI of *Calanus spp.* were prepared for heavy metal detection, for which about 200 individuals were needed for each measurement. A total of about 440 sorted samples were obtained from all cruises for metal determination. As can be seen in Fig. 12 for instance Cd levels in *Calanus spp.* increased significantly from 0.68 mg kg⁻¹ in the German Bight to 11 mg kg⁻¹ at some stations around Scotland above 59°N, in line with ZISCH-data reported for the benthic hermit crab, *Pagurus bernhardus* (Karbe et al 1989).

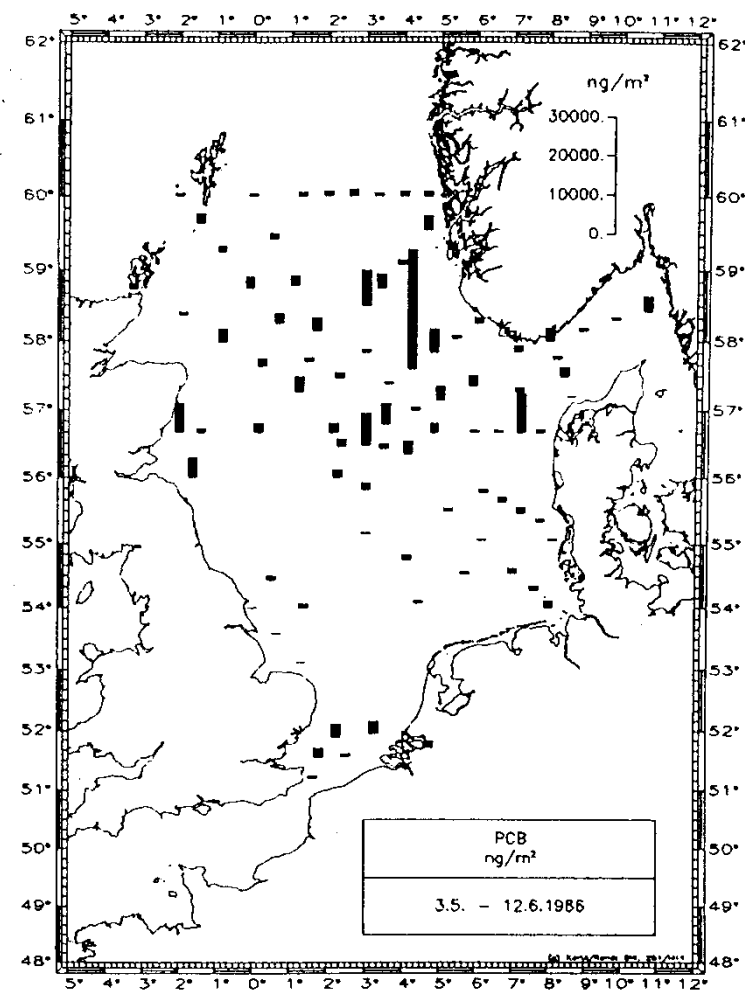
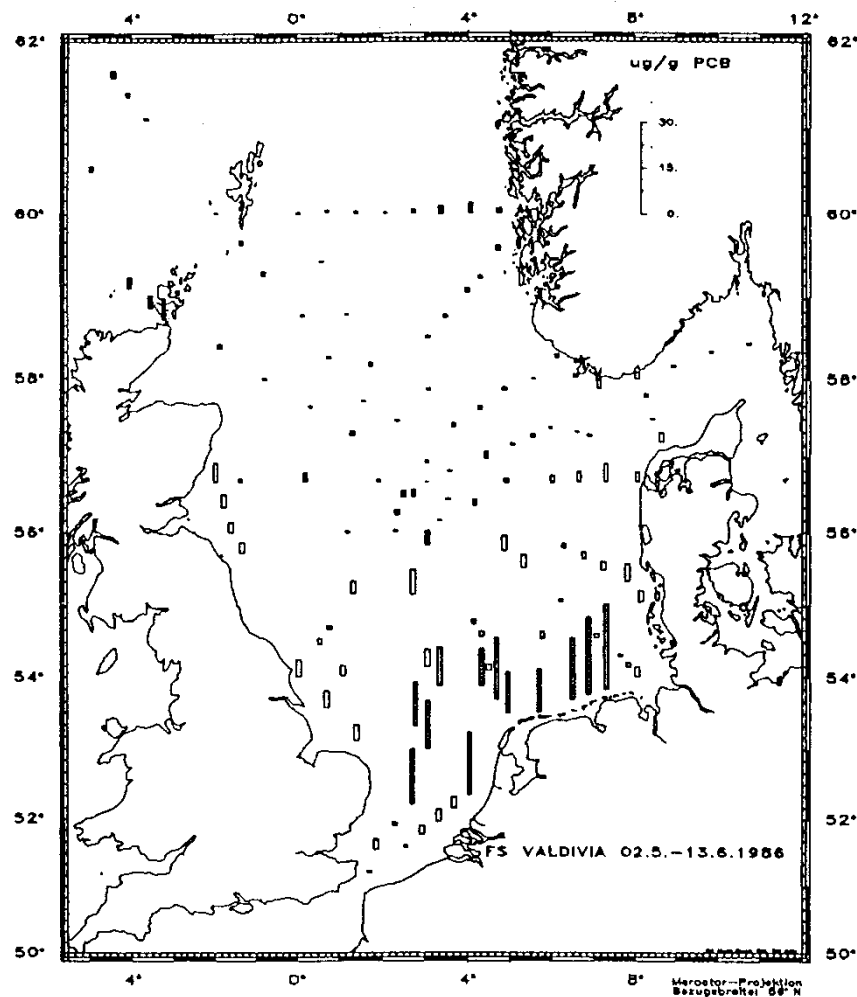
Karbe et al (1994) and Heyer et al. (1994) published their results from the ZISCH surveys, supplying comparative results on contaminant concentrations (organochlorines, heavy metals) and their accumulation in the various ecosystem compartments in the German Bight and the entire North Sea. Haarich et al (1993) used PRISMA data to compare heavy metal loads in zooplankton (*Calanus spp.*), particulate matter and water in northwestern North Sea.

Further investigations on the contaminant concentrations in zooplankton were carried out in the North Sea e.g. by Topping (1972), who investigated heavy metals in zooplankton from Scottish waters. Ten-Berge & Hillebrandt (1974) investigated uptake and accumulation of organochlorines through marine organisms in the North Sea and Dutch Wadden Sea. Witzel (1989) studied heavy metal concentrations in copepods of the German Bight and found, among other things, that in general higher heavy metal concentrations were measured in the inner German Bight, whereas the more offshore regions, influenced by water of the central North Sea, showed decreased values. The author found indications that physiological processes can regulate the uptake and retention of heavy metals in copepods.

In addition, there are a number of experimental studies concerned with the effects of contaminants on plankton which were mostly carried out in mesocosms. Usually, species shifts in phytoplankton and zooplankton were found after addition of petroleum (e.g. Dunstan et al. 1975; Parsons et al. 1976; Kuiper et al 1984), copper (e.g. Thomas et al. 1977; Thomas & Seibert 1977), cadmium (e.g. Kuiper 1981) organochlorines (e.g. O'Connors et al. 1978) as well as plant nutrients (e.g. Gamble et al. 1977). In general, in the contaminated tanks there was a phytoplankton species shift away from large centric diatoms towards small microflagellates and pennate diatoms which, according to the authors, are more resistant to contaminants. This, of course, also has consequences for the species composition of the consumers, the herbivorous zooplankton.

Zooplankton also showed species shifts in the contaminated mesocosms. Reeve et al. (1977a+b) are of the opinion that the toxicity of heavy metals in copepods is proportional to their size, and Gibson & Grice (1977) report that the small copepod *Pseudocalanus sp.* dominated in tanks contaminated with copper. This was also observed by Gamble et al. (1977) and Davies & Gamble (1979) in copper and in mercury contaminated tanks. Other authors such as Reeve et al. (1976) showed, however, that based on laboratory studies, predatory zooplankton organisms such as ctenophores reacting more sensitively to a number of contaminants than their prey organisms, could also be responsible for a stock shift towards smaller copepods following the reduction of predators due to contaminant effects. Thomas et al. (1977), however, hypothesised on the contrary that the small zooplankton in the copper contaminated tanks was inhibited in its development in such a way that its food organisms, the microflagellates, could reproduce in masses.

Impairment of one organism group through contaminants has effects on all trophic levels of the food web in the form of a chain reaction. Ryther (1969) found that the production of resources usable by humans, e.g. fish, has a relationship to the length of the food chain. If a phytoplankton community is, for example, dominated by small flagellates, there is a relatively long chain of



Quelle: ZISCH, Teilprojekt C4/G8

MUDAB (Meeresumwelt-Datenbank)
UBA-UMPLIS/DHI

Fig. 11: comparison of the concentrations of Σ PCB (left side) and the load of Σ PCB (right side) in zooplankton during the ZISCH - North Sea Survey in spring 1986 (Knickmeyer & Steinhart 1989; Krause & Knickmeyer 1992).

Trace Metals in Mesozooplankton of the North Sea

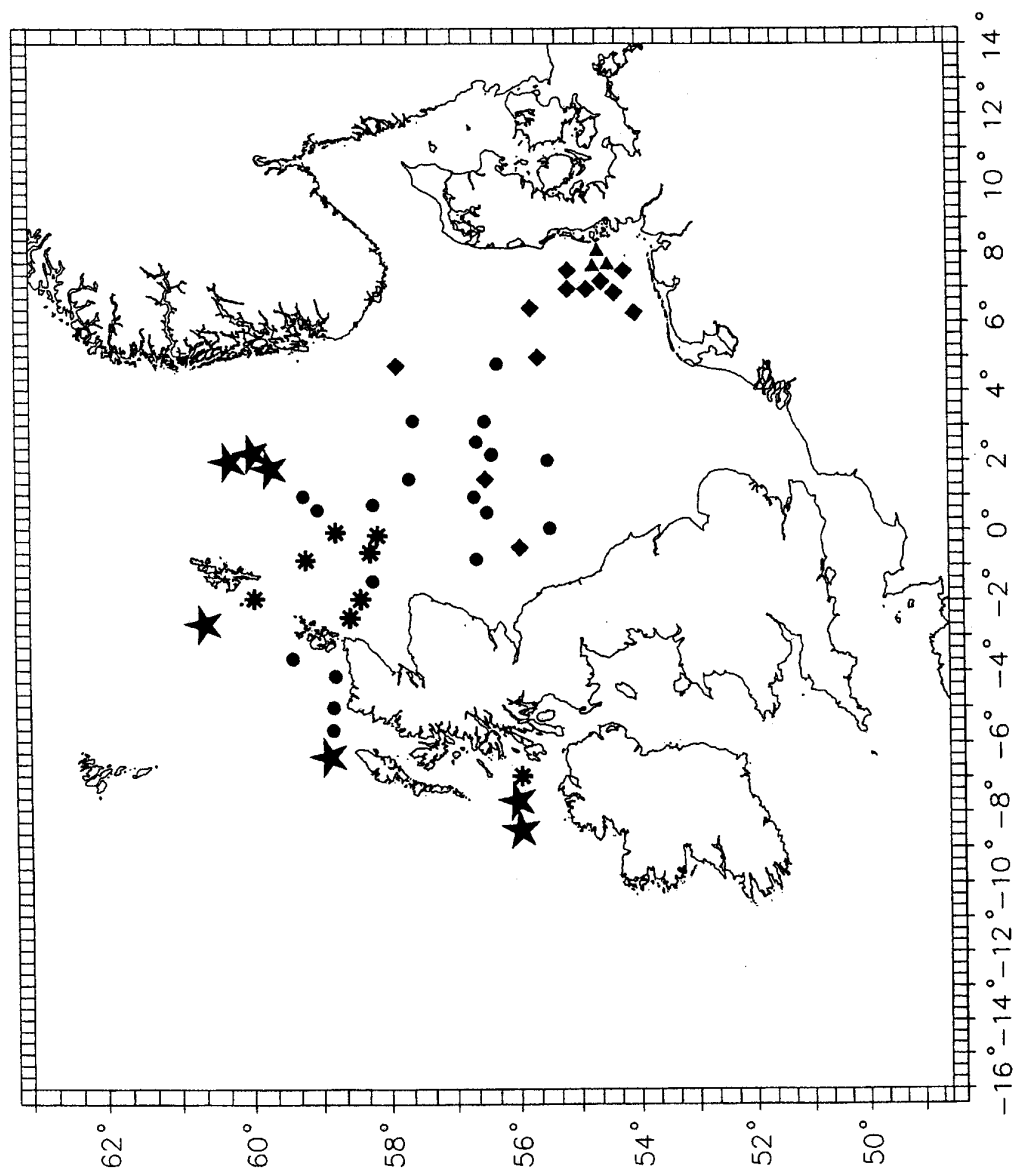


Fig. 12: Spatial heterogeneity of Cd in *Calanus spp.* in different regions of the North Sea and adjacent Atlantic waters during PRISMA stock mapping. Group 1 (▲) 0.7 mg Cd kg⁻¹; group 2 (◆) 1.8 mg Cd kg⁻¹; group 3 (●) 3.2 mg Cd kg⁻¹; group 4 (○) 5.0 mg Cd kg⁻¹ and group 5 (✱) 11 mg Cd kg⁻¹ (Zaucke et al. 1996).

★

✱

subsequent links to the fish. In the case of large diatoms as primary producers, the energy is passed on in one or two trophic steps to fish and the efficiency is higher. Greve & Parsons (1977) hypothesised two basically different pathways for energy transfer in the food chain:

- Large phytoplankton cells (centric diatoms, dinoflagellates) are caught and eaten preferentially by large copepods, corresponding to their relatively coarse filter apparatus. Such copepods, as for example *Calanus finmarchicus*, are preferred by the various juvenile fish larvae and pelagic fish species (e.g. Herring).
- Small zooplankton, on the other hand, eats preferentially small algae (e.g. flagellates) and is eaten primarily by medusae and ctenophores. These predators can thus develop particularly well, since large copepods would probably be capable of damaging their tentacles and might control their population strengths whilst eating their juvenile stages.

Therefore, if increased inputs of plant nutrients and diverse contaminants cause massive developments of small primary producers, this would promote development of the small zooplankton, which could ultimately lead to a „switch“ in the food web from a fish production to a jellyfish production system. There is definitely a need for research on this matter.

3.1.6. Stock data from the projects in Hamburg

In the interdisciplinary marine research projects carried out in Hamburg since the beginning of the 1970's, the North Sea and its adjacent waters had a high priority in the investigations. In physical oceanography, hydrographic data during field investigations have been gained with the help of IT-supported sensor systems for some time now. In the SFB-94 and the ZISCH, PRISMA and KUSTOS projects, which were led and mainly planned by physical oceanographers, the zooplanktological working group always tried to produce zooplankton data sets with a similarly high resolution as that of the physical data sets. Using traditional methods, this was only possible with a tremendous effort expended to collect and evaluate the samples during the many cruises. While the physical oceanographers already had their data in the computer when they got home, the zooplankton data could only be assembled during years of intensive work at the microscope. This time lag in the availability of the different data sets had the practical consequence that the cooperative evaluation of the data was often reduced to a minimum. This has led to the bizarre situation that, on the one hand there is a considerable „hunger“ for stock data on marine organisms while, on the other hand, large data sets exist which are in danger of becoming unavailable.

Table 5 gives a summary of the stock data for zooplankton gained in the Hamburg projects. Project name, research vessels, times and areas of investigation, collection devices and existing data quantities are given. In total, nearly 700 000 stock data are available. This number is constantly increasing as samples from the last projects continue to be evaluated. In addition, there are thousands measurements of the lengths of investigated organisms, heavy metal concentrations for selected taxa, dry weight and lipid determinations for individual developmental stages of important copepods as well as measurements of respiration and excretion which were carried out at various seasons on a copepod mix.

As can also be seen from Table 5, samples were usually collected by means of water bottle series and the simple WP-2 net (mesh size: 200 µm). This was not only because more sophisticated equipment was not available. It was also important to try to reduce the time necessary for taxonomic identification to fit the constraints of short-term projects. This was achieved partly by apportionment of this work. It was already possible to derive results on the stock size and horizontal distribution of the mesozooplankton by evaluating the WP-2 net hauls. If then, for example, information about stratification phenomena of the zooplankton or diurnal vertical migration was needed, in a further step the water bottle series, which were collected in parallel to the net hauls, could be evaluated. Good results had already been achieved with the water bottle series during the Fladen Ground Experiment (FLEX '76). In addition, these samples, which are filtered through a fine gauze of 70 µm, also contain the smaller zooplankton components.

Interdisciplinary Projects	vessel	time of investigation	Sea area	sampling gears	existing data	data form
Norwegian Sea '69	ANTON DOHRN	08.08.-15.08.69	62°59'N 3°44'E	LH-Plankton-Recorder	ca. 53 000	counting lists
PREFLEX '75	METEOR I	03.07.-14.07.75	58°55'N 0°32'E	water-bottle series	ca. 7 680	EXCEL
FLEX '76	METEOR I	26.03.-13.06.76	Fladen Ground	water-bottle series	ca. 220 000	EXCEL
POSER '79	VICTOR HENSEN	02.03.-05.04.79	Rossfjord/Skagerrak	WP2-Net/water-bottle series	ca. 49 800	counting lists
SEAPLAD '82-85	VALDIVIA 2	27.04.-01.05.82	58°55'N 0°32'E; 56°N 6°E	WP2-Net/water-bottle series	ca. 600	counting lists
	VALDIVIA 4	17.06.-22.06.82	58°55'N 0°32'E; 56°N 6°E	WP2-Net/water-bottle series	ca. 10860	counting lists
	VALDIVIA 8	02.10.-12.10.82	58°55'N 0°32'E; 56°N 6°E	WP2-Net/water-bottle series	ca. 14630	counting lists
	VALDIVIA 9	01.03.-11.03.83	58°55'N 0°32'E; 56°N 6°E	WP2-Net/water-bottle series	ca. 2180	counting lists
	VALDIVIA 11	26.04.-06.05.83	58°55'N 0°32'E; 56°N 6°E	WP2-Net/water-bottle series	ca. 13240	counting lists
	VALDIVIA 14	17.08.-27.08.83	58°55'N 0°32'E; 56°N 6°E	WP2-Net/water-bottle series	ca. 12700	counting lists
	VALDIVIA 17	12.10.-20.10.83	58°55'N 0°32'E; 56°N 6°E	WP2-Net/water-bottle series	ca. 7710	counting lists
	VALDIVIA 18	22.02.-02.03.84	58°55'N 0°32'E; 56°N 6°E	WP2-Net/water-bottle series	ca. 11960	counting lists
	VALDIVIA 19	25.04.-05.05.84	58°55'N 0°32'E; 56°N 6°E	WP2-Net/water-bottle series	ca. 3320	counting lists
	VALDIVIA 24	19.02.-28.02.85	58°55'N 0°32'E; 56°N 6°E	WP2-Net/water-bottle series	ca. 31970	counting lists
	VALDIVIA 27	16.04.-25.04.85	58°55'N 0°32'E; 56°N 6°E	WP2-Net/water-bottle series	ca. 1260	counting lists
	VALDIVIA 31	13.06.-27.06.85	58°55'N 0°32'E; 56°N 6°E	WP2-Net/water-bottle series	ca. 12230	counting lists
NORSCVATN '83	VALDIVIA 10	21.03.-20.04.83	Norwegian Trench	WP2-Net/water-bottle series	ca. 41 000	EXCEL
MIZEX '84	VALDIVIA 21	15.06.-25.07.84	Fram-Strait	MC-Net/water-bottle series	ca. 25300	counting lists
ZISCH I (Spring)	METEOR II	02.05.-13.06.86	whole North Sea	Multi-Closing-Net	ca. 8 380	counting lists
ZISCH I (Winter)	METEOR II	28.01.-05.03.87	whole North Sea	Multi-Closing-Net	ca. 75000	EXCEL
ZISCH II	VALDIVIA 76	29.11.-08.12.88	Heligoland Bight	WP2-Net	ca. 4000	EXCEL
	VALDIVIA 77	20.01.-23.01.89	Heligoland Bight	WP2-Net	ca. 1960	EXCEL
	GAUSS 127	27.02.-03.03.89	Heligoland Bight	WP2-Net	ca. 1510	EXCEL
	VALDIVIA 79	21.03.-23.03.89	Heligoland Bight	WP2-Net	ca. 450	EXCEL
	SENCKENBERG	10.04.-13.04.89	Heligoland Bight	WP2-Net	ca. 1420	EXCEL
	GAUSS 131	03.05.-06.05.89	Heligoland Bight	WP2-Net	ca. 1870	EXCEL
PRISMA	VALDIVIA 103	18.09.-04.10.90	Scottish Waters	WP2-Net	ca. 2110	EXCEL
	VALDIVIA 110	15.04.-29.04.91	Heligoland Bight	WP2-Net	ca. 4840	EXCEL
	GAUSS 180	17.04.-30.04.91	Heligoland Bight	WP2-Net	ca. 4550	EXCEL
	HEINCKE 15	18.08.-28.08.91	Heligoland Bight	WP2-Net	ca. 3010	EXCEL
	GAUSS 189	15.08.-30.08.91	Heligoland Bight	WP2-Net	ca. 3130	EXCEL
OPTINOM /TUVAS	METEOR 19	02.10.-10.10.91	North Sea/Hel. Bight	WP2-Net	ca. 3300	EXCEL
	VALDIVIA 123	07.09.-11.09.92	Heligoland Bight	WP2-Net	ca. 3000	EXCEL
KUSTOS	VALDIVIA 147	26.07.-11.08.94	Heligoland Bight	WP2-Net	ca. 5310	EXCEL
	HEINCKE 62	25.07.-11.08.94	Heligoland Bight	WP2-Net/water-bottle series	ca. 5200	EXCEL
	GAUSS 258	25.04.-11.05.95	Heligoland Bight	WP2-Net	ca. 6120	EXCEL
	HEINCKE 69	26.04.-10.05.95	Heligoland Bight	WP2-Net/water-bottle series	ca. 6500	EXCEL
	HEINCKE 74	15.08.-22.08.95	Heligoland Bight	WP2-Net	ca. 2100	EXCEL
	VALDIVIA 156	20.08.-22.08.95	Heligoland Bight	WP2-Net	ca. 3670	EXCEL
	ALKOR 11/96	23.02.-06.03.96	Heligoland Bight	WP2-Net/water-bottle series	ca. 6960	EXCEL

Tab. 5: List of stock-data of mesozooplankton from the North Sea and adjacent areas collected during the Hamburg- Projects.

Further more, through the continuous use of the same collection devices in the different projects it was possible to compare the stock sizes in the different investigated marine areas and seasons.

In spite of a number of publications and many impulses for the other disciplines participating in the projects, there is still a tremendous amount of potential evaluation which could be carried out with this material. It was collected in the context of interdisciplinary projects within which zooplankton was only one component of many. An optimal evaluation of interdisciplinary projects must involve collaborative work on the different data sets.

For this, it is not sufficient to encourage the colleagues to produce interdisciplinary output each from his or her separate niche. A true interdisciplinary collaboration requires support. This would include, for example a functioning central data bank with experts who are capable of transforming the various data sets so that they are compatible and of storing them in such a way that they do not become unavailable or unuseable. Another necessity for successful scientific work is the building of trust. For example, the willingness to expend such effort to compile the huge data sets on the abundances of zooplankton in the North Sea grew out of the trust in the know-how and will to cooperation on the part of the physical oceanographers to handle such data sets. It is only in the past few years that PC hardware and software have developed to such a degree that single persons with enough IT competence can carry out such work alone. In the private economy it is now a matter of course to reduce the time factor for the output of products based on division of labour and teamwork.

3.2. Vertical migration

Diurnal vertical migrations of zooplankton populations were observed and described very early (e.g. Cuvier 1817; Brady 1883; Tizard et al. 1885; Loeb 1893). Their ecological function was also considered. Nelson (1912), Cronin et al. (1962) and Bosch & Taylor (1973), were of the opinion that vertical migrations help estuarine zooplankton to control its horizontal distribution, i.e. to remain in the same sea area in which they originated and not be transported out into the open water. Kimmerer & McKinnon (1987) found that in Western Port (Victoria, Australia), the adults of the most abundant resident species, *Acartia tranteri*, maintain their horizontal distribution by undergoing vertical migration in synchrony with the tides. There, where currents and countercurrents are superimposed upon each other, vertical migrations can also help to maintain the horizontal distribution. It is thus quite conceivable that – as Backhaus et al. (1994) assume – the reproduction stocks of *Calanus finmarchicus* in the mixed layer of the Northeast Atlantic Current drift to the north while the overwintering stocks, after having „transferred“ to the transitional zone between Atlantic Water and Arctic Bottom Water (see Fig. 4), are subject to a southward drift.

Nevertheless, Hardy (1956) suggested that vertical migrations make it possible to reach new environments for the passively drifting organisms. Lane (1975) supposed after a comparative study of the zooplankton of four diverse lakes that vertical migrations reduce interspecific competition by providing a mechanism enabling species to select habitats that are occupied by fewer competitors or are rich in food. McAllister (1969) supposed that vertical migration reduces intraspecific competition in zooplankton by enhancing algal production during daylight and giving the phytoplankton time to recover from herbivory. There are, however, numerous publications in which reverse diurnal vertical migrations of zooplankton are described, where the organisms are in the surface layer at daytime and at depth at nighttime.

In the last century, an enormous volume of literature (646 registered publications) about diurnal and seasonal vertical migrations of zooplankton and about their reasons has been accumulated. Several theories have been advanced concerning the adaptive advantages of vertical migration. But apparently we still are not equipped with a universally satisfying explanation. In his publication „Aspects of diel vertical migration in zooplankton, and its enigma variations“ Bayly (1986) summarised different observations and thoughts and came to the conclusion „that diel vertical migration should be treated as having multiple causation and different major adaptive functions in different situations“.

Influence of light: Early investigations on the vertical migration of zooplankton (e.g. Rose 1925; Russell 1925, 1926, 1927, 1928 a,b, 1934; Kikuchi 1930; Clarke 1933, 1934a+b; Bogorov 1946; Hardy & Paton 1947) attributed the vertical movements mainly to changes in the light intensity. The notion of an “optimum” light intensity was first developed by Rose and was later very actively explored by Russell, who came to the conclusion that for instance *Calanus sp.* prefers a particular light optimum. But Clarke already questioned this. Based on his field investigations in the Gulf of Maine he ascertained pronounced differences in vertical migration of *Calanus sp.* at two stations within a distance of 100 miles. Clarke assumed that the different behaviour of the organisms must be attributed to environmentally caused physiological differences.

Roe (1984) ascertained that slow movement and/or diffuse distributions of the copepods make it unlikely that populations investigated by him maintained themselves within particular light regimes throughout the diel cycles. Enright (1977) and Enright & Honegger (1977) also found little correlation between sky state and migration in *Metridia pacifica* and *Calanus helgolandicus*. They concluded that change in light intensity was more important to migration timing than absolute intensity, and they suggested that the daily light cycle acted as a “presumptive entraining regime for endogenous biological rhythmicity”. Likewise Forward (1976) as well as Bainbridge (1961) believed “that light may act as an initiating, a controlling and/or an orientating cue in the vertical movements”.

Influence of water stratification: According to in vitro experiments by Harder (1954a+b), ctenophores and medusae “float” in a salinity gradient cylinder at the pycnocline, since their specific weight is greater than that of the water above and less than that of the water below. Harder (1952, 1954) demonstrated experimentally that also an accumulation of motile copepods in density gradients is possible, whereby it was clear that the density gradient alone was the factor determining the distribution of the organisms.

According to Banse (1959), a salinity gradient of 0.2-0.3 ‰ per 10 m of depth is sufficient to cause smaller copepods up to the size of *Calanus finmarchicus* to refrain from diurnal vertical migrations. On the basis of field investigations in the summer surface layer of the southern Norwegian Sea, Krause (1978) also observed a significant reduction in the magnitude of diurnal vertical migrations of certain species (e.g. *Calanus finmarchicus*) with salinity increases of 0.2-0.4 ‰ at most. However, Banse (1959) also admits that many observations on seasonal migrations indicate that copepods can overcome pronounced density gradients. Diurnal migrations through thermoclines have also been observed repeatedly. Esterly (1912) showed that *Calanus sp.* off the coast of California ascends from 9°C deep water to 17°C surface water in the course of one day. Clarke (1934a+b) demonstrated that *Calanus sp.* could surmount a thermocline spanning 6°C at Georges Bank. Krause (1978) described diurnal vertical migrations of *Metridia sp.*, *Pleuromamma robusta* and *Euchaetides*, as well as of *Spiratella retroversa* and *Clione limacina*, which regularly crossed the thermocline (approximately 5°C), whereby the organisms covered distances up to 2 times 200 m per day. On the other hand, Banse (1957) pointed out that pronounced biological stratification must not necessarily be accompanied by hydrographic stratification but can also occur in almost homogeneous water column.

Thus, it seems that vertical migrations of zooplankton organisms are sometimes limited by density gradients in the water column, but sometimes the organisms seem able to overcome strong density gradients, and, finally, sometimes pronounced biological stratification was observed in an almost homogeneous water column.

Influence of food supply: The food supply has been considered by several authors to be a stimulus for diurnal vertical migration. Hardy & Gunther (1935) hypothesized that the time spent at the surface by migratory herbivores might be inversely proportional to food availability, because satiated animals would descend. A logical corollary to this hypothesis is that unsatiated animals would stay longer in the surface water, either ascending earlier or descending later than usual; in the extreme case they might remain at the surface continuously. Similar statements – partly based on enclosure experiments – are given by several workers like Singarajah et al. (1967), Daan & Ringelberg

(1969), Pearre (1973), Forward (1976), Mackas & Bohrer (1976), Boyd et al. (1980), Bohrer (1980), Huntley & Brooks (1982).

Influence of fat content: According to Marshall et al. 1934, copepodite stages V and VI of *Calanus finmarchicus* have a high fat content in spring and therefore cannot perform vertical migrations during this period (Bainbridge 1952, 1953). Because of the high fat content, the density difference between *Calanus finmarchicus* and sea water approaches zero, and the diurnal vertical displacement of the population is negligible. Rudyakov (1970) also attributed seasonal variations in the amplitude of migration and the fact that migration is only pronounced in some age groups of a species at a particular location to differing fat contents of the individuals. Marshall et al. (1934) cited fat contents for *Calanus finmarchicus* in July of 5% for females, 9% for males and 12% for the copepodite stage V. According to Nicholls (1933) at this time vertical migration behaviour is only pronounced in females; in males it is slight and in the copepodite stage V practically non-existent. Sushkina (1961) obtained similar results. According to their data, the fatter copepodite stages IV and V perform no vertical migration.

Influence of activity cycles: Numerous investigations have shown that animal activity, as is the case with many other biological processes, does not remain constant during a 24 h period (Park 1940; Harker 1958; Allen 1966; Woodhead 1966). Exhaustive studies (Aschoff 1960, 1966; Büning 1967) have demonstrated that, in the majority of cases, physiological cycles and activity cycles are preserved under constant laboratory conditions, proving their endogenous nature. The existence of endogenous activity cycles in plankton organisms was first shown by Esterly (1917), then assumed by Russell (1927), and finally proven experimentally by Harris (1963) and Duval & Geen (1976).

Harris (1963) observed swimming of *Calanus sp.* in enclosures: Short bursts of swimming alternated with periods of passive sinking. Haury & Weihs (1976) assumed that this “hop and sink” behaviour saves energy relative to continuous swimming at a fixed depth. According to Harris (1963) the short alternating spells of swimming and sinking took place entirely in the vertical direction. If these are of equal extent, the animals will remain at a constant depth; if swimming predominates, they will gradually rise towards the surface; if the sinking phase predominates, the animals will descend. Changes in activity will therefore be reflected on the whole in a rising or sinking of the population, and a diurnal cycle of activity will thus result in a cyclic vertical displacement of the population.

Based on such results, also Rudyakov (1970) assumed that diurnal vertical migrations of plankton organisms must be regarded as a simultaneous functioning alternation of passive sinking and active rising phases. In principle he assumed the following pattern for diurnal vertical migration of planktonic organisms: The life of a single individual is composed of alternating phases of high and low activity. During the phase of low locomotory activity, the animals are subject to a passive displacement, the direction of which depending on the level of activity, on the direction and rate of vertical transport, on changes in water density and viscosity, and on diurnal variations in the specific gravity of the organisms. During the high activity phase the organisms migrate actively upwards or downwards, depending on the direction of motion in the passive phase.

Regulation of high and low activity phases is determined by the periodic changes in environmental factors acting as time cues. These synchronize the daily activity cycles with the periodic changes in the environment, which usually results in a 24 h period, and they also synchronize the individuals of the same population. The most effective synchronization factor is illumination (Aschoff 1960), the increase of which is held responsible for the withdrawal of migratory organisms to greater depths.

However Rudyakov also pointed out that this simple explanation is contradicted by numerous cases, e.g. when populations begin to descend long before day-break or when migratory organisms are found at the surface in bright sunlight, also due to inverse migrations.

Influence of predator pressure: At present one of the most popular theories about diurnal vertical migration might be the 'predator avoidance hypothesis'. Dagg et al. (1998) wrote: "After at least two decades of accumulated evidence, it should be accepted that downward diel migration of copepods during daytime is a response to visually orienting predators". This theory supposes that zooplankton avoid upper photic zone predators like fish by moving into relatively great depths at dawn and by rising again towards the surface to feed on phytoplankton only at night when they cannot be detected by visual predators.

Bayly (1986) mentioned that it is not certain who originated this hypothesis. It was briefly raised as a possibility by Hardy (1956). Subsequently, the theory was discussed by McLaren (1963), Hutchinson (1967) and Zaret & Suffern (1976). McLaren assumed that an escape from predators could be an element in the adaptive value of migration. According to him it might be probably the essential reason for descent by day rather by night. The most important results leading to the predator avoidance theory stem from investigations made in limnic ecosystems. So, Zaret & Suffern found that predation could be an important factor in the adaptive significance of vertical migration patterns among zooplankton: In both Gatun Lake in Panama and Fuller Pond in Connecticut the diurnal vertical migration patterns of prey populations assumed distributions which resulted in lessened predation by the dominant lake planktivores. It was concluded that such patterns of vertical migration result when prey populations are under intense selective pressure from visual predators. They even showed that *Daphnia galeata mendotae*, unlike in summertime, undergoes only feeble migration during winter when the intensity of predation by planktivorous fish is considerably reduced. A significant relationship between the strength of diurnal vertical migration of the marine copepod *Calanus pacificus* and the abundance of predatory fish in the upper 50 m was also shown by Bollens & Frost (1989).

Based on investigations with daphnids also Stich & Lampert (1981) assumed that certain species carry out diurnal vertical migrations to avoid ingestion by predators. This migratory behaviour would be the result of a genetic selection, caused by a predator pressure in the surface layer. Among others, the authors showed in Lake Constance (Germany) that *Daphnia galeata* remained near the surface, whereas *Daphnia hyalina* underwent a pronounced vertical migration (except in winter and early spring). The birth rate of *D. galeata* having better food conditions in the surface layer was considerably higher than that of the migrating *D. hyalina*. The migration of *D. hyalina* was interpreted as an example of predator avoidance, whereas *D. galeata* adopted the alternative strategy of accepting severe predation by compensating it with high birth rates.

Vuorinen et al. (1983) found in experiments with young three-spined sticklebacks (*Gasterosteus aculeatus*) a significant preference for ovigerous over non-ovigerous female copepods of *Eurytemora hirundoides*. A field study in the upper 50 m depth of Finnish marine waters resulted in the finding that ovigerous females of *E. hirundoides* almost totally avoided the upper 20 m at 0900 h, but this layer contained significant numbers of non-ovigerous females. These results were considered to support the predator avoidance theory. Also Fancett & Kimmerer (1985) found that migration was most pronounced in ovigerous females of *Pseudocalanus spp.* occurring in Western Port (Victoria, Australia).

Wright et al. (1980) simulated growth and predation mortality of zooplankton populations under conditions of migration and non-migration. They computed that non-migrating zooplankton were decimated to a great degree by visual predators, whereas populations treated as migrating continued without extinction over a longer period. However, they noted also that migratory populations, which commonly move into a cold hypolimnion, suffer slower egg development times and lower growth rates.

Dodson (1990) tried to predict diurnal vertical migrations of zooplankton. Amplitude of diel vertical migration was predicted by water clarity measured by Secchi depth. The model assumes that vertical migration serves to minimize mortality from visually feeding fish and to maximize grazing rate within this predation context. Most observations in lakes showed diel vertical migration proportional to Secchi depth, with a correlation coefficient of about 0.880. The residual of the migration-water clarity relationship is significantly and inversely correlated with percent illumination of the moon.

Water clarity and moon intensity together account for 84% of the variation in migration amplitude for the observations.

On the other hand, a large number of observations are to be found in the literature which contradict the predation avoidance theory. Longhurst (1976) already noted that there are several reasons why the predation avoidance theory is neither complete nor universally applicable.

G.W. Begg (1976) investigated the relationship between the diurnal movements of some of the zooplankton and the sardine *Limnothrissa miodon* in Lake Kariba (Africa). Diurnal vertical movements of zooplankton was differently marked. The adults of *Mesocyclops leuckartii* showed the clearest movements followed by *Bosmina longirostris* which rose to the surface by night and descended long before dawn. Other zooplankton organisms like most rotifers appeared to be essentially epilimnic animals, seldom found below 30 m in any great numbers. The diurnal vertical movements of the sardine *Limnothrissa miodon* like its food organisms rose to the surface of the lake at the approach of dusk and thus showed a similar pattern of diurnal vertical migration. The author therefore believes that migrations of fish and food organisms are independent responses to light intensity stimuli, with the result that the two occur at the same depths at certain times of the day and night. At such times *L. miodon* feeds mainly on *B. longirostris*. Although planktivorous fish are known to be visual feeders, studies of the feeding habits of *L. miodon* have shown that it feeds on *B. longirostris* by both day and night (Begg 1974).

Hamza et al. (1993) studied the diurnal vertical distribution of plankton in Lake Candia (Italy) in May and September 1991, in relation to the diurnal grazing impact of two herbivorous zooplankton communities on the natural phytoplankton. They stated that neither diurnal vertical migration nor diurnal horizontal migration could be explained as a predation avoidance mechanism.

Bayly (1986) summarised important facts that speak against the predation avoidance theory:

- In oceanic situations, some migrants do not go sufficiently deep to avoid being seen by potential visual predators. Clarke (1936) showed the possibility of potential predators seeing their prey in light values as low as 10^{-10} times those at the surface during daylight, and on this basis the daytime depths of many migrants would be adequately lit for location by predators. Clarke calculated the depth of minimum illumination for vision of fish for several marine waters. The mean of these values was just over 200 m and the maximum (for the Sargasso Sea) was 430 m.
- Some oceanic migrants descend to much greater depth than would be necessary to avoid visual predators. So, Waterman & Berry (1971) showed that some species ascend from 1400 to 1000 m at dusk. There exist evidence of diurnal vertical migrations between 1000 and 2000 m depth. In the Norwegian Sea Krause (1978) found that the overwintering stocks of *Calanus finmarchicus* in 400-800 m of depth carry out diurnal vertical migrations in August as well.
- Many zooplankters subject to predation do not migrate from brightly lit waters. For example, many planktonic organisms live continuously near the surface during 24 h daylight in polar regions. Normally migratory species are sometimes found at the surface in full sunlight. Nicholls (1933) noted: "The occurrence of *Calanus* in large quantities at the surface during the day, often under conditions of brilliant sunshine, has been recorded on several occasions in different regions. Also, the immature stages of many migrant species are themselves non-migratory".
- Last but not least, Bayly alludes to the fact that there additionally exists a considerable number of non-visual predators in the surface layer which hunt most efficiently at night, so as Chaetognatha; Medusae; Ctenophora, and predatory copepods like *Labidocera* sp. and *Euchaeta* spp.

Influence of metabolic benefits: McLaren (1963) already supposed that a zooplankter receives an energy bonus by feeding at night in warm water, in which the efficiency of food assimilation would be high, and by the more efficient harnessing of energy for growth at lower temperatures found at daytime depth. So, an animal which does all necessary feeding in warm surface water and “rests” in cooler water gains a benefit which may be put into fecundity. Also Enright (1977) and Enright & Honegger (1977) showed that, from a metabolic point of view, it is more profitable for herbivorous zooplankton to feed at the surface during a few hours at night, when the phytoplankton biomass is at its maximum, and then to rest in deeper cooler water during daytime, where its metabolism is lower. Williams & Conway (1980) assumed that the most important requirement of the young copepodites is to direct the net energy gain obtained from their food towards growth, while the older stages (CV and CVI) need to build and store energy reserves for reproduction. Therefore, it would seem to be advantageous for the younger stages to stay in close contact with their food supply, while the older stages after feeding seek the environment most favourable for maximizing the conversion of the food to an energy store. The authors referred to the investigations by Petipa (1964a), who showed that at a temperature of 7°C (below the thermocline) food passes through the gut in 3 to 4 hours, while above the thermocline it takes 10 minutes. Therefore Williams & Conway found it likely that stage V copepodites and adults would have evolved a feeding and migratory strategy which maximizes the use of ingested food in the formation of lipid reserves necessary for reproduction.

Enright (1977) supplied an alternative hypothesis to the predator avoidance theory which emphasizes the photosynthetic rather than the visual significance of the day-night cycle. Enright stated that photosynthetic rate is great enough for algal biomass to increase appreciably from dawn to dusk; that the metabolic needs of grazers can be reduced by resting during nonfeeding hours in cooler waters at depth; and that the grazing rate of herbivores, following an extended interval of nonfeeding, is initially greater than steady state rate and then declines in a matter of a few hours. Enright's calculations based on these assumptions demonstrate that nocturnal feeding by a grazer might be able to provide a greater net energy gain for growth and reproduction than continuous feeding.

According to Enright it is an unexpected prediction of this approach that if maximizing net energetic gain is of greater selective importance than avoidance of visually orienting predators, grazers ought to migrate upward and begin feeding well before sunset, rather than afterwards, as the predation avoidance hypothesis presumes, namely that grazers migrate upward and begin feeding in darkness, after sunset. The exact timing of the postulated feeding optimum depends on assumed values of several parameters but most of the calculated advantage seems attainable by an onset of grazing 1-2 h before sunset. Enright & Honegger (1977) found in field investigations confirmative results. In most of their sampling program, that means in late spring and at highest herbivore abundance, the onset of migration for adults as well as immatures of *Calanus helgolandicus* (*pacificus*) began consistently an hour or two before sunset, suggesting that predator avoidance was relatively unimportant under that set of circumstances. Only in early summer and at lowest herbivore abundance, migration began after sunset, for both adults and immatures, suggesting that avoidance of predators was of overriding importance under those circumstances. Migration of immatures in a third sampling program, in midspring, began one hour or two before sunset but that of adults began only after sunset, suggesting that the appropriate trade off between survivorship by predator avoidance and possible metabolic advantage may depend on the developmental stage of the animal.

According to Huntley & Brooks (1982) diurnal vertical migration behaviour in *Calanus pacificus* and perhaps in other planktonic herbivores is a conditional response to two levels of stimuli: The primary stimulus appears to be hunger. When food availability is low and competition for food is high, the copepods modify their migration behaviour by remaining in the relatively food-rich surface waters and feed to satiation. The secondary stimulus, which operates under conditions of high food availability and low competition for food appears to have regular, circadian periodicity. Thus, when the copepods are able to satisfy their nutritional requirements by nocturnal feeding alone, they respond to the secondary stimulus and perform regular diurnal migrations. Authors like Enright & Honeg

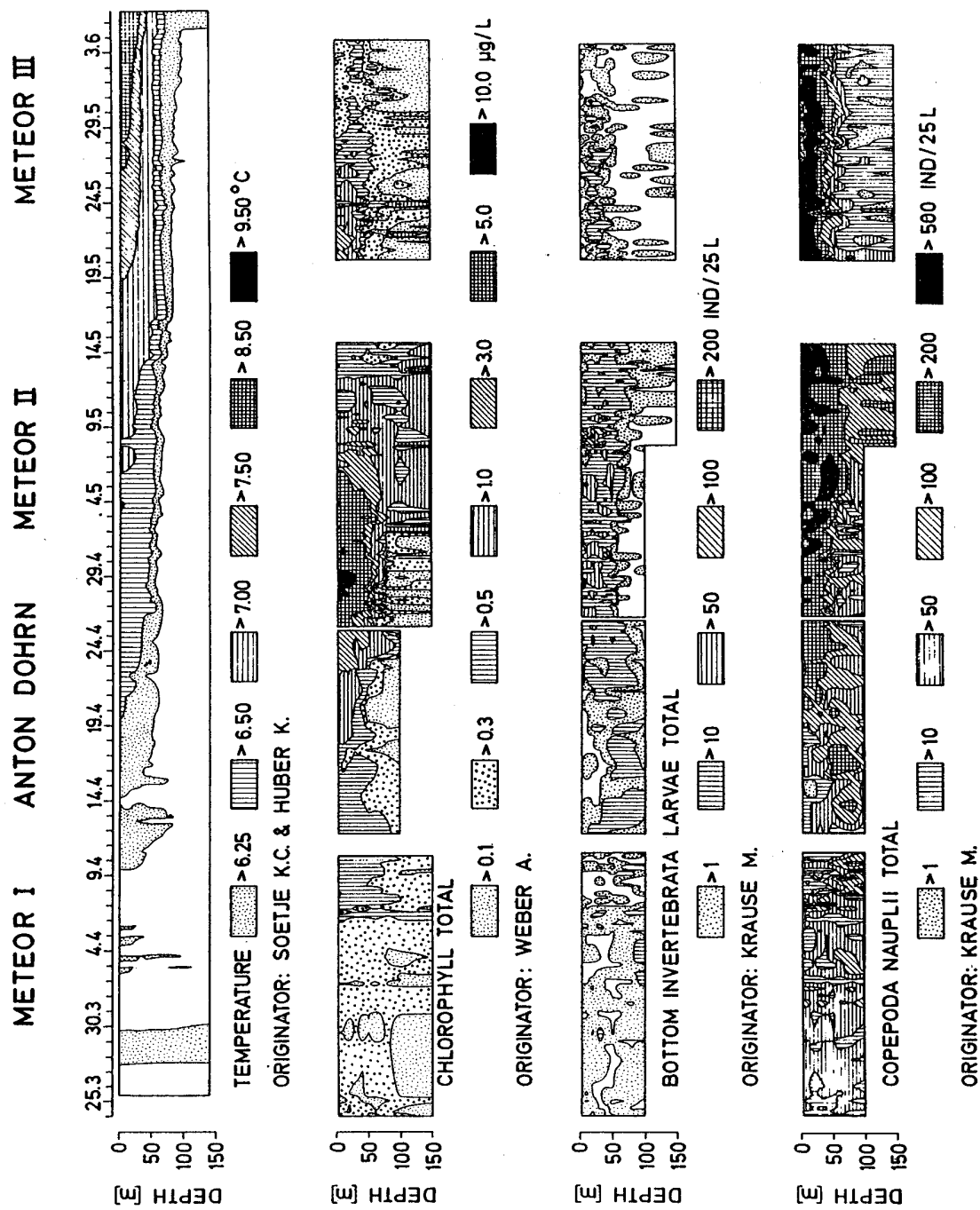


Fig. 13: Isograms of temperature and chlorophyll measurements as well as of the countings of the bottom invertebrate larvae (total) and of the copepoda nauplii (total) from the FLEX'76 material over time and depth (from Krause & Radach 1989).

ger (1977) and Huntley & Brooks (1982) concluded that hunger overrides other stimuli, such as high light intensity or avoidance of predation, which might otherwise induce a downward day migration.

Nevertheless, these results do not conform with observations of other authors like Vinogradov (1970), who demonstrated that during spring at the time of reproduction, *Calanus finmarchicus* carries out no vertical migration. The reproduction period of *Calanus*, however, corresponds with the period of intense algal blooms (Marshall & Orr 1952; Tande & Hopkins 1981). Not until late summer, when the algae stocks are small and the animals begin to leave the surface layer, do the older copepodite stages begin with intensive diurnal vertical migrations.

During the Fladen Ground Experiment (FLEX'76) at a fixed station the spring development of physical environmental parameters as well as of phyto- and zooplankton stocks were studied by means of water bottle series over 2 ½ months (26.3 – 5.6.1976). According to Krause & Radach (1989), at the end of winter the zooplankton organisms were sporadically distributed throughout the homogeneous, completely mixed water column of the Fladen Ground. With the formation of the thermal stratification and the simultaneous exponential development of the algae bloom the organisms like bottom invertebrate larvae and copepod nauplii began to accumulate in the warmed and food rich surface layer (Fig. 13). The same was the case for most of the planktonic organisms such as the very important copepod species *Calanus finmarchicus*, *Oithona similis* and *Pseudocalanus elongatus* (Fig. 14). With the exception of *Calanus finmarchicus*, whose naupliar stages first appeared during the algae bloom – according to Marshall & Orr (1952, 1955) and Tande & Hopkins (1981) *Calanus* females require algae blooms as a trigger for spawning – all copepod nauplii were distributed randomly over the wintertime mixed water column. But, during the formation of the thermocline and the start of the phytoplankton bloom an accumulation of the organisms took place, which as a rule was directed into the surface zone. Only *Microcalanus pusillus*, which is well known as a detritus feeder and a coprophage, moved with all its developmental stages into deeper water layers at that time.

Pronounced diurnal vertical migrations of zooplankton species were firstly recognizable eight or ten days after the decline of the phytoplankton bloom. Particularly wax ester producing copepods like *Calanus finmarchicus*, *Pseudocalanus elongatus*, *Microcalanus pusillus*, and *Metridia lucens* started those migrations. As an example, in Fig. 15 the vertical centres of gravity of the *Calanus finmarchicus* stock from the FLEX'76 material are presented. At first, the vertical movements of those centres took place in a random manner. Earliest at 15 May, after the decline of the phytoplankton bloom (see also Fig. 16), marked diurnal vertical migrations of all stages commenced. The movements of the species and their stages occurred synchronously, leading in the same direction, and persisting in deeper and cooler water layers during daylight. But, the amplitude of migration increased with each maturity stage reached. During a second smaller phytoplankton bloom the amplitudes of migration decreased again in most investigated developmental stages (see Fig. 15). Similar result also was obtained by Huntley & Brooks (1982), who found that “the onset of vertical migration behaviour already occurred in the first feeding stage, Nauplius III. The amplitude of vertical migration gradually increased with age, becoming maximal in the late copepodite stages. Night depth remained constant with age while daytime depths increased”. In the Fladen Ground copepod species like *Acartia clausi* and *Oithona similis* showed only weak vertical movements. These species are known to be able to feed also carnivorously if necessary.

Huntley & Brooks (1982) stated that the migratory behaviour of *Calanus pacificus* late copepodite stages was influenced by food availability. When phytoplankton was abundant and individual ingestion rates were high, copepodites performed high-amplitude migrations. As food availability declined, however, and the competition for food increased, migration amplitudes decreased and then ceased altogether so that copepodites remained in the relatively food-rich surface waters at all times. The authors suggest that hunger is the

primary factor controlling vertical migration. Nevertheless, based on their observations Krause & Radach (1989) speculated that the periodic vertical displacements of zooplankton populations might be explained on the basis of nutritional states and metabolic cycles in that way, that in the unstratified water during late winter the organisms, being present in relative small numbers, are distributed randomly over the entire totally mixed water co

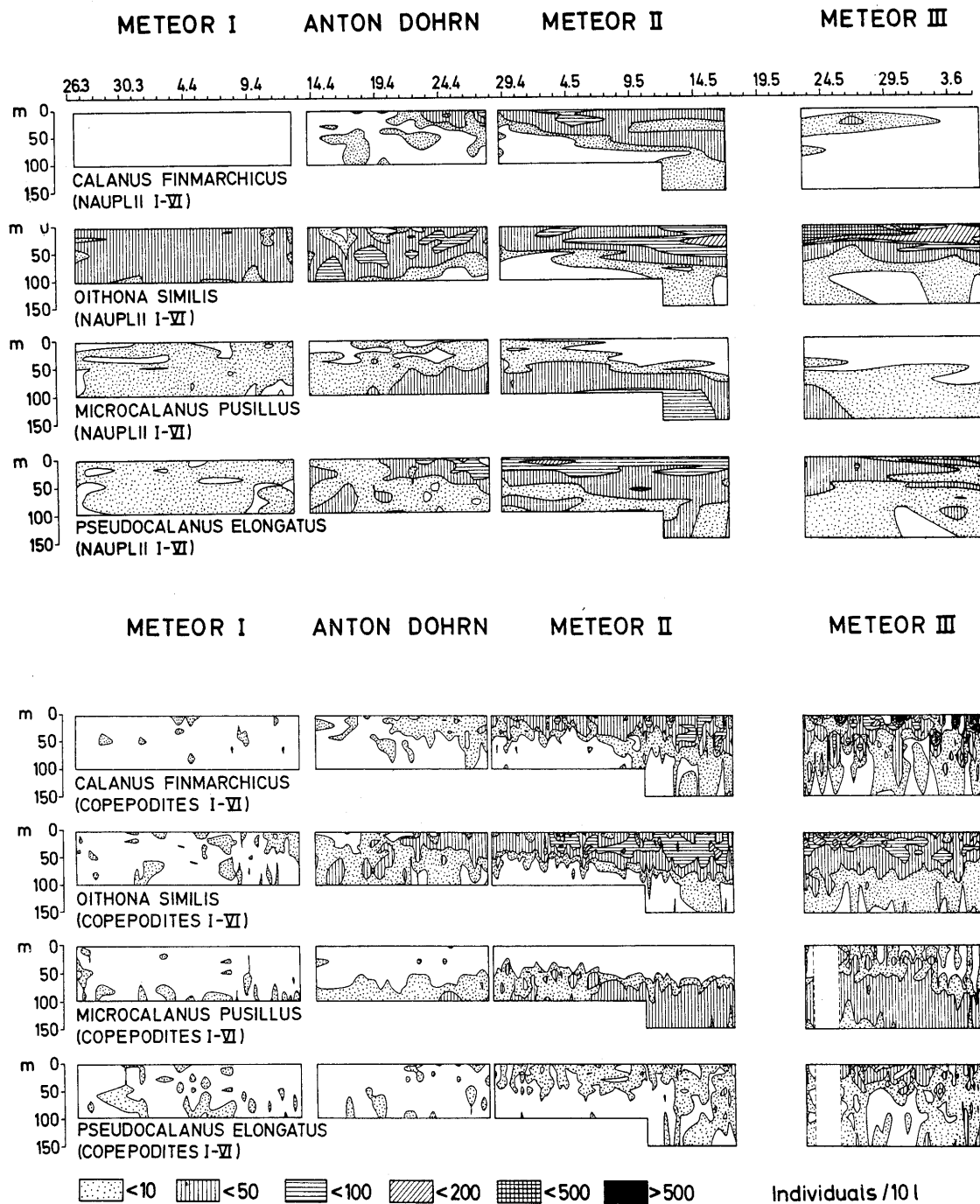


Fig. 14: Isograms of the 4 most abundant copepod species (nauplii NI-NVI) and copepodites CI-CVI) from the FLEX'76 material over time and depth (from Krause & Trahms 1982).

lumn. At that time these organisms might represent starvation forms, which likely display a neutral buoyancy. With the begin of stratification, the phytoplankton spring bloom starts in the euphotic zone, which leads to a development of a rich food supply for herbivorous zooplankton. The various zooplankton organisms could store light algal fat to attain enough buoyancy to accumulate in the surface zone and graze on phytoplankton without exerting themselves. From this it also becomes clear that by contrast all stages of *Microcalanus pusillus* have to accumulate in deeper layers at this time (see Fig. 14). That might be because its special food (detritus; faecal pellets) is not equipped with enough lipids like living algae.

Nevertheless, some days after the decline of the phytoplankton bloom the surplus algal fat in the animals has been reduced or transformed, so that their bodies became more dense, especially since meanwhile the organisms have put on weight due to the synthesis of dense proteins. Consequently, the animals have to sink in their probably light controlled passive phases into water depths which correspond to their body densities. It might be imaginable that an alternating synthesis of heavy proteins (in the surface layer) and of extremely light wax esters (in the deep layer) would cause the up- and downward displacements of the populations.

The reduction of the amplitude of migration of the younger stages (CI-CIV) during the last phase of the FLEX'76-Experiment (see Fig. 15) is probably caused by the onset of a second (smaller) algae bloom, since the copepods could store up on buoyant fat anew. The number of faecal pellets per individual found in the water column may point to the varying grazing activities of the zooplankton organisms. Hence, these numbers could reflect the nutritional state of *Calanus finmarchicus*. From the FLEX'76-Experiment the depth-integrated time series of the phytoplankton stock (mg chlorophyll a m^{-2}) compared with that of the number of faecal pellets per *Calanus* individual found in the water column is documented in Fig. 16. Both time series are highly significant correlated. So it can be concluded, that in periods of sufficient phytoplankton concentrations the diurnal vertical migrations did not happen or were at least reduced.

The considerations mentioned above are supported by numerous observations found in the literature. Although they have already been reviewed in Krause & Radach (1989), they will briefly be mentioned here:

If *Calanus* is living under favourable trophic conditions, Cushing & Vucetic (1963) found out that the copepods may have a daily food intake of up to 390% of their body weight. Gaudy (1974) suggested by *Calanus helgolandicus* a maximum daily ingestion rate of 250 to 300% of its body weight, and Paffenhöfer (1971) assumed in *Calanus* Stage V "only" 195%. Petipa (1964b) ascertained that, when there was an increase in the amount of food consumed, more fat was deposited along the intestine and *vice versa*. In *Calanus*, deposition along the intestine in form of fatty droplets takes place under conditions of superfluous feeding, when faeces are excreted every 5 to 15 minutes. At such times fat is stored away as reserves within minutes after it has been extracted from the food consumed. Such a rapid deposition of fat reserves in animals is apparently due to an ability to absorb the fat, without breaking it down, in the form of a fine fatty emulsion (Ginetsinskii & Lebedinskii 1956). According to Petipa, a deposition of fat along the intestine in form of tiny fatty droplets of 0.5 microns in diameter in *Calanus* takes place within 7 to 15 minutes as the food moves along inside the gut. Petipa believed that marine poikilothermic organisms, which often feed to excess, commonly have the ability to rapidly store fat away in reserves in little changed form and that this is a normal and widespread phenomenon.

Biochemical studies by Sargent et al. (1972) and Gatten & Sargent (1973) have shown that the three major dietary constituents, protein, fat and carbohydrate, all serve as precursors in the *de novo* biosynthesis of wax esters in the copepod *Euchaeta sp.*, a finding in support of the earlier conclusion that *Calanus helgolandicus* can elaborate wax esters from diets entirely lacking this lipid (Lee et al. 1971, 1972). Thus, the formation of wax esters in copepods may represent a mechanism whereby large dietary inputs can be converted efficiently and rapidly to unusually large lipid reserves. According to Lewis (1970), wax esters have an extremely low average density of only 0.86, while proteins average 1.33. Thus, a conversion of proteins and carbohydrates to wax esters might increase the buoyancy significantly.

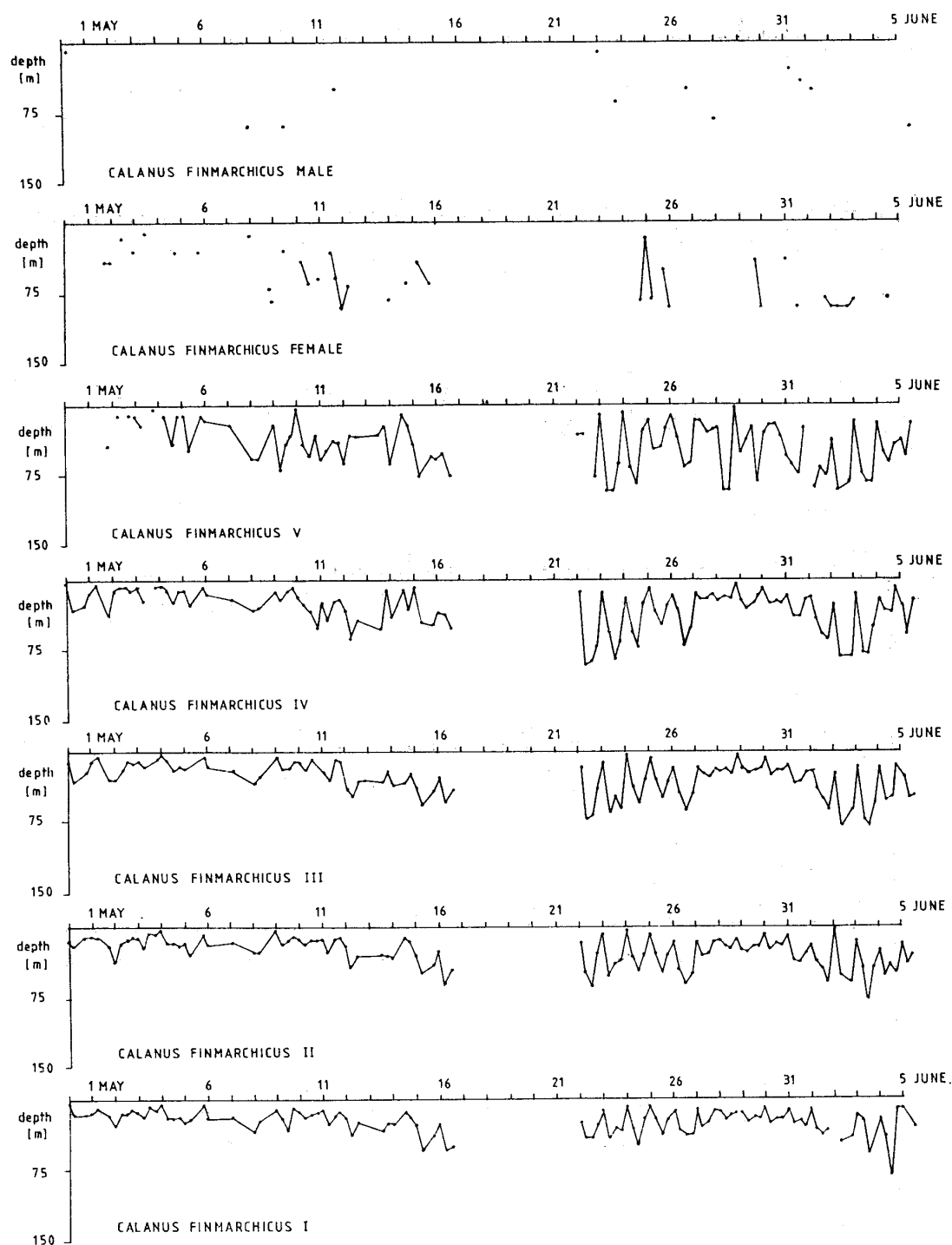


Fig. 15: Vertical centres of gravity of *Calanus finmarchicus* (copepodite stages and adults) from the FLEX76 material over time and depth (from Krause & Radach 1989). For females and males these calculations could not be conducted because of a shortage of individuals in the water column.

Lowe (1935) already referred to the oil sac of *Calanus finmarchicus* as a “hydrostatic organ”. Brandes (1941) supported this idea. He studied *Calanus* from the stomachs of herring caught off Iceland and came to the conclusion that the oil sacs of these copepods must contain a homogeneous mixture of wax esters and proteinaceous substances. Childress & Nygaard (1974) ascertained that lipids and proteins are the major organic components of the crustaceans and therefore show an inverse relationship. They assumed that the relative buoyancies are largely accounted for the balance between the buoyancies of the lipids and the proteins. Indeed, several authors like Nevenzel (1970) Lee, et al. (1970), Malins & Barone (1970), Morris (1971, 1972, 1973), Lee, Hirota & Barnett (1971) have already pointed out that organisms commonly have adaptations for maintaining a given position in the water column, and they assumed that lipids are accumulated by many organisms for buoyancy regulation as well as for energy storage.

Like Childress & Nygaard (1974) Krause & Radach (1989) think that the balance between proteins and wax esters plays an important part for buoyancy regulation of the organisms. But, moreover it is imaginable that metabolic rhythms of either protein or wax ester synthesis may cause alterations of the specific weight of the individuals producing diurnal displacements of the populations and giving them so ecological benefits. For, with this mechanism the planktonic organisms are able to “choose” their optimal water layers in a diurnal rhythm during periods of poor food supply.

But, after all, it seems that diurnal vertical migrations of *Calanus finmarchicus* represent an unstable transitional period between stable periods of grazing in the surface layer during diatom bloom and overwintering in deep water layers.

It is well known that *Calanus finmarchicus* after having filled up its oil sacs with wax esters can sink already during summer into greater depths to hibernate there until next phytoplankton spring bloom in February/March (e.g. Sömme 1934; Marshall & Orr 1955; Östvedt 1955). As an example for this, Fig. 4 presents vertical profiles of *Calanus finmarchicus* stocks from a continuous station in the southern Norwegian Sea superimposed by the corresponding temperature curves of the water column. It is conspicuous that the concentration maxima of the animals occurred exclusively in the two water layers with strong temperature (and density) gradients. Are they kept here corresponding to their specific weights? In the upper warm mixed layer in summertime, all larval developmental stages as well as sexually mature females and males (=reproduction stock) could be found. In the deep layer, the transition zone between Atlantic Water and cold Arctic Bottom Water, on the contrary, only the overwintering stocks consisting of the older copepodite stages V as well as, in much lower numbers, CIV were met. While the reproduction stock in the mixed layer performs diurnal vertical migrations, the older stages, which are in excellent nutritional condition, apparently are subject to a process of “selection”. That means that those individuals which have achieved an advanced state of development possess large wax ester reserves but likewise rather large protein contents. Hence the organisms become more and more heavy and the magnitude of their migrations steadily increases. At some point their weight causes them to sink out of the surface layer and into a depth zone which corresponds to their body density. It is highly probably that these are water layers with strong density gradients (see Fig. 4).

Some authors assumed that a large amount of energy from lipids is used during diurnal vertical migrations (Marshall & Orr 1955; Hardy 1956; Petipa 1964a). Rudyakov (1970) therefore concluded that zooplankton migration is not the result of an adaptation to the planktonic mode of life, but was already inherent in the ancestors of the recent plankton. Nevertheless, Klyashtorin & Yarzhombek (1973) and Klyashtorin (1978) stated that the relative energy losses for active movements do not exceed 20-40% of the standard metabolism of the crustaceans. Vlymen (1970) even suggested that the copepod *Labidocera* sp. expends remarkably little energy in swimming. More than 99% of the energy expenditure being used in basal metabolism. Foulds & Roff (1976) reported when *Mysis relicta* was induced to swim at speeds of 1.0 and 1.6 cm s⁻¹, which are similar to observed vertical migration rates in Lake Ontario, there was no significant increase in oxygen consumption over the ‘routine’ rate of 5.28 µg oxygen per animal and hour for a 5 mg animal (dry weight). Veiga & Castel (1986) found that the energy expended by the estuarine copepod *Eurytemora hirundoides* for constant velocity swimming only represents 0.26% of the metabolic rate (but considering the escape reactions it can be reach up to 50%). Mechanisms should therefore be sought which might support

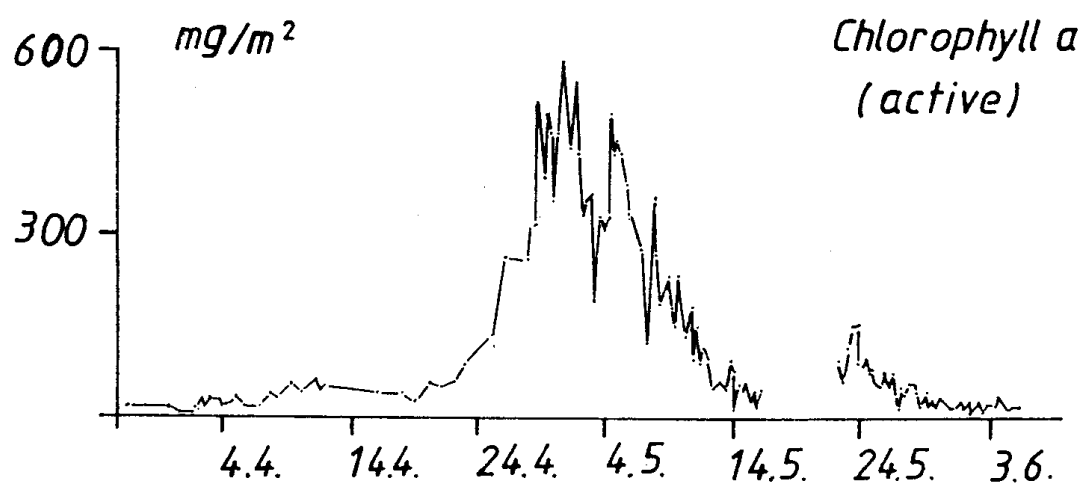
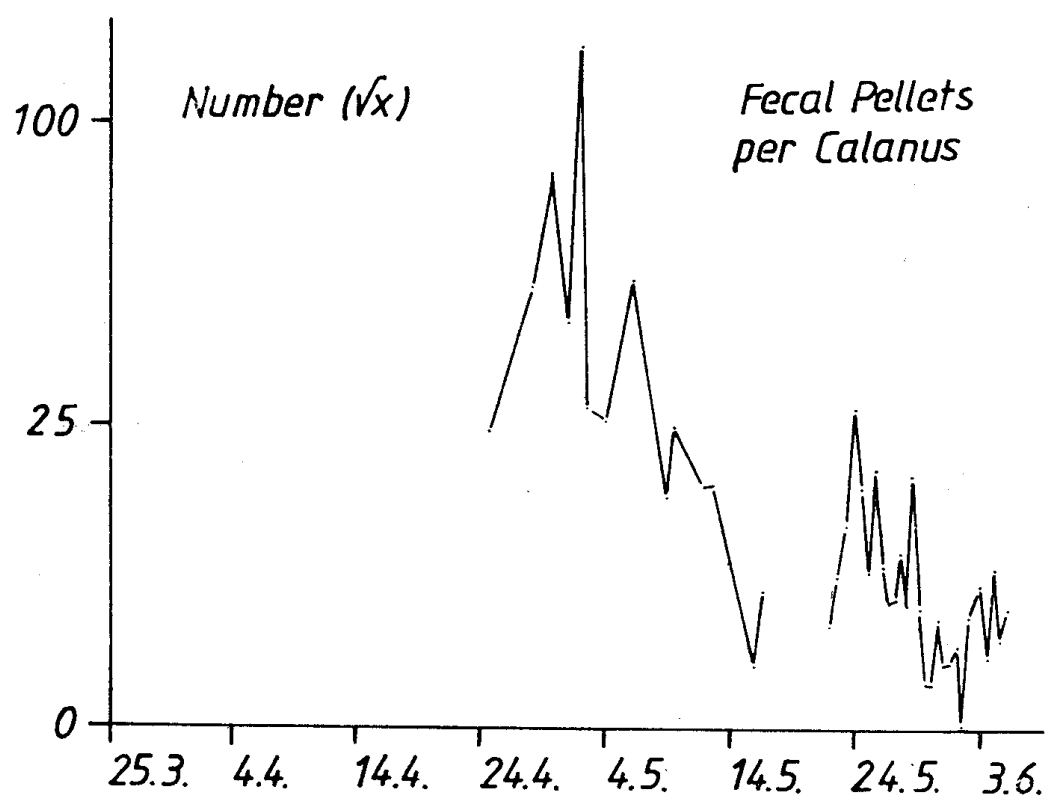


Fig. 16: Depth-integrated time series of numbers of *Calanus* faecal pellets per *Calanus* individual and chlorophyll a measurements (mg m^{-2}) in the 100 m water column from the FLEX'76 material (Krause 1981; Krause & Radach 1989).

diurnal and seasonal migrations.

During descending and ascending, the organisms are probably utilizing a particular property of wax esters reported in the literature: Brandes (1941) already found that the lipids in the oil sacs of *Calanus* can “crystallize”, thus increasing their specific weight drastically. Yayanos et al. (1978) ascertained that lipids are more expandible and compressible than water. The density and the specific volume of the wax esters change far more with temperature and pressure than does that of water. The coefficient of thermal expansion of the wax ester mixture of *Calanus plumchrus* were 6 to 10 times that of sea water. The likely reason for this large value is that the mixture is in part undergoing a first-order phase transition (liquid-solid) with change in temperature.

Yayanos et al. (1978) assumed that information on the pressure and temperature dependence of the density of wax esters of *Calanus plumchrus* could reveal how its physical properties affect buoyancy in these and other animals which contain wax esters. They consider: “ Presumably an organism could benefit energetically by moving upwards with an empty gut and then by using food to assist its downward movement. Migration to the warmer surface temperature would be facilitated as a result of the large coefficients of thermal expansion of the wax esters. Thus, a vertically migrating hungry animal could approach the grazing grounds of the photic zone with a savings in fuel consumption”. Certainly, the authors subsequently rejected their considerations again, because of some uncertainties. But at least for the lipid-containing eggs of *Calanus plumchrus* - laid in deep water and passively moving towards the sea surface (Fulton 1973) – they let this mechanism pass.

It is thought by Krause & Radach (1989) that the data gained during the Fladen Ground Experiment and other projects performed at the University of Hamburg will support the considerations of Yayanos et al. (1978). Temperature and pressure induced physical changes in the filled oil sac can augment the sinking trend (as well as the ascent) of the organisms, once the motion has begun. The animals do not stop sinking until the densities of the animals and of the surrounding water are the same. This is most conspicuous in layers with strong temperature and density gradients.

It appears that the coupled consideration of diurnal vertical migrations and the nutritional state of the animals can explain the many very different and sometimes confusing observations such as light-independent vertical migrations or the fact that populations sometimes do not migrate at all but remain in the surface layer or that the migratory amplitude increases with increasing developmental stage or that already slight increases in the water salinity can drastically reduce migratory amplitudes. Here there is certainly a need for further research.

3.3. Physiological parameters

Physiological data give information on life processes in organisms and their rates. Together with the data of stock sizes, knowledge about the physiological capacity of zooplankton species gives insight into their role in the turnover of substances in the ecosystem. Important physiological parameters are feeding, ingestion, respiration, excretion, growth and reproduction rates.

A look at the existing literature shows that there has already been a lot of work done on physiological processes (Table 1), particularly with copepods (Tables 2 and 3). The information and data to be found here are of great value. They need to be thoroughly analysed in order to go beyond the multitudinous details and arrive at general principles which then can be used, for example, in ecosystem models. However, the physiological rates of zooplankton organisms are subject to great variability effected by numerous biotic and abiotic environmental factors. In the following it will be attempted to survey this area, although an exhaustive treatment is not possible within the framework of this project.

3.3.1. Respiration

Raymont & Gauld (1951) already pointed out that the respiratory rates of zooplankton organisms are of considerable interest as they permit an assessment of the metabolic requirements of the

zooplankton, which forms a vital link in the economy of the sea. Petipa (1966) writes that the study of the oxygen consumption of marine planktonic organisms is necessary for determining the level of their energy metabolism and food requirements in relation to environmental factors. It assists in explanation of the ways energy is transformed in the lower links of food chains.

Methods

Respiration measurements were carried out in the past using a modified Winkler method or oxygen electrodes, which have so improved in the course of time that they hardly show any oxygen consumption themselves (e.g. Mikro-Clark electrodes) and have become ever more accurate. In some cases CO₂ release has been measured as an alternative to oxygen (e.g. Rakusa-Suszczewski et al. 1976; Johnson et al. 1993) as an gauge for respiration. Evidently the first respiration measurements were made per individual and time units. Later the results were related to weight (e.g. mg dry weight)) and time units.

Packard (1971) proposed a further method where the in vitro activity of the respiratory electron system (ETS-activity) was used to estimate the in situ respiratory rate of phytoplankton. This was modified by Kenner and Ahmed (1975) to yield the maximum velocity (V_{\max}) of electron transfer for phytoplankton, and by Owens & King (1975) for zooplankton.

King & Packard (1975) measured respiratory oxygen consumption and respiratory electron transport activity for 15 species (from five phyla: Annelida, Chaetognatha, Arthropoda, Ctenophora, Coelenterata) and several mixed populations of marine zooplankton. A high correlation ($r > 0.97$) was found that was only weakly affected by size of the animals and temperature. Båmstedt (1979) studied respiratory rate and ETS-activity of zooplankton from deeper part of Kosterfjorden, Sweden to compare both techniques. According to this the respiratory rate and ETS-activity of zooplankton varied considerably over the year, with maxima usually in spring and minima in summer. The ETS-activity was much more variable than the respiratory rate and the seasonal variation of the two were only weakly correlated. The ratio between ETS-activity and respiratory rate was neither constant between different species nor constant over the year. Båmstedt believes that these findings cast some uncertainty over ETS-activity as a predictive tool for estimating population or community metabolism.

There are many difficulties involved in experimental measurements of respiration rates in zooplankton organisms. Berner (1962) and Ikeda (1977a) ascertained that remarkably high oxygen uptakes occurred in the first few hours of the experiments. The respiratory rate then decreased rapidly until a steady low rate was established after about 30 h. He assumed that the higher initial respiratory rates, which were observed in all experiments, are caused from excitement when the animals were transferred to the experimental bottles. Likewise, Marshall (1973) refers to the „effect of time after capture”: It has often been observed that oxygen uptake is higher during the first hours after capture than subsequently, and to avoid this period experiments are often made on animals which have been kept 24 h or so in the laboratory. But it is not certain whether the excitement of capture and handling raises oxygen uptake above normal, or whether under laboratory conditions there is a decline from normal values.

Zeiss (1963) pointed out a further potential source of error when measuring respiratory rates in living organisms: Measurements of respiratory rates of two species of zooplankton were made under varying degrees of confinement simulating conditions imposed on the organisms by varying population densities and in experimental techniques for respiration measurement. It was found that when *Daphnia* sp. is confined to a small space its respiratory rate is much increased, but that *Calanus* sp. does not seem to have the same response to confinement. Measurements of oxygen consumption were also carried out by Razouls (1972a) on *Temora stylifera* and *Centropages typicus*. Two different experimental conditions were varied, namely, degree of confinement and length of time spent in the laboratory. According to Razouls it appears from these results that particular attention must be paid to the effect of experimental conditions in the determination of absolute values of metabolism of copepods.

Pavlova (1975) has also shown that degree of crowding may be important in *Pseudocalanus* sp. Rates of O₂ consumption by uncrowded adults were $0.225 \pm 0.032 \mu\text{g O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ for males and $0.190 \pm 0.223 \mu\text{g O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ for females; for crowded adults, they were 0.092 ± 0.030 and $0.086 \pm 0.037 \mu\text{g O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ respectively. Thus, in Pavlova's experiments crowded organisms showed much lower respiration rates than uncrowded. Although Marshall (1973), in her review about respiration and feeding in copepods, supposed a falsification of respiration measurements due to the transfer to the incubation chambers of the test organisms, since she did not find the results in the literature to be consistent, she was not able to make an unequivocal statement in this regard. Corbett & McLaren (1978) believe: whatever measurements might be made, the experimental violence done to such tiny animals by crowding them into small volumes of sea water and perhaps forcing them to be abnormally active may make any result somewhat unnatural.

Respiration of copepods

In the following an attempt will be made to briefly survey the respiration measurements that have been made for copepods. By far the most investigations about oxygen consumption in zooplankton were carried out for this group. The low number of publications regarding other large taxonomic groups of zooplankton indicate a need for future work (see Table 3).

According to Marshall (1973) copepods are very important in the sea because they are the main convertors of the phytoplankton into food suitable for higher organisms. The first measurements of the respiration of a selected species (*Calanus finmarchicus*: females, males and Stage CV) were already made by Marshall et al. (1935). In 1939, Clarke & Bonnet published a further series of measurements of the *C. finmarchicus* Stage CV, giving values slightly higher than those of Marshall et al. (1935). Raymont & Gauld (1951) measured the respiration rates of the copepods *Calanus finmarchicus*, *Euchaeta norvegica*, *Centropages typicus* and *C. hamatus* (adults and Stage CV) at temperatures between 16 and 19°C. The rate for *Calanus finmarchicus* Stage CV at 17 °C was found to be $0.52 \mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ and agreed well with the results found by Marshall et al. (Stage CV: $0.44 \mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) and Clarke & Bonnet. (Stage CV: $0.80 \mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$). The respiration rate for females of *Calanus finmarchicus* was on an average $0.86 \mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$. For *Centropages* sp. the authors found a respiration rate of $0.11 \mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$.

Petipa (1966) compared own data on the respiration of *Acartia* spp. with the material of other investigators like Gauld & Raymont (1953), Conover (1956) and Pavlova (1961), and could present fairly good agreement of the majority of the results:

Authors	species	Temp.	ml O ₂ ind. ⁻¹ h ⁻¹
Gauld & Raymont (1953)	Acartia clausi	20°C	$9.45 \cdot 10^{-5}$
Conover (1956)	Acartia clausi	15°C	$1.76 \cdot 10^{-5} - 3.06 \cdot 10^{-5}$
Conover (1956)	Acartia clausi	20°C	$3.65 \cdot 10^{-5} - 5.00 \cdot 10^{-5}$
Conover (1956)	Acartia clausi	25°C	$3.30 \cdot 10^{-5}$
Pavlova (1961)	Acartia latisetosa (female)	20°C	$3.90 \cdot 10^{-5} - 5.46 \cdot 10^{-5}$
Petipa (1966)	Acartia latisetosa	20°C	$3.50 \cdot 10^{-5}$

Effect of body size: The relation of respiration to body length, volume or weight has been discussed by many authors, e.g. by Raymont & Gauld (1951), Gauld & Raymont (1953), Conover (1959, 1960), Berner (1962); Marshall (1973); Corbett & McLaren (1978).

Conover (1959) measured the respiratory rate and weights of marine calanoid copepod species at the same temperature, and an attempt was made to find a basis for comparison of respiration in zooplankton crustaceans of different size. For the experiments *Centropages hamatus*, *Temora longicornis*, *Pseudocalanus minutus*, *Acartia bifilosa*; *Acartia discaudata*, *Acartia tonsa*; *Acartia clausi* from Southampton (England) and *Acartia clausi* from Long Island Sound (U.S.A.) were used. When the respiratory rates of all these species were plotted against their individual dry weights a linear correlation coefficient $r = 0.978$ was obtained.

Berner (1962) measured feeding and respiration in the adult marine copepod *Temora longicornis*. Respiration experiments were done at 10°C. In 19 experiments the respiration rate varied considerably between 0.0153 and 0.0537 $\mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$. It could be seen that the oxygen consumption is very dependent upon the body size. The values of respiration measurements in *Centropages hamatus*, *Temora longicornis* and *Acartia clausi* at 10°C found by Gauld & Raymont (1953) were for *Centropages* in the same time of year slightly below, for *Temora* slightly above and for *Acartia* decidedly above those of Berner. Shushkina & Vilenkin (1971) measured the respiration of eleven copepod species in the tropical Pacific. A significant relation between respiratory rate and body weight was found.

Corkett & McLaren (1978), in a review about the biology of the common calanoid copepod *Pseudocalanus minutus*, referred to the factors influencing the rate of oxygen consumption and tried to find a formula explaining optimally the relationship between respiration and body size:

According to this, Raymont & Gauld (1951) already found a fairly close agreement between respiration and body length over a size range of about an order of magnitude with the formula:

$$\text{Log } R = 2.19 \log L - 0.928$$

However, Conover (1959) presented a closer correlation of respiration with body dry weight than with length (respiration rate $R = \mu\text{l O}_2 \text{ ind.}^{-1} \text{ d}^{-1}$; body weight $W = \text{mg dw}$) for a number of copepod species:

$$\text{Log } R = 2.068 + 0.856 \log W$$

Because weight of an organism may be variously made up of metabolically inactive material, such as stored oil, ripe ova or gut contents, cephalothorax length might be a better predictor of like-shaped animals. Raymont (1959) assumed that respiration followed a “surface law”, and that it could be proportional to the square of length, and therefore corrected respiration rates of copepods accordingly. However, within the size range of *Pseudocalanus* used by him (adults of both sexes 0.94 – 1.13 mm) no correlation of respiration rate and length was noted. Conover (1959) fitted a relationship of respiration rate (R , in $\mu\text{l O}_2 \text{ ind.}^{-1} \text{ d}^{-1}$) to cephalothorax length (L , in mm) for a variety of copepods:

$$\log R = 0.353 + 2.713 \log L$$

The less reliable regression coefficient for *Pseudocalanus* alone was 1.645. Corkett & McLaren (1978) criticized that there are no data for respiration of nauplii and copepodites of *Pseudocalanus* from which to derive an intraspecific relationship, and such experiments as conducted by Conover (1959) demonstrate that it is difficult to use adults or copepodites of a narrow size range to derive an accurate relationship between respiration and body size of *Pseudocalanus*. It is better to use a general, interspecific relationship, making use of a wide size range of animals. Probably the best available interspecific relationship to date is that fitted by Ikeda (1974) to “boreal” zooplankton, including *Pseudocalanus*:

$$\log R = 1.437 + 0.783 \log W$$

Again R is $\mu\text{l O}_2 \text{ ind.}^{-1} \text{ d}^{-1}$ and W is dry weight mg. Corkett & McLaren (1978) transformed this for cephalothorax length (L in mm) by using a given length-weight relationship [dry weight in $\mu\text{g} = 11.9 (\text{cephalothorax length in mm})^{3.64}$]:

$$\log R = 2.850 \log L - 0.070$$

Last but not least, Marshall (1973) wrote about the effect of body size: Many attempts have been made to find a constant relationship between oxygen uptake and some measurement of the copepod body, length, surface area, or weight. The equations most often used are:

$$R = KL^2 \text{ or } R = KW^{0.667}$$

Where R is metabolic rate (or respiration) and K is a constant of proportionality. Surface area is taken to vary as L^2 , and volume (or weight) as L^3 , and oxygen uptake is assumed to occur through the surface of the copepod. Conover (1959) has found that oxygen consumption is directly related to weight, although later (1960) he used log-transformed data. Many authors have measured respiration in copepods of varying size and have calculated regression equations either directly or after a log-transformation.

Nevertheless, Marshall (1973) reported also in her review that when oxygen uptake is expressed per unit of dry body weight the small forms are usually found to be more metabolically active. The same tendency is seen when the developmental stages of a single species are compared.

That was already found by Marshall & Orr (1966) who stated in small copepods higher metabolic rates than in the large, e.g. *Calanus finmarchicus* or *C. hyperboreus*. Petipa (1966) noted a definite tendency towards decrease of oxygen consumption with age in *Acartia* sp. Investigations of Haq (1967) from the Gulf of Maine showed that the smaller *Metridia lucens* respired at a higher rate than the larger *Metridia longa*. Both species are common in the northern North Sea and adjacent waters. Also Mullin & Brooks (1970) found that generally respiration per unit body carbon decreased as body carbon increased.

Champalbert & Gaudy (1972) described the results of 281 respiration analyses of pelagic copepods sampled in the South Moroccan and Canarian area. The species used in experimentation were collected from various bathymetric levels: hyponeustonic species, e.g. *Anomalocera patersoni* and *Labidocera wollastoni*; epipelagic species, e.g. *Centropages typicus*, *Temora stylifera*, *Calanus helgolandicus* and *Acartia clausi*, as well as bathypelagic species, e.g. *Pleuromamma xiphius*, *Pleuromamma abdominalis* and *Euchaeta acuta*. Most of the named species live also in the North Sea and in the adjacent areas. When all species are studied together, a strong negative correlation exists between the log of respiration and the log of weight. Similar results were found from Champalbert (1973). These are further indications that smaller species have greater respiration rates per weight and time unit and thus a higher turnover of matter than larger species.

Effects of temperature and seasons: Gauld & Raymont (1953) measured respiratory rates of the copepods *Acartia clausi*, *Centropages hamatus* and *Temora longicornis*. Most of the experiments were conducted at temperatures ranging from 10 to 20°C. Measurements took place at four different temperatures. The results showed that in general an increase in respiratory rate followed a rise of temperature for all three copepods. However, the three species were probably not affected to the same extent by the same rise in temperature. Marshall et al. (1935) worked at temperatures down to 0°C, and they found that between this temperature and 10°C the respiratory rate for males and Stage CV *Calanus* was approximately doubled (Q_{10}). In females, however, the increase was considerably less. Between 10 and 20°C the curves for all *Calanus* steepened. Clarke & Bonnet (1939) found considerable variation in the respiratory rate of stage CV *Calanus*, but their results indicate a rise from 0.32 to 0.91 $\mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ for an increase in temperature from 5.5 to 16.8°C.

Gauld & Raymont (1953) noted a marked change between the respiration of *Centropages* from 4 to 13 June and those caught from 14 to 26 June. Although the length had decreased from an average 0.977 to 0.854 mm the oxygen consumption (corrected for body length) had nearly doubled. They considered that they were dealing with different generations and emphasised that this is a factor which should always be taken into account.

Seasonal variation in metabolism independent of temperature was demonstrated by Conover (1959) for several species of copepods. Painstaking investigations of the oxygen consumption of *Acartia clausi*, *A. tonsa*, *A. discaudata* and *A. bifilosa* were carried out by Conover (1956, 1959), who showed the link between the respiration rate of these species and temperature and the seasons in two areas of the Atlantic coast of the USA. Marshall & Orr (1958) found maximum respiratory rates in *Calanus finmarchicus* in April, coinciding with the diatom spring increase. Berner (1962) found a marked seasonal variation in respiration rate of *Temora longicornis*. Because the

spring diatom increase was over before observations began, his measurements could not be closely correlated with either phytoplankton or change in generations. Marshall (1973), considering the publications of e.g. Marshall & Orr (1958), Conover (1959), Haq (1967) and Gaudy (1968), summarized the knowledge about respiration and seasons of that time: From this, there can be seen a marked seasonal variation in oxygen consumption. That means, from a low value in winter months there is a sharp rise (per individual) in spring. Gaudy (1977) studied the respiratory metabolism of the copepod *Acartia clausi* at different temperatures using the environment of a power plant during an annual cycle. Seasonal variations in respiration intensity were observed, with a spring maximum. Q_{10} varied with temperature and time of year, suggesting seasonal regulation of metabolism.

Anraku (1964) tried to compare measurements of respiratory and grazing rates of *Calanus finmarchicus*, *Pseudocalanus minutus*, *Labidocera aestiva*, *Acartia tonsa* and *Acartia clausi*. For this, he exposed the organisms in different seasons to different temperatures, namely 2°C, 8°C, 15°C and 22.5°C, and determined the respiratory and grazing rates and their reaction to the incubation temperature.

From these experiments, it appears that the species studied showed a seasonal adaptation, but their reactions cannot always be attributed to temperature alone. Though *Acartia tonsa* has warm-water affinities, the winter population was partially acclimatized to its environment. For *Acartia clausi*, which has somewhat stronger cold-water affinities than *A. tonsa*, less oxygen was consumed in winter than in summer (a reverse acclimation). Except for the May population, *Pseudocalanus minutus* partially adjusted to their environment. The animals during the cold months respired at a relatively high rate at low temperatures as compared with the summer population. Thus, there were obvious changes in the slope of the metabolism-temperature curves with season, namely, the Q_{10} is: 16 February = 1.33; 16 August = 3.72, and 12 December = 1.72. The low Q_{10} for the winter *Pseudocalanus* seems to indicate an adaptation to cold, a fact that reveals its strong cold-water affinities. For *Calanus finmarchicus* little acclimation was observed between summer and winter populations. The high respiratory rates for *Calanus* in May and June are perhaps due to metabolic changes during the breeding cycle or to plentiful food supply. A high respiratory rate in spring, followed by a gradual decrease to a low level in winter, has already been observed for *C. hyperboreus* and is possibly related to the breeding cycle and the amount of food available (Conover 1962). This may explain the high metabolic rate in spring, which was unrelated to the environmental temperature alone.

Respiration, feeding, and assimilation in the two copepod species *Metridia lucens* and *Metridia longa* from the Gulf of Maine were studied by Haq (1967). *M. lucens* – a temperate form – demonstrated a normal increase of respiratory rates up to 18°C and *M. longa* – a boreal form – up to 14°C. Above 14°C the respiratory rates of *M. longa* declined, and at 18°C (range of lethal temperature) the animals died within 12 to 18 hrs. *M. lucens* became at 20°C sluggish and their oxygen consumption was reduced, although they survived more than two days. Maximum respiration occurred during spring for both species and tended to decline in fall and winter. Also the rates of oxygen consumption for *Calanus finmarchicus* found by Anraku (1964) increased with temperature, but at 22.5°C all individuals died having obviously reached their lethal range of temperature.

Marshall (1973) stated that temperature is the factor which has perhaps been most studied, since it is continually varying in the environment. Oxygen uptake rises with rising temperature up to a maximum which varies from copepod to copepod and, in some species, from one season to another. A temperature which is high enough to be injurious in winter can be endured without harm in summer. In some of these cases the copepod may belong to a different generation but some acclimatization can take place. The temperature/respiration curve is rarely linear, usually rising more steeply at the upper end and falling as the lethal temperature is approached. Q_{10} varies considerably from 2.0 (Comita & Comita 1964; Comita 1965, 1968) and in one copepod, *Pseudocalanus minutus* (Anraku 1964), varied from 1.33 in February to 3.72 in August.

Hirche (1987) studied the effect on respiration and swimming activity as well as temperature tolerance and respiration rates of the dominant copepods *Calanus finmarchicus*, *C. glacialis*, *C. hyper-*

boreus and *Metridia longa*, collected in the Fram Strait in July 1983. Temperature tolerance in the boreal *C. finmarchicus* was slightly higher than in the three Arctic species. Respiration rates at lower temperatures followed the Arrhenius equation in all species, with values for μ (temperature characteristics) between 11.05 and 22.95, corresponding to a Q_{10} between 2.05 and 4.5.

This increase in metabolic rate with rising temperature was not related to an increase of swimming activity. Average swimming speed remained unchanged at all temperatures and was ca. 1 cm s^{-1} for all species, when only periods of active swimming were considered. The time spent with active swimming did not change with temperature in *M. longa* and *C. finmarchicus*, but decreased in *C. glacialis*. In *C. hyperboreus* it increased at 5°C and decreased again at higher temperatures. Hirche suggested that the increase in oxygen consumption with rising temperature is fully accounted for by the basal metabolism.

Effects of feeding and food concentration: Measurements of the quantity and type of food assimilated by adult female *Calanus helgolandicus* during summer months and calculations of oxygen consumption were conducted by Corner (1961). This was based on the volume of oxygen required to metabolize lipid ($1 \text{ g} \equiv 2.03 \text{ l O}_2$) and carbohydrate ($1 \text{ g} \equiv 0.75 \text{ l O}_2$) present in the total quantity of food assimilated. The author wrongly assumed that protein must not be considered in the calculation because he thought that in normal circumstances it is not used primarily as a fuel. So, according to Corner the average amount of food digested daily accounted for 25.3% of body dry weight and was equivalent to an average respiration rate of $26.5 \mu\text{l O}_2 \text{ ind.}^{-1} \text{ day}^{-1}$.

Marshall & Orr (1966) made observations on the feeding and respiration of the common small copepods in the Clyde Sea area, using cultures labelled with ^{32}P for feeding experiments and the Winkler method of oxygen determination for respiration measurements. In all species, e.g. *Pseudocalanus elongatus*, *Centropages hamatus*, *Temora longicornis*, *Acartia clausi*, *Paracalanus parvus*, *Metridia lucens*, *Diaixis hibernica*, except possibly in *Oithona sp.*, there is a rise in oxygen consumption following the spring diatom increase. The authors believe that this is linked with the increased size of the copepods at that time. *Oithona sp.* was found to feed little on diatoms or flagellates but was able to take *Calanus* nauplii.

Omori (1970) studied variations of length, weight, respiratory rate and chemical composition of *Calanus cristatus* (North Pacific) in relation to its food and feeding. Positive correlations were observed between body length and the quantity of food available during its growth. The average weight of animals decreased when food became scarce. Respiratory rate was reduced to less than half due to adaptation to the unpleasant condition.

Under conditions of prolonged starvation *Oithona sp.* can reduce its metabolism (Marshall & Orr 1966). From observations on *Calanus finmarchicus* (Marshall et Orr 1958) and *C. hyperboreus* (Conover 1962) the same was found. Ikeda (1971a) measured food uptake, respiration rate and assimilation efficiency of ingested food by *Calanus cristatus* Stage CV in a continuous flow system. Food uptake varied from 0.22 to $10.90 \mu\text{g organic matter ind.}^{-1} \text{ h}^{-1}$ with positive correlation to the flow rate of water through the system. The respiration rate observed was as high as two times (1.26 to $4.25 \mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) that measured by Ikeda (1970) using closed bottle without food (1 to $2 \mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$). Ikeda (1971 a+b) found that under starvation conditions the oxygen consumption of *Calanus cristatus* rose for the first six days then fell considerably. The variable results may depend on the general level of feeding and the length of time since the copepod has fed. Marshall (1973) recapitulated that in general, respiration is lower in copepods living in water with an inadequate supply of food, than in the same species living in a nutrient rich environment. But under experimental conditions feeding sometimes raises oxygen consumption and sometimes has no effect.

Tsuda (1994) investigated starvation tolerance of all stages of *Pseudocalanus newmani*. Carbon content and respiration rate of the copepod increased exponentially with developmental stages and body length. The respiration rate of adult females decreased exponentially with days starved. Tsuda suggested that respiration rate decreased with starvation period at the rate of 11.4% per day. Although the author could not determine if this response was a behavioural or a physiological one,

it prolonged the survival period of starvation. Further authors like Raymont (1959), Mayzaud (1976), Ikeda (1977b), Vidal (1980b), Porter et al. (1982), Hiller-Adams & Childress (1983), Skjoldal et al. (1984), Surendranath et al. (1987) have observed a decrease of respiration rate and other metabolic activities during starvation in many organisms.

Gaudy (1974) found that increased daily food intake affects respiration and oviposition of copepods. The minimum quantity of organic matter required by copepods to balance their respiration expenditure is considered to be nearly $20 \mu\text{g dw d}^{-1}$ in *Calanus helgolandicus*, $8 \mu\text{g dw d}^{-1}$ in *Centropages typicus*, and $10 \mu\text{g dw d}^{-1}$ in *Temora stylifera*. These values are equivalent to 25, 50 and 50% of the copepods' body weight, respectively.

Conover (1960) suggested that carnivorous forms had a higher respiration per unit weight than herbivorous. This is for Marshall (1973) understandable since they must move more actively than herbivores to capture their prey.

Herbivorous species like *Calanus plumchrus*, *Paracalanus parvus* and *Euphausia pacifica* and carnivorous species like *Parathemisto pacifica* and *Pleurobrachia pileus* collected from Saanich Inlet, British Columbia, were maintained in the laboratory under fed and starved conditions by Ikeda (1977). Respiration rate and excretion rate of ammonia and inorganic phosphate were measured. The respiration rate remained at a constant level or increased during the feeding experiment but decreased progressively in starved individuals. In general, the level of excretion rates of fed species was higher than that of starved ones.

Lampitt & Gamble (1982) investigated the diet and respiration of the small neritic cyclopoid copepod *Oithona nana*. This species differs from other common copepods in having a wide food-particle size spectrum and a low metabolic rate. It is suggested that these adaptations constitute the strategy whereby *O. nana* maintains its population levels throughout the year. The seasonal pattern of respiration rate of *O. nana* is characterised by a sharp increase in June, followed by a gradual decline to reach a winter minimum. The data were converted into metabolic cost in terms of ingested carbon, using an RQ of 0.9 (Parsons et al. 1977). Metabolic requirements were calculated as between 6 and 40% of the food material estimating as being eaten.

Båmstedt & Tande (1985) studied respiration and excretion of *Calanus glacialis* in Arctic waters of the Barents Sea. The respiration and excretion rates of *Calanus glacialis* copepodite Stages III, IV, V and adult females from the drift-ice area east of Svalbard (Barents Sea) were measured in ship-board experiments during the period from 27 May to 13 June, 1983.

The phytoplankton biomass and abundance varied considerably between localities, but these variations were not generally reflected in the respiration and excretion rates of the copepods. The respiration and excretion rates of *C. glacialis* at the ambient temperature of -1.8°C (average respiration rates of 0.95, 0.73, 0.57, and $0.60 \mu\text{l O}_2 \text{ mg}^{-1} \text{ dw h}^{-1}$ for Copepodite Stage III, IV, V, and adult females, respectively) were similar to those previously reported for other large-sized copepods from cold or temperate areas. Average respiration and excretion rates tended to decrease with incubation time or time after capture.

Rates of oxygen consumption, ammonia excretion and phosphate excretion were measured by Ikeda & Skjoldal (1989) on a hydromedusa (*Aglantha digitale*), pteropods (*Limacina helicina*, *Clio-ne limacina*), copepods (*Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia longa*), an amphipod (*Parathemisto libellula*), an euphausiid (*Thysanoessa inermis*) and a chaetognath (*Sagitta elegans*), all of which were dominant species in the Barents Sea during early summer 1987. Oxygen consumption rates ranged from 0.33 to $13.8 \mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$, ammonia excretion rates, from 0.0072 to $0.885 \mu\text{g N ind.}^{-1} \text{ h}^{-1}$ and phosphate excretion rates, from 0.0036 to $0.33 \mu\text{g P ind.}^{-1} \text{ h}^{-1}$. In general, higher rates were associated with larger species, but considerable differences were also seen between species. The ratios between the rates (O:N, N:P; O:P) exhibited a wide species-specific variation, indicating dominant metabolic substrates. Typical protein orientated metabolism (predators) was identified only in *S. elegans*. From the results of metabolic rate measurements and

elemental analyses, daily loss of body carbon and nitrogen were estimated to be 0.50 to 4.15 and 0.084 to 1.87%, respectively, showing faster turnover rates of carbon than that of nitrogen.

Respiration, ammonium and phosphate excretion and phytoplankton consumption of mesozooplankton were examined by Christou & Moraitou-Apostolopoulou (1995) biweekly in a coastal area of the eastern Mediterranean from January 1989 to January 1990. Taking into account the ambient temperature, the metabolic rates estimated (4 to $31.2 \mu\text{l O}_2 \text{ mg}^{-1} \text{ dw h}^{-1}$, 0.4 to $3.5 \mu\text{g NH}_4\text{-N mg}^{-1} \text{ dw h}^{-1}$ and 0.1 to $0.6 \mu\text{g PO}_4\text{-P mg}^{-1} \text{ dw h}^{-1}$) were lower than those reported for the western Mediterranean, which might be related to the higher oligotrophy in the eastern Mediterranean. Maxima for these metabolic rates and that for zooplankton community respiration ($7 \text{ mg O}_2 \text{ m}^{-3} \text{ d}^{-1}$) were all observed during the period of higher temperatures. Simple and multiple regression models suggest that temperature was the most significant variable affecting zooplankton metabolism. Body weight and population composition were also important variables. Feeding activity, sometimes showing an increase with food concentration, seemed to increase metabolic rate, but temperature may mask this effect. The low O:N-ratio indicated a protein metabolism. Furthermore, the O:N, N:P and O:P fluctuations indicated a dissimilarity in zooplankton dietary pattern, probably due to the low phytoplankton levels and differing exploitation of other supplementary food sources. The results stress the importance of temperature, rather than food or other factors, for zooplankton metabolism in coastal areas of the oligotrophic eastern Mediterranean, which during summer is comparable to oligotrophic tropical seas.

For gelatinous zooplankton also a positive relationship between food concentration and respiration was found. Volovik et al. (1994) used the hyperbolic equation

$$R_{ro} = R_{rb} + R_{rmax}(F/(K_s + F))$$

to estimate this relationship for *Mnemiopsis* sp., for which F indicates food availability (prey l^{-1}). Comparable results were found for *Mnemiopsis mccradyi* by Kremer (1982), where starved ctenophores respired $6.0 \mu\text{M O}_2 \text{ h}^{-1}$ and fed specimen increased respiration to $26.4 \mu\text{mol h}^{-1}$, respectively.

Effect of microbial respiration: For herbivorous feeding in frontal systems respiration rates are often higher than expected by means of the observed increase in Chl a . In such areas depth integrated respiration amounts to 30-50% of daily primary production (Martinez 1997). The increase in respiration probably can be related to increased conjoint microbial respiration, since bacterial and microbial respiration constitutes a major part of respiration and is stimulated by copepod grazing (van Wambeke et al. 1996). Microbial respiration is both food and temperature dependent and food limited at low temperatures (Pomeroy & Wiebe 1993). The Respiration-to-ETS ratio is negatively related to temperature and positively related to Chl a since ETS does not increase much in Chl a maxima (Alcaraz & Packard 1989). The ratio (1.8 to 3.3, $r=0.64$) reflects metabolic state on a ocean-wide scale - on a short-term scale these measurements both reflect the animals activity level (Hernandez-Leon & Gomez 1996).

Effect of pressure: Investigations on the influence of water pressure on the respiration are of great interest, not the least with respect to possible explanations for diurnal and seasonal vertical migrations of zooplankton.

Bishop (1968) studied populations of cladocerans and of migrating copepods (*Diaptomus* spp., *Cyclops* spp.) in a freshwater lake. Respiration rates were measured. Animals from the epilimnion, mostly cladocerans, and from the hypolimnion, mostly copepods, respired at similar rates in their respective habitats. When the animals were placed in the same habitats, copepods from the hypolimnion had the greater rates of respiration. Copepods, which migrated over an extensive vertical distance daily, were less sensitive to changes in depth than cladocerans, which remained within a narrow vertical range. The copepods were less affected by changes in pressure and temperature within than outside their range of migration. Summarizing the results, it was found that increasing pressure depressed respiration but that temperature, being higher in the upper layers, raised it. On

the other hand, Percy & Small (1968) found that pressure had no effect on the respiration of some larger migrating crustaceans (*Euphausia* sp.; *Thysanoessa* sp.; *Sergestes* sp.).

Childress (1977) measured oxygen consumption rates on the carnivorous and vertically migrating midwater copepod *Gaussia princeps* at different temperatures and at different atmospheres. Zones of minimum oxygen are found at intermediate depths in most of the world's ocean and, although the dissolved oxygen in some of these "oxygen minimum layers" is considerably less than 0.5 ml/l, populations of metazoans exist there (Schmidt 1925; Sewell & Fage 1948; Banse 1964). The copepod *Gaussia princeps* cannot satisfy its metabolic needs by oxygen uptake at 0.20 ml O₂ l⁻¹ (as it was found in the oxygen minimum layer off California), although it is frequently found there. The question arises how *G. princeps* is able to survive in the low-oxygen environment.

The rate of oxygen consumption of *G. princeps*, at any temperature and pressure combination normally encountered, is much lower than that of shallower living copepods. This supports the theory that deeper living crustaceans consume oxygen at much lower rates than do shallower living forms. Because of an anaerobic adaptation to the minimum layer, it seems likely that this species may be comparable to the „lethargic vertical migrators“ described by Barham (1971). Q₁₀ is greater at lower temperatures and higher pressures. Based on the data, a predicted relation between depth and oxygen consumption by this species is presented. This shows a higher oxygen consumption rate at the nighttime depths in upper layers (feeding time) and a much lower, partially anaerobic metabolism at the daytime depths. The question here is whether such migrations might be an answer to food limitation in the mixed layer, whereby the transfer to a deeper zone would be a way to reduce metabolism.

Pavlova (1994) investigated diel changes in copepod respiration rates. Measurements of respiration in adult copepods at optimum concentrations in a respirometer were made at different hours of day. The migratory species (*Pleuromamma xiphius*, *Calanus euxinus*) were found to increase respiration rate late in the evening and early in the morning. No statistically reliable daily difference in the estimates of respiration were observed in copepod species like *Acartia clausi* and *Temora discaudata*, which do not make long-distance migrations. The author assumed that in the given experimental conditions the respiration rate appeared to represent changes in locomotory activity resulting from the sustained natural migratory rhythm and movement in food search.

It should be critically noted here, however, that during the investigations apparently respiration measurements were not carried out between midnight and 4 in the morning. Therefore it is not necessarily the case that *Pleuromamma xiphius* and *Calanus euxinus* exhibit two separate respiration maxima. Rather, the respiration rate may have increased toward evening and only decreased toward dawn. In this case respiration would not reflect the rhythm of vertical diurnal migration, which generally occurs during dusk and dawn, but would be an indication of a nocturnal feeding rhythm.

Hirche (1978) found in resting stages of *Calanus* sp. in a Swedish fjord between August and February no activity of the digestive enzyme trypsin. Amylase was very low in comparison to summer values elucidating that no feeding took place. In addition, the respiration values were the lowest recorded for *Calanus* sp. Calculations based on these values gave a possibility of survival for 194 days for lipid assimilation accepting a reduction in lipid content from 45% to 15%.

Hirche (1983) noted that many calanoid copepod species overwinter in deep water generally as Stage CV. There is, however, conflicting published information concerning the physiology and behaviour of the overwintering stages. For example, Marshall & Orr (1958) and Butler et al. (1970) concluded from respiration and excretion measurements on *Calanus finmarchicus* and *C. helgolandicus* that although the overwintering stages utilized little oxygen, there was a requirement for food intake during winter when phytoplankton is scarce. They therefore suggested that microzooplankton and detritus formed the overwintering diet. Detrital feeding was also suggested by Harvey (1950) and Corner et al. (1974). Comita et al. (1966) found even increases in weight and calorific content of the hibernating animals and assumed that it could only be the result of winter feeding. On the other hand, several workers failed to detect stomach contents in overwintering stages of *C.*

finmarchicus (Ussing 1938), *C. hyperboreus* (Conover 1962), *Calanoides acutus* (Andrews 1966), *Calanus cristatus* (Omori 1970) and *C. plumchrus* (Fulton 1973). Hirche (1983) assumed that these contradictory findings concerning food uptake by overwintering stages possibly result from ecological differences in the respective samples or populations. Evidence for winter feeding, particularly in *Calanus finmarchicus* and *C. helgolandicus* (Marshall & Orr 1958; Butler et al. 1970), comes from specimens caught in the upper water layer in rather shallow areas, whereas evidence for fasting stems from deep-water samples.

Hirche's paper reports in-situ measurements of respiratory and digestive enzyme activities in *Calanus finmarchicus* and *C. helgolandicus* from two fjords (120m and 650 m deep, respectively). In addition, experiments were carried out to study the influence of external stimuli such as food, light and temperature on respiration, digestive enzymes and development of copepods from different water depths. In the deep Norwegian fjord two populations were found in late summer and autumn: in the surface layer the copepods were smaller and more active with high respiratory and digestive enzyme activities. The deep population, consisting of copepodite stage CV and a few females, was torpid, had large oil sacs and empty guts. Their respiratory and digestive enzyme activities were very low. In the shallow Swedish fjord CV in deeper layers weighed much less than those in the Norwegian fjord. Weight-specific respiration was intermediate between deep and surface populations in the Norwegian fjord. Hirche concluded that overwintering copepodites do not feed. Metabolic rates allowed successful overwintering only in the deep Norwegian fjord.

Båmstedt et al. (1990) studied nutritional condition of copepods and pelagic production during autumn in Kosterfjorden, western Sweden. At this among others electron transport system (ETS) activity of copepods from surface – and deep water in Kosterfjorden were measured.

Calanus finmarchicus from the above 30 m depth exhibited values between 2.5 and 12.5 $\mu\text{g O}_2 \text{ mg}^{-1} \text{ dw h}^{-1}$, without any temporal or diurnal trend. *Acartia clausi* from the surface-water had an ETS-activity between 9.0 and 32.9 $\mu\text{g O}_2 \text{ mg}^{-1} \text{ dw h}^{-1}$, on an average 2.3 times higher than that of *C. finmarchicus* in the surface-water. Copepods collected in the deep-water displayed different characters. *C. finmarchicus* exhibited uniformly low ETS-activity, with a range from 1.8 to 6.3 $\mu\text{g O}_2 \text{ mg}^{-1} \text{ dw h}^{-1}$, corresponding on average 42% of the surface-collected animals. *A. clausi* from the deep-water exhibited ETS-activity ranging from 9.3 to 17.3 $\mu\text{g O}_2 \text{ mg}^{-1} \text{ dw h}^{-1}$, corresponding on average to 85% of the surface-collected *A. clausi*.

For the purpose of estimating the active transport of carbon and nutrients by diurnal vertical migration of zooplankton Steinberg et al. (2000) have measured CO_2 -respiration and dissolved organic carbon (DOC) excretion by individual species of common vertically migrating zooplankton. On average, excretion of DOC makes up 24% (range = 5 – 42%) of the total C metabolized (excreted + respired) and could represent a significant augmentation to the vertical flux that has already been documented for respiratory CO_2 flux by migrant zooplankton.

Effect of light: Marshall (1973) summarized that full sunlight is lethal to *Calanus* as to many other marine animals (Huntsman 1925). Bright sunlight raises oxygen consumption of *Calanus finmarchicus* considerably. Light could influence the activity and therefore oxygen consumption of copepods. It appears according to the experiments of Pavlova (1975) that respiration is higher (and more variable) in the light. But Bishop (1968) states that sunlight had no effect on the oxygen consumption of some freshwater copepods (e.g. *Diaptomus sp.*, *Cyclops sp.*).

Effect of salinity: The effect of lowered salinity has been measured in a few copepods. In *Calanus finmarchicus* (Marshall et al. 1935; Anraku 1964) and in *Centropages hamatus* (Anraku 1964) oxygen uptake is lower in diluted sea water.

Miliou & Moraitou-Apostolopoulou (1991) investigated variations of respiratory rate of *Tisbe holothuriae* (Copepoda, Hapacticoida) in relation to temperature, salinity and food type. According to their results oxygen consumption decreased with decreasing temperature, but with a greater rate of supra- or subnormal salinities.

Acartia clausi is one of the most abundant copepod species of the Gulf of Fos (Mediterranean) while *Acartia tonsa* constitutes the almost exclusive copepod species of the Berre lagoon, a neighbouring semi-closed brackish area communicating with the Gulf. To explain why these two species do not coexist in the same environment, Gaudy et al. (2000) performed comparative experiments on metabolism and feeding of these two species and investigated the influence of temperature and salinity. The respiration and ammonia excretion were measured in different combinations of temperature (10, 15 and 20°C) and salinity (15, 25 and 35‰). For each temperature at the salinity of 35‰, respiration rates were less in *A. clausi* than in *A. tonsa*, the contrary being observed at the lowest salinity. At any temperature ammonia excretion was greater at the intermediate salinity in *A. tonsa* and least in *A. clausi*. In *A. tonsa* Q_{10} of respiration and excretion were minimum at the lowest salinity, while in *A. clausi* they were unaffected by salinity variation. The atomic O:N-ratio (from respiration and ammonia excretion rates) was significantly more elevated in *A. clausi* (mean: 21.2, range: 13.6 – 28.7) than in *A. tonsa* (mean: 11.3, range: 4.2 – 25) suggesting a more proteinic orientated metabolism in the latter. Feeding experiments where *Dunaliella tertiolecta* was used as food showed that both species obtained the same specific daily food ration at marine (>30‰) or lagoon (<16‰) salinity. The relationships between ingestion and food concentration in the two species were not significantly different.

Effect of oxygen content: The oxygen content of water affects *Calanus finmarchicus* only when it falls very low; below 3 ml O₂ l⁻¹ the respiration fell off rapidly (Marshall et al. 1935). Some copepods, however, e.g. adults of *Cyclops varicans* (freshwater), can withstand complete anaerobiosis for as much as 36 h (Chaston 1969).

Geographical fluctuations: Conover (1959) found that *Acartia clausi* from Southampton waters had a statistically higher metabolic rate in laboratory experiments during the cooler months of the year than *Acartia clausi* from Long Island Sound at the same season. Rakusa-Suszczewski et al. (1976) measured oxygen consumption and CO₂-production of *Rhincalanus gigas* (Antarctic Ocean) during the Austral winter. O₂ uptake was lower than for low latitude species. But, Shushkina & Vilenkin (1971) measured the respiration of eleven copepod species in the tropical Pacific. The intensity of respiration of tropical copepods at 30°C proved to be similar to that crustaceans in the temperate latitudes at 20°C.

Champalbert (1972) showed that an analysis of the respiration/temperature curve makes it possible to describe different modes of adaptation in relation to geographical distribution, altitudinal repartition, and dietary characteristics. Champalbert (1973) measured respiratory rates of the hyponeustonic copepod *Anomalocera patersoni*, sampled in the Gulf of Marseilles, during the cold period and compared the results to those of individuals of the same species from South Morocco and Canarian area. Optimal temperature ranges are different for subtropical and temperate populations.

Båmstedt (1988) studied ecological significance of individual variability in copepod bioenergetics. High interstage variability in body length and mass, reproductive state and metabolic activity is characteristic of copepod populations from the Barents Sea and coastal waters in Sweden and Norway. The dry weight of a given copepodite stage, sampled at a given time from a homogeneous water mass, may vary by a factor of 4 – 5 between extreme individuals, protein and particular lipid content being even more variable. Similarly, high variability in gut fullness and grazing rate within defined copepodite stages typically occurs at all times of the year, both when measured as in-situ rate or experimentally determined rate, using homogeneous food suspensions. In accordance with this, maturation state (measured as length of gonads) and spawning (measured as length of egg production over 24h) are highly variable factors at the individual level. Since all these factors also influence the metabolic rate of the animals the respiratory rate (measured as ETS-activity) of comparable individuals may vary as a factor of 5 or more. The results indicate that high individual variability in size and activity parameters is universal. Båmstedt assumed that this can not be explained by existing models of feeding behaviour, growth and development, and calls for new models, in which the nutritional history of the individual may play an important role.

Gaudy et al. (2000) have measured the respiration and ammonia excretion of *Acartia clausi* and *Acartia tonsa* in different combinations of temperature (10-, 15-, 20°C) and salinity (15-, 25-, 35‰) to explain why these two species do not coexist in the same environment. Respiration rates were maximum at the highest temperature tested (20°C), but the effect of temperature varied according to species and salinities. That means, in *Acartia clausi*, respiration increased regularly with temperature. In *Acartia tonsa* this was observed only at the salinity of 35‰, while at 15- and 25 ‰ respiration was least at the intermediate temperature. In *Acartia clausi* the respiratory rates were slightly increased at low salinities, a tendency which is opposite to the results obtained in *Acartia tonsa*.

In both species, ammonia excretion rates showed a small range of variation between 10 and 15°C but increased markedly at the highest temperature tested. The salinity variation had no marked effect on the ammonia excretion rates in *A. clausi*, at any temperature. In *A. tonsa*, the excretion rates were relatively homogeneous at low and medium salinity for a given temperature but decreased (10- and 15°C) or increased (20°C) at 35‰.

Summarizing it can be said that the metabolic rate of copepods (and surely of other zooplankton) is affected by a multitude of parameters, e.g. by their body size and shape, temperature -, salinity -, light - and pressure effects, feeding habits, reproductive state, and by seasonal change.

Taxonomic differences in respiration: A comparison of metabolic rates of non-gelatinous and gelatinous zooplankton showed that gelatinous zooplankton had a comparably lower weight-specific metabolic rate than other zooplankton. On the other hand, carbon content in gelatinous zooplankton dry weight is smaller than for crustacean zooplankton: 1 - 32% compared to 24 - 67%, respectively (Schneider 1992). The resulting carbon-specific metabolic rates showed no difference between the two groups. This indicates that primary metabolic processes are similar in both groups, but gross differences are achieved by means of functional morphology.

Respiration of total zooplankton community

In the literature there are only very few examples of attempts to measure oxygen consumption of a whole zooplankton community. The main publications to be named in this connection are those by Martens (1986, 1992). Zooplankton was caught in vertical net hauls from the pycnocline to the surface with a WP-2 Net (200 - or 250 µm mesh size). The sample was divided in two equal parts. A subsample was incubated in the dark in 500 ml sea water of the same location at actual water temperature for about 4 hours. The other subsample was treated with additional 100 mg MABA (Sandoz) to anaesthetize the zooplankton and measure the phytoplankton- and microbe-oxygen uptake. Both bottles were locked with polarographic oxygen sensors (Mikro-Clark-Electrode), the oxygen content of the bottles being measured continuously. The difference between these two measurements gave the oxygen consumption of the mesozooplankton caught by the WP-2-Nets.

In the North Sea Martens (1986) found with this method weight specific respiration rates which showed diurnal variation during spring and winter but not during summer. In spring maximum respiration occurred in the early morning, while in winter the maximum was at noon. Martens (1992) employed his method further on five drifting stations in the North Atlantic (18°N to 72°N). The weight specific respiration rate decreased from south to north parallel to the water temperature, whereas the amount of mesozooplankton increased. No significant difference in the total oxygen uptake ($\mu\text{g O}_2 \text{ h}^{-1} \text{ m}^{-3}$) of the zooplankton community between the five stations could be found.

This method certainly involves some difficulties. A main problem is the automatic inclusion of dead biomass in the sample material when calculating the respiration rates relative to dry weight.

Measurements of respiration rates during the KUSTOS experiments

The measurements of zooplankton respiration rates in the German Bight were carried out using a digitally controlled electrode system similar to that used by Martens. However, in this case there was no question of measuring the respiration of the whole zooplankton community due to the con-

siderable proportion of detritus and other particulate material in the net samples. The main emphasis was therefore placed on measuring the oxygen consumption of the copepods, which dominate the mesozooplankton in the German Bight throughout the year. The proportion of copepods in the mesoplankton was 54% in summer of '94, 69% in spring of '95 and 96% in winter of '96.

The animals were obtained by careful vertical hauls with the WP-2 net (200 µm mesh size). Using a point light source, they were concentrated and removed from the rest of the sample, which often contained considerable amounts of phytoplankton and detritus, by pipette. Taking advantage of the phototactile response of the animals ensured that only healthy and active individuals were selected and that practically no phytoplankton and detritus got into the holding containers. The organisms were then briefly examined under the microscope in order to eliminate foreign matter and unintended species so that there was finally a mixture of the small copepods typical for the German Bight such as *Acartia* sp., *Temora longicornis*, *Centropages hamatus*, *Pseudocalanus elongatus* and *Paracalanus parvus* remained. The animals were then held in the dark and at a constant temperature in bacteria-free filtered and oxygen-saturated sea water. The measurements of O₂ consumption were carried out continuously over 4 to 8 hours using a digitally controlled electrode system developed by the firm Meerestechnik Elektronik GmbH (Mikro Clark electrodes).

During six cruises in the German Bight experiments were carried out on board involving a total of 172 individual measurements of the "copepod-mix" at the ambient mean temperatures of the surface layer (1.5, 8, 10, 12, 16 and 17.5 °C). The individual measurements were averaged for each experiment (maximum of four measurements) and are presented in Fig. 17. In spite of a good deal of variability they show a highly significant correlation to water temperature ($p < 0.005$). With increasing temperature there was an exponential increase in O₂ consumption, by a factor of around 2.6 for an increase of 10°C (Q_{10}). Considering the stock size in the station grid, which was converted to biomass, the O₂ consumption in summer of '94 was roughly calculated to be on the average 12.3 mg O₂ m⁻²h⁻¹ (Krause et al., in prep). These data were also used to estimate the productivity of the copepods in the German Bight (see section on Production).

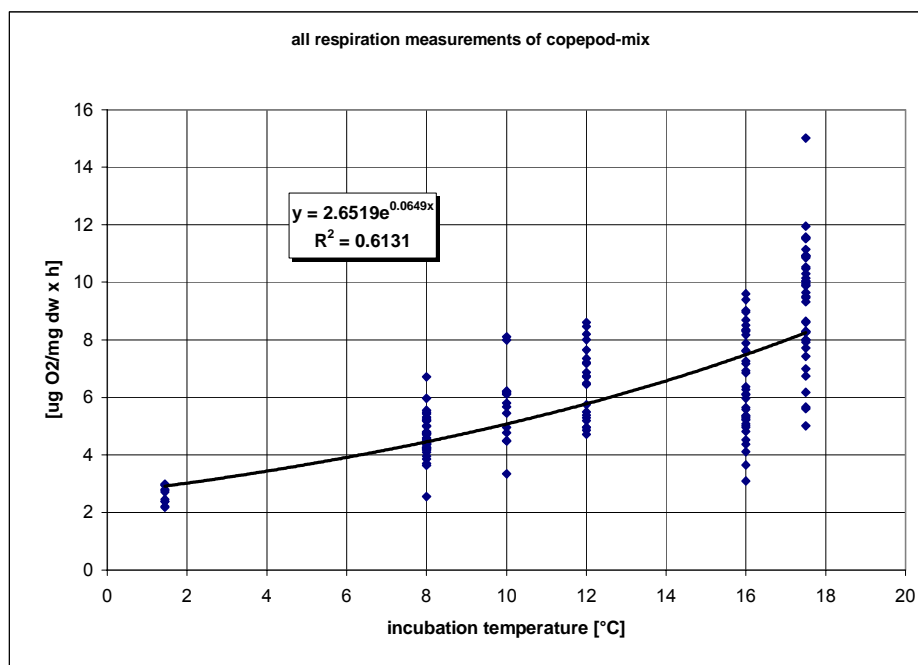


Fig. 17: Respiration measurements upon the copepod-mix in the German Bight at different seasons.

average O ₂ -consumption of the copepods in the German Bight					
Season	temperature [°C]		Copepoda-mix [µgO ₂ mg dw ⁻¹ h ⁻¹]	Calanus sp. [µgO ₂ mg dw ⁻¹ h ⁻¹]	position
26 Feb. - 5 March '96	1.5	MIN MAX MEAN st. deviation var. coeff. n	2.18 2.99 2.62 0.30 11.63 11	1.82 1.99 1.91 0.12 6.31 2	different positions
28 April - 7 May '95	8.0	MIN MAX MEAN st. deviation var. coeff. n	2.55 6.72 4.63 0.72 15.66 37	-----	drift station
29 May - 1 June '95 and 29 May - 1 June '96	10.0	MIN MAX MEAN st. deviation var. coeff. n	3.35 8.11 5.69 1.30 22.79 14	-----	different positions
29 July - 10 Aug. '94	16.0	MIN MAX MEAN st. deviation var. coeff. n	3.09 9.60 6.49 1.73 26.63 38	-----	drift station
15 - 22 August '95	17.5	MIN MAX MEAN st. deviation var. coeff. n	5.01 15.01 9.30 2.04 21.90 39	-----	different positions
1 - 5 October '96	12.0	MIN MAX MEAN st. deviation var. coeff. n	4.72 8.61 6.48 1.26 19.45 22	3.92 1	different positions

Tab. 6: average respiration rates of the copepod-mix in the German Bight during different temperatures (seasons) from Krause et al. (in prep.).

In Table 6 mean values are given for the respiration measured during KUSTOS. The measurements were generally made using the copepod-mix composed of small copepods typical for the German Bight. The table also shows results of measurements made on the large copepod *Calanus* sp. The results show the small copepods to have a distinctly higher respiration rate relative to body weight.

The following critical remarks must be made with respect to the method used:

- Respiration was only measured for a part of the zooplankton spectrum, namely the copepods. Mass balances and turnover rates, as they were aspired to in the KUSTOS project, would require measurements for the entire zooplankton community.
- The composition of the species and stages in the sample might not correspond to that in the water, since the different species and stages might react differently to the light source.
- A statistical analysis revealed that the O_2 consumption in $mg\ dw^{-1}h^{-1}$ was significantly positively correlated with the biomass used. This result supports the argument by various authors that crowding in the experimental container causes the organisms additional stress and leads to increased O_2 consumption.

Modelling respiration

Size and density dependence: In most models size dependence, i.e. application of allometric relationships, is used to scale respiration (Anderson 1992). This is based on baseline work of Banse (Banse 1979; Banse 1982).

The general form is

$$q = aM^b$$

where M is the biomass. Banse (1982) could show that the factor b is almost 0.75 irrespective of the taxon. Where biomass data are not available, the 'equivalent spherical diameter' (ESD) can be applied. Moloney and Field (1991) created a discrete model based on ESD-size classes, where the average ESD was calculated as geometric mean:

$$ESD_{average} = \sqrt{ESD_{min} * ESD_{max}}$$

For the aforementioned model 4 size classes were selected in logarithmic intervals from 0.2 μm to 2000 μm , each one separated in auto- and heterotroph guild, with the size class 200-2000 μm representing zooplankton. From the ESD spherical volumes were calculated with the conversion factor of 1 pg wet weight = 1 μm^3 , in order to calculate biomass. Further conversion factors were applied. 0.07 to calculate carbon weight from wet weight. A more complicated estimation of the average weight for a size class was provided by Blanco et al. (1998). Besides general size-dependence (e.g. Ikeda 1978) also density dependence can be found Razouls (1972b).

Stoichiometry: Excretion rates of P and N are strongly correlated ($r^2 = 0.88$) and consequently each predicts the other best. Respiration rate is also highly significantly correlated with P and N excretion rates and is the second best predictor (see also Volovik et al. 1994; Finenko et al. 1995). The former apply a formula for inorganic to organic release of $C_{tot}=66\% CO_2$ and 33 % DOC. Although body size explained relatively less overall variability, the inclusion of temperature, container volume, and experimental duration as independent variables in multiple regressions substantially improved the predictive power of models based on body size. The models can be corrected for taxonomic biases in zooplankton, but these biases were usually small (Wen & Peters 1994).

3.3.2. Grazing and feeding

Grazing -, feeding – and ingestion rates give information about the uptake of biomass. Filtration rates inform about the water volume filtered by the organisms per time unit. Rates of food assimilation and food efficiency quantify the degree of utilization of the ingested food. Feeding rates of

zooplankton organisms are mainly dependent on food concentration, food quality and water temperature (e.g. Kiørboe et al. 1982).

There is a great deal of literature about the general topics of grazing and feeding by zooplankton. We have registered more than 1800 papers regarding this area up to now (see Tab. 2). For grazing and feeding of copepods alone we found 809 papers. Work on feeding has also been carried out for most of the other taxonomic groups but these investigations are far fewer in number (see Tab. 3). It would certainly be useful to collect all data on grazing, feeding and ingestion rates and to compare them, whereby careful attention must be paid to the methods and experimental conditions applied. In this way it would probably be possible to arrive at meaningful dynamic factors for budgets and models. Furthermore, such a compilation of existing data would make it easier to identify weaknesses and gaps which should be filled by future investigations.

Feeding and feeding behaviour of filter feeding copepods have been extensively studied in the laboratory by many workers, e.g. by Conover (1966), Mullin & Brooks (1967), Paffenhöfer (1971, 1976), Nival & Nival (1976), Frost (1977), and Poulet (1974, 1977) to mention at least some of them. Grazing and feeding of zooplankton have been reviewed several times (e.g. by Cushing 1958; Anraku 1963; Joergensen 1966; Mullin 1967; Marshall 1973; Corkett & McLaren 1978; Poulet 1983; Huntley 1988; Kleppel 1993; Fransz et al. 1991a; Mauchline 1996). The 'Hydrobiological Bulletin', volume 19(1) compiled the reports of various authors regarding methodological problems with grazing and ingestion measurements for zooplankton.

Dealing with the North Sea, Gamble (in Fransz et al. 1991a) noted that it truly can be stated that, at some time or other, observations have been made on copepods grazing in most areas of the North Sea, but the observations are very sparsely distributed. Further, no measurements have been made in the North Sea proper of the nutrition of copepods during winter. These reservations still apply to a certain degree today. Most of the numerous publications on copepod grazing report on laboratory experiments, which are, by nature, represent artificially constructed systems and are thus not necessarily comparable to field conditions.

Methods

Grazing and feeding rates in zooplankton have been measured using very different techniques up to now:

- In laboratory experiments, the reduction in the number of potential food particles in the incubation vessels due to the grazing activity of the experimental organisms was determined. This can be performed by photometric measurement of the chlorophyll concentration, if only herbivorous grazing is to be determined, or by particle counters (Coulter Counters), which give information on food selection in terms of food particle size spectra and hence indicate food preference (e.g. Gamble 1978).

Nevertheless, Kersting (1985) reported that an important problem of electronic particle counters is count loss by coincidence of passage of particles through the orifice and caused by dead time of the instruments. Kersting found out that the count losses were much higher than the ones predicted by the manufacturers. A maximal counting frequency of 200 counts/second is recommended for accurate work. Also Baretta & Malschaert (1985) listed some problems which have occurred in grazing experiments on natural particle assemblages using electronic particle counters. These include, among others, variance between samples due to statistical causes (especially caused by large particles), differences between experimental bottles and between experimentals and controls at start of experiment, shifts in particle distribution during the experiment due to an increase in small particles, growth of bacteria and other organisms, and breakage during handling by grazers into fragments. Klein Breteler (1985) found fixation artifacts of phytoplankton in grazing experiments caused by drastic losses of cells and changes of size after fixation of flagellates. Even in diatoms changes in size were noticed to a certain degree.

- The flow cytometer developed for phytoplankton research by Yentsch et al. (1983) can be used for grazing studies on zooplankton. Van Ierland (1985) gave a short description of the cell analyser based on light scattering properties. Beside particle counting, the apparatus has the capability to distinguish different types of cells.
- Using the radioactive tracer method, the food (e.g. phytoplankton) is marked with radioactive isotopes (^{14}C , ^{15}N ^{35}P) and can be measured after uptake by the experimental animals. The ^{14}C -technique for grazing measurements was developed by Daro (1978) and can be used to estimate grazing of either individuals or small groups. Thus with this e.g. comparing studies of the trophic role of different developmental stages are feasible. It can also be used for study of diurnal feeding rhythms.

Gulati (1985), however, examined the technical problems which appear by investigating zooplankton grazing using radioactive tracers. For example, it was found that because of the respiratory loss of the assimilated radiotracer in experiments lasting a few hours serious underestimates of assimilated rates may occur. Baars & Oosterhuis (1985) reported about problems in grazing with *Calanus finmarchicus* using ^{14}C bicarbonate.

- With the gut fluorescence method the vegetable proportion of the intestinal content of zooplankters can be measured by fluorescence analysis, permitting conclusions about the grazing rate (e.g. Mackas & Bohrer 1976). This method has the advantage that during field investigations freshly caught organisms can be used, and no laboratory experiments are necessary.

Considering, however, the fact that it is becoming ever more evident that most copepods which were previously considered to be herbivorous can utilize animal nutrition independently of the food supply available (see below), this method will not, on the rule, pick up the full spectrum of ingested food. Further, Baars & Helling (1985) reported about methodical problems in the measurement of phytoplankton ingestion rate by gut fluorescence.

- Measurements of digestive enzyme activities can give indications with regard to herbivorous or carnivorous food preferences of zooplankton organisms (e.g. Mayzaud and Conover 1976).

Nevertheless, Oosterhuis & Baars (1985) studied the usefulness of digestive enzyme activity as an index for feeding activity in copepods. They concluded, also because the literature about this reveals conflicting results, that the technique cannot be used as index for feeding activity.

- Ayukai & Nishizawa (1986) reported about the use of defaecation rates as a possible measure of ingestion rate of *Calanus pacificus*. Båmstedt et al. (1999) showed that the production rate of faecal pellets can be used as a quick and robust method to estimate grazing rate in *Calanus finmarchicus*.
- Some authors have also drawn on egg production rates when estimating ingestion rates (e.g. Kiørboe et al. 1985; Daro & Baars 1986; Kiørboe & Tiselius 1987).

But, Gamble (in Fransz et al. 1991a) criticized that grazing rate inferences from egg production can only be made directly on adult females and the method itself integrates a previous period of feeding.

Principally, Gamble (in Fransz et al. 1991a) thinks that by most of these methods measurements are made on animals which have been isolated in small containers and the results thus obtained could be unrealistic. Likewise, Mauchline (1996) stated that laboratory experiments about grazing and feeding rates can be criticised, because these methods ignore the higher variability in the natural environment in space, time, abundance and diversity of food items.

Gamble (in Fransz et al. 1991a) also emphasised that grazing measurements are naturally highly variable, because a variable number of animals in the experimental bottles do not feed and thus reduce the total grazing potential of the population. Furthermore, it is obvious that for populations

with many developmental stages of several co-occurring copepod species feeding on natural phytoplankton assemblages, single value estimates of grazing rate can be highly inaccurate and grossly misleading. Poulet (1983) also criticised the typical laboratory experiments for determining grazing and feeding rates, stating that the one-link design in laboratory experiments is not necessarily realistic. Rather, a combination of pathways seems to provide a more probable utilization of the food existing in nature. According to Poulet the quality of food, expressed in terms of respiration, assimilation, growth or reproduction, has been explored for only a few species of phytoplankton. The trophic value of most of the naturally occurring particles on which copepods feed is still unknown.

Consequently, recent emphasis has been directed towards making measurements on animals immediately after collection. Such methods however have their own drawbacks. For example, the gut fluorescence technique depends on a laboratory-bench estimate of digestion time. Additionally, this method measures only the ingested phytoplankton and lacks the heterotrophic food items (Harris 1994; Harris 1996). Further criticism of the gut pigment approach is based on the apparently variable degree of pigment destruction during gut passage (Lopez et al. 1988; Penry & Frost 1990). Digestive enzyme activity according to Oosterhuis & Baars (1985) could not be used as an index of feeding activity.

To ensure a better interpretation of feeding rates, more than one method should be carried out at the same time. Dam et al. (1994) proposed additional measurements of metabolic rates like respiration, excretion and egg production. The evidence of omnivorous feeding could be shown by estimation of carbon demand from respiration on the one hand and from minor carbon ingestion measured from herbivorous feeding on the other hand. Mauchline (1996) believed that ingestion rates derived from conventional grazing experiments together with evacuation rates leads to a more realistic view of the feeding process in copepods.

Feeding of copepods

Feeding behaviour and selective feeding

In the past it was imagined that filter feeding planktonic organisms swirl up suspended food particles in a passive way. In the case of *Calanus finmarchicus* food was thought to be obtained from a filter current which was diverted from the swimming current (Esterley 1916; Cannon 1928; Lowndes 1935; Marshall & Orr 1955; Gauld 1966). In this case a selection of the food according to particle size would take place, corresponding to the specific construction of the filter apparatus. Nevertheless, e.g. Richman and Rogers (1969) assumed that besides passive filtering, copepods like *Calanus helgolandicus* are able to hunt actively larger food particles.

For food uptake copepods use five pairs of extremities: 2nd antennae, mandibles, 1st and 2nd maxillae and maxillipedes. In copepods there is a close correspondence between the morphology of the mouth parts and the feeding behaviour. Within the group of the copepods there are two different basic types of food acquisition: 1) filtering type, which is primarily found in herbivores and 2) raptorial type, which is characteristic for carnivores. The setae and setulae of the 2nd maxillae constitute the filter apparatus in the filterers. The space between the setulae is significant for the minimum size of the food particles retained (Schnack 1975).

Anatomical structure and the use of feeding appendages determine feeding behaviour to a great part. The antennules having sensilla (mechanoreceptor) that are used in the detection of prey, primarily function in predatory feeding (Mauchline 1980). Chemoreceptors are used more in particle-feeding like herbivory and detritivory. In this way selectivity of particles is possible. Rejection and avoidance of particles is a negative response of chemoreceptors, while escape behaviour is an negative response of mechanoreceptors (Landry 1980). Additionally three broad types of mouthparts occur: one for particle feeders, second of omnivores and the last one of predators, divided up by segmentation and setation of the mouthparts (Turner 1978; Schnack 1989). Cinematographic study determine animal to animal variability in the feeding behaviour of *Calanus finmarchicus* (Turner et al. 1993). Flow fields and feeding currents generated by the copepods has been investigated

for more omnivore, predatory species (Yen & Fields 1992) and for herbivorous species (Bundy & Paffenhöfer 1996). Strickler (1982) conceived a model of the copepod feeding current. The authors pointed out that further studies are necessary to define intra- and interspecific differences in the generation and capabilities of flow fields.

Huntley (1988) reviewed the feeding history and its integrative forcing functions (past and present) of copepods in a behavioural view instead of a mechanical determination of feeding only. This is supported by findings of Gill & Poulet (1988) showing that *Temora longicornis* shows mechano- as well as chemosensorial reactions to food particles. On the other hand feeding behaviour can be influenced by the occurrence of predators. For example grazing of *Acartia* spp. is reduced under high light and at presence of fish predator exudate in order to reduce visibility and by this to avoid the risk of predation (Cieri & Stearns 1999).

Mullin (1963) reported that *Calanus* spp. removed large phytoplankton cells at higher rates than small ones when feeding on a mixture of two species of phytoplankton. The large cells contributed by far the greater fraction of the total volume of food ingested by the copepods, even when considerably less abundant than the smaller cells. Paffenhöfer (1971), investigating filtration and ingestion rates of all stages of *Calanus helgolandicus*, found that filtration and ingestion performances of all stages increased with increasing particle size. Furthermore, filtration rates decreased and ingestion rates increased with increasing food concentrations.

Poulet & Chanut (1975) have shown that the feeding of *Pseudocalanus minutus* on peaks in the particle spectrum is not a selective process based on sizes, but rather an active opportunistic mode of feeding based on the most concentrated stock of particles within a given size range. When feeding on particles, copepods generally feed on peaks in the particle spectrum but shift grazing pressure to other parts of the spectrum according to the occurrence and succession with time of biomass peaks. Poulet & Marsot (1980) assumed that such results clearly demonstrate considerable flexibility in copepod feeding and strongly suggest that this shifting process demonstrated by Poulet (1973) and Richman et al (1977) depends on behavioral phenomena. Poulet & Marsot (1980) believed that the concept of a fixed sieve deduced from the theoretical performance of the filtering apparatus (Boyd 1976) does not seem to correlate with experimental results (Richman et al. 1977; Poulet 1977; Allan et al. 1977). In addition, this concept logically extends the classical hypothesis according to which the mouth parts of copepods (second maxilla) act as filters or sieves (reviewed by Marshall 1973).

It has been shown by several workers that feeding among copepods was related to chemoreceptors (e.g. Ong 1969; Friedman and Strickler 1975; Paffenhöfer et al. 1995) to mechanoreceptors (e.g. Strickler 1975; Landry 1980) and to the taste of the particulate food (Fernández 1979; Poulet & Marsot 1978, 1980). Thus, Fernández (1979) could show that using mixtures of planktonic algae and plastic beads of different or similar sizes, the nauplii of *Calanus pacificus* strongly selected the algal cells, consuming them almost exclusively. Poulet & Marsot (1978) fed the copepods *Acartia clausi* and *Eurytemora herdmanni* with artificial food particles consisting of microcapsules that were either enriched with an encapsulated homogenate of naturally occurring phytoplankton or nonenriched. The copepods preferentially ingested the enriched capsules. The observations demonstrated that filter-feeding in these species is a behavioural process, under sensory control, and that the copepods are able to discriminate between enriched and non enriched food particles. Sykes & Huntley 1987 observed selection against particles like the toxic dinoflagellate *Gonyaulax grindleyi* by *Calanus finmarchicus*. That means, copepods fed *G. grindleyi* regurgitated after 45 to 120 min and, in nearly all cases, did not maintain full guts.

Poulet & Marsot (1980) studied chemosensory and food-gathering by omnivorous marine copepods. They found that feeding processes of copepods are neither passive nor automatic phenomena. Raptorial feeding and impaction feeding are most likely the two basic modes of food capture existing among copepods. The intensity of capture depends on the size of the particles and both on the anatomical and dynamic properties of the feeding appendages. The flexibility noticed in the regime of particles consumed over the entire size spectrum is related to the capability as well as to the length of time with which copepods can operate one mode of capture and can switch from one

mode to the other. Small and large size particles can be retained either with the same or with variable efficiencies, depending on the abundance of each particle category in the water and also on the capture ability of the copepod species. Selectivity for food results from the stimulatory effects of physical and chemical agents on receptors presumably located in the filtering chamber and on the feeding appendages. Identification of food through sensory mechanisms seems to be more important than selectivity for size alone, as far as the dynamic equilibrium of the pelagic food web is concerned. Poulet & Marsot (1978, 1980) thought that sensory selection should allow copepods to obtain their energy requirements with the least effort from the heterogeneous mixtures of particles, a fraction of which constitutes potential food resources.

Poulet & Marsot further explained that many workers generally suggested that copepods are indiscriminate filterers whose retention efficiency for different particle sizes depends on their filter structures, which retain larger particles more efficiently than smaller ones. These workers also admit that larger particles are preferentially selected by copepods (Mullin 1963; Richman & Rogers 1969; Wilson 1973; Frost 1972, 1977). In contrast, experiments performed with natural particles show that the highest rates of ingestion occur at or near the biomass peaks observed in the size spectrum (Parsons et al. 1967, 1969; Poulet 1973, 1974, 1977; Richman et al. 1977).

Harris (1982) made a comparison of the feeding behaviour of the large copepod *Calanus pacificus* and the small copepod *Pseudocalanus minutus* in two experimentally manipulated enclosed ecosystems (CEPEX'78). The feeding behaviour of the two different sized copepods was examined in relation to the particle size composition of naturally occurring phytoplankton populations (dominated by diatoms and flagellates). The hypothesis was tested that the larger copepods feed on larger sized particles. It was found over a series of experiments lasting 72 days, that on average *Calanus pacificus* fed on slightly larger particles (1.2 x diameter) than *Pseudocalanus minutus*. However, despite the large difference in body size (x 10 dry weight) there was evidence that on most occasions both species were competing for the same food resource over a wide range of the particle-size spectrum.

Laboratory experiments with copepod nauplii showed that ingestion rate of early stages may be related to size of algae (Rey et al. 2001). Even if more cells are ingested in the case of small algae (faster rate of filtration), the ingestion rate is higher with large algae than small ones. Similar results on the ingestion of copepodites have been reported by Mullin & Brooks (1970a), Paffenhöfer (1971a), and Allan et al. (1977). Arashkevich & Drits (1984) investigated the influence of food particle size on ingestion rates as a function of food concentration. For food, monocultures of planktonic flagellate algae *Pyramidomonas* sp., *Exuviella cordata*, *Gymnodinium wulfii*, *Prorocentrum micans*, and also nauplii *Artemia salina* (thus food of different size) were used. It was shown that feeding rates of *Calanus helgolandicus* were inversely proportional to food particle size.

Peters & Downing (1984) reported that ingestion rate was found to increase significantly with animal size, food concentration, and temperature. Filtering rate also increased with animal size and temperature, but declined as food concentration increased. The analysis suggests a difference in particle size preference between cladocerans and copepods. Cyr & Curtis (1999) reported that the range in size of grazed algae increased with increasing mean zooplankton body size, but differed systematically with their taxonomic composition. Copepod-dominated communities followed the same general relationship as cladocerans in freshwater.

The small cyclopoid copepod *Oithona* spp., three species of which form large stocks in the North Sea, differs distinctly from the other copepods mentioned up to now by the form of the 2nd maxillae. The setae are short and dagger shaped and have only a few, sturdy setulae. These 2nd maxillae appear most certainly to be less suitable for filtering than for grasping and holding of prey. For this reason, a carnivorous way of life is usually attributed to this species (Schnack 1975).

Nevertheless, from a study of the mouth parts of *O. similis*, Gauld (1966) came to the conclusion that it was a raptorial herbivore with preference for larger phytoplankton. During gut-content analysis, Lebour (1922) found "green remains and bits of diatoms". Eaton (1971) found that the survival of *O. similis* was enhanced by the presence of a number of species of cultured phytoplankton,

and that egg production was increased. Marshall & Orr (1966) noted that the nauplii of *Calanus* sp. disappeared when *O. similis* was present. Lampitt (1978) provided the first quantitative data on the carnivorous feeding behaviour of *O. nana*, with Stage I of *Acartia clausii* nauplii as prey. *O. nana* differs from other common copepods in having a wide food particle size spectrum and a low metabolic rate. It is suggested that these adaptations constitute the strategy whereby *O. nana* maintains its population level throughout the year. Lampitt & Gamble (1982) conducted an extensive investigation about diet and respiration of the small planktonic marine copepod *Oithona nana*.

Despite the great number of studies on feeding there is still a paucity of information on several aspects of the natural diets of the copepods and the question how they adjust their selective feeding to attain an optimal growth and reproduction efficiency.

Diurnal periodicity in feeding activity

Although e.g. Richman and Rogers (1969) found no innate diurnal feeding rhythm in *Calanus helgolandicus*, other workers could describe those fluctuations in copepod feeding. For example, Marshall & Orr (1955b) noted that *Calanus finmarchicus* feeds better in the dark than in the light. The diurnal feeding rhythm of the Black Sea *Pseudocalanus elongatus* was found by Zagorodnyaya (1974) to be closely related to vertical migrations and illumination, with heavy feeding recorded during the dark period, when the population rises to the surface, and practically no feeding observed during daytime. Daro (1980) measured differences of a factor of 4-10 between nocturnal feeding and diurnal feeding in *Calanus finmarchicus* during FLEX'76. Baars & Oosterhuis (1984) found a diel rhythmicity in the gut fluorescence level of *Calanus* spp., *Temora longicornis* and *Pseudocalanus* sp. Baars & Fransz (1984) showed that measurements of gut fluorescence indicated that large stages of calanoid copepod ingested ca. 6 times more chlorophyll containing particles by night than by day in the Oyster Ground area of the North Sea. Tiselius (1988) has demonstrated that community grazing by copepods in the Skagerrak and Kattegat was 2-5 times higher at night than during the day.

Head et al. (1985) studied the effect of day length and food concentration on in situ diurnal feeding rhythms in Arctic copepods. Levels of chlorophyll and phaeopigment were measured in several stages of *Calanus hyperboreus* and *Calanus glacialis* at 4h intervals to examine diurnal feeding behaviour in copepods which do not vertically migrate on a daily basis. All stages examined for each of the two species showed diurnal variations in feeding activity. In addition, different stages and species always started to feed synchronously, although timing of the onset of evening feeding was different at each of the three stations. On each occasion feeding started when incident light intensity decreased to $<4 \text{ W m}^{-2}$. Cessation of feeding in the morning, however, was not linked to a particular intensity of incident light and may, according to the authors, be controlled by satiation of appetite. Levels of three digestive enzymes – protease, laminarinase, and amylase – were measured in two stages of *C. hyperboreus* and *C. glacialis* at 4h intervals over a 48h time series. There were no rhythmic changes in amount of enzymes in any of the stages. Further, maximum levels of gut pigment were not necessarily correlated with ambient chlorophyll concentrations.

Effect of food concentration

Several workers have ascertained that the grazing (ingestion) rate of copepods increases with increasing food concentrations. For example, Irigoien et al. (1998) estimated *Calanus finmarchicus* daily ingestion of phytoplankton to be about 2% of body carbon prior to the bloom, 30% during the bloom and 14% thereafter. But this is not a linear process. Adams & Steele (1966) showed that at growing chlorophyll a the filtration rate of *Calanus finmarchicus* first rose rapidly to decline again later on. For example, Gamble (1978), Daro (1980, 1986) and Nicolajsen et al. (1983) found similar results with several copepod species (e.g. *Calanus* sp.; *Temora longicornis*, *Pseudocalanus* sp. and *Centropages* sp.). Gamble assumed that such a pattern would result in a saturation relationship between ingestion rate and food concentration. The relationship between grazing rate and food concentration has been differently described: Gamble (1978) found based on his data a double rectilinear model. Daro (1986) recognized an Ivlev-Parsons relationship, and Kiørboe et al. (1982) showed a sigmoidal curve. Gamble (in Fransz et al. 1991) pointed out that the choice of the

sigmoid model assumes that no threshold food concentration (see next paragraph) is necessary to initiate feeding. Arashkevich & Tseytlin (1978) ascertained that two factors – the ceiling number of phytoplankton cells in the faeces and the frequency of excretion of a particular copepod – determine a copepod's maximum food intake per unit of time. This intake cannot be increased, no matter how high the food concentration in the environment is. Food intake per day thus can be determined by multiplying the number of defaecations per day with the average number of cells in the faeces.

Nevertheless, the experimentally gained data sets about grazing rates often supported the assumption that at low food concentration no feeding occurred. Thus, there exists a concentration of food below which copepods either cease or sharply reduce feeding intensity. Those threshold food concentrations were found e.g. by Adams & Steele (1966), Frost (1975), Mullin et al. (1975), Conover (1978), Gamble (1978) and by Daro (1980). Arashkevich & Drits (1984) in conducting experimental feeding studies in the copepods *Calanus helgolandicus* and *Calanus glacialis* at various food concentrations could confirm these results. They found that food consumption does not occur in any species of algae at concentrations below a minimum value C_{th} which is called threshold concentration. With increased concentrations of food particles higher than C_{th} , the rate of consumption increased to a specific maximum with further increase in quantity of food in the medium. Data obtained is quite accurately described by an Ivlev-equation, modified by Parsons. The authors found at food concentrations lower than threshold the crustaceans produced either none or an insignificant quantity of faecal pellets, indicating empty peritrophic envelopes. Only in experiments where the animals fed on large food particles (large algae or nauplii) was no threshold established. This was also reported by Gamble (in Fransz et al. 1991). On the other hand, Deason (1980) concluded from grazing experiments with *Acartia hudsonica* feeding on *Skeletonema costatum* that threshold values of 39 and 59 cells ml^{-1} were not significantly different from zero. However, filtration rates were depressed at low food concentrations. And Baars & Fransz (1984), measuring grazing pressure of copepods on the phytoplankton stock of the Central North Sea (Oyster Ground), assumed that during summer most of the copepod species studied were feeding below threshold concentrations, and, if not consuming detritus and microzooplankton, suffered from starvation.

Superfluous feeding

Several field studies of secondary productivity in the sea have indicated that herbivorous zooplankton feed to excess in high algal concentrations (Harvey et al. 1935; Riley 1946; Cushing 1959b; Cushing & Vucetic 1963). Cushing & Vucetic (1963) believed that herbivores feeding in excess may not necessarily ingest the plant cells captured, but may destroy these cells outside the body. They regard the broken material as a source of soluble nutrients supporting the further growth of phytoplankton. Beklemishev (1957, 1962) considered that this superfluous feeding leads to the production of large quantities of undigested material in form of faecal pellets. Beklemishev and others strongly emphasized the loss of plant production as faecal pellets that sink below the euphotic zone. However, if it is right that most copepod faecal pellets will be remineralized in the upper layer (e.g. Krause 1981; Hofmann et al. 1981; Martens & Krause 1990) the feeding and excretion activities of copepods may promote the nutrient cycling in the euphotic layer and thus prolong the phytoplankton blooms in the stratified water column (e.g. Colebrook 1981). Nevertheless, Conover (1966) stated that superfluous feeding does not normally occur in nature. Likewise, Arashkevich & Tseytlin (1978), falling back on their experiments, did not believe that any excess feeding occurs in copepods.

A further possibility for secondary producers to influence primary production by grazing and excretion is reported for example by Porter (1976). The author pointed out that, in contrast to the wide-spread view that herbivorous zooplankton reduce the abundance of algae during grazing, some studies have shown that primary productivity and the numbers of certain algal species increase in the presence of grazers. Nutrients, such as phosphorus, that are excreted by zooplankton may stimulate the growth of algae not cropped during grazing. Porter found in the freshwater cladoceran *Daphnia magna* that during gut passage, viable phytoplankton cells can take up nutrients, both from algal remains and from *Daphnia* metabolites. This nutrient supply stimulates algal carbon fixation and cell division. Enhanced algal growth, observed after gut passage, can compen-

sate for the minor losses to the population caused by grazing. Also, Sterner (1986) found that the increase in algal reproductive rates caused by nitrogen regeneration from herbivorous zooplankton approximately equaled the zooplankton-caused mortality. Sterner concluded that this result demonstrates that nutrient regeneration by herbivores is at least sometimes a strong indirect effect in natural communities.

Effect of food quality on feeding rates

Food quality is often described in terms of selective feeding and preferred particles, but there is a great lack in quantifying food quality. For example, Fernandez (1979) defined food selection by the nauplii of *Calanus pacificus* as the ability to ingest certain kinds of particles in behavioural preference to others that occur simultaneously in the same environment. Huntley (1988) proposed as the best expression the dependence of ingestion on food quality in an equation but rarely applied it to define the quality of entire natural particle aggregations. Gamble (1978) tried to define food quality as the ingestion rate and the following gain of body carbon out of the available food particles. Libourel-Houde & Roman (1987) and Kiørboe et al. (1988b) measured food quality as egg production rate of *Acartia tonsa* under various environmental conditions. The definition of food quality is one of the least understood areas of copepod feeding biology (Huntley 1987). Therefore it would certainly be important to establish the food requirements of different species under comparable conditions, using standard methods (Harris 1996).

Temperature effects on feeding rates

Increasing temperature also causes an increase of all metabolic functions (Vidal 1980) and filtering rate. Those observations were made e.g. on the filtering rates of the freshwater cladoceran *Daphnia sp.* by Burns & Rigler (1967). Mullin & Brooks (1970) noted that the calanoid copepods *Rhincalanus nasutus* and *Calanus helgolandicus* fed on the diatoms *Ditylum brightwellii* and *Thalassiosira fluviatilis* ate and grew more slowly at 10° than at 15°C, but did not necessarily grow to larger size. Deason (1980) found in grazing experiments with *Acartia hudsonica* feeding on the diatom *Skeletonema costatum* that maximum ingestion rates increased exponentially with temperature, reaching a maximum with copepods collected at 14° - 15°C, and then declining again. Peters & Downing (1984), calculating multiple regression analysis of published filtering and feeding rates of cladocerans and marine calanoid copepods, found that ingestion rates increased significantly with animal size, food concentration, and temperature. Filtering rates also increased with animal size and temperature, but declined as food concentration increased.

Food sources

In the past, there was a tendency to separate the different species of copepods rather strictly into the herbivorous or carnivorous categories. Omnivorous status was imparted to only a very few species based on unequivocal experimental results. Recently, it has become more and more evident that it is not possible to strictly separate herbivores and carnivores, particularly in the large group of copepods, but that they must largely be assumed to have a mixed diet which varies in the course of the seasons and the larval development.

Poulet (1983) thought that marine copepods can potentially obtain food from any known stock of organic matter, in either dissolved or particulate form. Filtering mechanisms utilized by these crustaceans allow them to capture particles of various sizes, in the form of detritus and living prey. Contrary to phytoplankton, the role of detritus, bacteria, ciliata and flagellates in the diets of copepods is still poorly known, despite the relative importance of their standing stocks. Generally, data on the chemical composition of natural diets and on the digestion strategy of copepods are scant.

In the following, a brief and non-comprehensive summary of the potential food sources for copepods are given:

Utilization of diatoms and dinoflagellates: Much attention has centred on copepod feeding in order to estimate grazing pressure on phytoplankton blooms (Gamble 1978; Mauchline 1996). Copepods

of the genus *Calanus* were found to be effective grazers on diatom spring blooms. *Calanus finmarchicus* attains its maximum stocks shortly after the decline of the phytoplankton bloom, and in the second half of June the older copepodite stages already begin to migrate to their winter refuge in greater depths. This seasonal migration of the organisms continues into October/November (e.g. Marshall & Orr 1955; Vinogradov 1968). The animals do not reappear in the mixed layer until February/March to mate as mature males and females and to produce eggs in time for the onset of the diatom spring-bloom.

Mullin (1963), investigating the grazing of three *Calanus* species (*C. finmarchicus*, *C. glacialis*, *C. hyperboreus*), found that filtration rates (wrongly termed as grazing rates) varied inversely with phytoplankton concentration. Paffenhöfer (1971) studied filtration and ingestion rates of all stages of *Calanus helgolandicus*. Prey species were the chain-forming diatom *Lauderia borealis* and the unarmoured dinoflagellate *Gymnodinium splendens*. In a log-log system, filtration and ingestion rates increased almost linearly with increasing body weight. Ingestion rates increased from 0.2 µg to 0.8 µg C/day/nauplius stage IV to 18 µg to 69 µg C/day/female. Filtration and ingestion rates per unit body weight decreased gradually with increasing body weight. The daily ingested amount of food decreased from 292 - 481% of the body weight of nauplius V to 28 - 85% of the body weight of adult females. Paffenhöfer & Harris (1976) cultured the copepod *Pseudocalanus elongatus* over multiple generations at 12.5 °C on a diet of the chain forming diatom *Thalassiosira rotula*. The average daily ration ranged from 63% of the body weight at a food concentration of 25 µg C l⁻¹ to 148% at 200 µg C l⁻¹. Paffenhöfer & Harris (1976) found that at the same diet juvenile copepod stages were slightly more efficient feeders than adults. Zagorodnyaya (1974) studied the feeding and migrations of the Black Sea *Pseudocalanus elongatus* in winter. The animal is shown to feed on phytoplankton and to prefer diatoms less than 10 µ.

During the Fladen Ground Experiment (FLEX'76) Gamble (1978) showed in his experiments that small copepods had slightly higher ingestion rates than *Calanus finmarchicus*. Further, he observed a rapid environmental change in the phytoplankton population structure from diatoms to small flagellates and pennate diatoms. The ingestion rate of *C. finmarchicus* feeding on the smaller particles was considerably reduced and achieved a daily intake of about 20% of the body carbon compared with 50% at the same food concentration with the larger diatoms.

Huntley (1981) found out that *Calanus finmarchicus*, *Calanus glacialis*, and *Calanus hyperboreus* removed all phytoplankton in direct proportion to their abundance at chlorophyll a concentrations ranging from 0.53 to 12.1 µg liter⁻¹. For phytoplankton >20µm in diameter there appeared to be no selective ingestion according to the size, shape, or species of cell. The filtration rate for a given copepod species did not change over time or space. Weight-specific ingestion rate increased as copepod body weight increased. Evans (1981) found coherences between changes in size of *Temora longicornis* off the north English coast with the availability of the diatoms *Thalassiosira* and *Chaetoceros* as food. Gifford et al (1981) fed *Calanus finmarchicus* on two forms of the diatom *Thalassiosira weissflogii*: normal cells, which are spinose, and cells which did not have spines. Filtration rates of *Calanus* on the spinose form were on the average 1.7 times higher than on cells with no spines.

Peruyeva (1984) calculated the daily ration of Stage IV copepodites *Calanus glacialis* from the values characterizing gut filling with the use of the experimental data on defaecation rate and taking into account condensation of non-assimilated food in the back part of the gut. The daily ration of copepodites is 6 - 9% of body weight in the 12 - 30 m layer and about 1% in the 30 - 75 m layer. The difference is attributed to temperature and trophic conditions in the environment. Baars & Fransz (1984), measuring grazing rates with labelled food, noted that *Pseudocalanus* and *Calanus* had lower daily ingestion rates of chlorophyll (4-8% of body carbon) than *Temora* and *Centropages* (ca. 25% of body carbon). Gamble thus concluded (in Fransz et al. 1991) that similar sized calanoid copepods have similar feeding relationships. Berggreen et al. (1988) showed that the optimal size of preferred food increased during the development of *Acartia tonsa*.

Båmstedt et al. (1999) have studied the utilization of small-sized food algae by *Calanus finmarchicus*. According to this, the copepod could utilize small algae like the cryptophyte *Rhodomonas bal-*

tica (ca. 8 µm diameter), and the haptophyte *Emiliania huxleyi* (ca. 4 µm diameter). The results show that *C. finmarchicus* is capable of efficiently converting nanoplankton carbon to secondary production, that it can achieve an optimal production during nanoplankton blooms and that the low summer concentrations of nanoplankton algae in temperate waters can sustain low but continuous reproduction. Nevertheless, reproduction is limited in subbloom concentrations of small algae.

The role of dinoflagellates in the diet of copepods increasingly attracts attention. At present, results on dinoflagellate diets are equivocal. Huntley et al. (1986) and Sykes and Huntley (1987) found chemically mediated rejection of dinoflagellate prey by the copepods *Calanus pacificus* and *Paracalanus parvus*. Although *Calanus finmarchicus* rejected the red tide dinoflagellate *Alexandrium excavatum*, the toxin was accumulated in the copepod (Turrieff et al. 1995). *Acartia tonsa* consumed an ichthyotoxic dinoflagellate and showed only erratic swimming behaviour (Mallin et al. 1995). *Acartia tonsa*, *Centropages hamatus*, and *Eurytemora herdmanni*, which commonly co-occur with toxic *Alexandrium* spp. dinoflagellates, could discriminate between toxic and non-toxic *Alexandrium* spp. cells by chemosensory means, suggesting that selective behaviour, rather than physiological effects, governs the grazing response of copepods exposed to toxic prey (Teegarden 1999). In contrast, other dinoflagellates are good diets in culturing *Calanus* in the laboratory (Mullin & Brooks 1967; Paffenhöfer 1971b; Gill & Harris 1987). Truely, Baars & Fransz (1984) suggested that phytoplankton populations in the central North Sea in July consisting equally of the dinoflagellate *Ceratium* sp. and microflagellates were unsuitable food for copepods. But, laboratory experiments from Nielsen (1990) showed that the larger copepod species like *Centropages hamatus* and *Centropages typicus* as well as cladocerans absolutely are able to graze dinoflagellates like *Ceratium* spp. The evident interspecific differences and the impact of red tides and algal blooms surely require further investigation.

Meyer-Harms et al. (1999) stated that *C. finmarchicus* selected diatoms throughout the study period and additionally selected dinoflagellates both before and after the spring bloom, despite the low abundance of both groups in the pre- and post-bloom phases. For *C. helgolandicus* off Plymouth, Irigoien et al. (2000) also observed a slight preference for diatoms, but there was generally little evidence of selective feeding on different phytoplankton in the seasonal study. For both species, haptophytes and cryptophytes formed a significant proportion of the diet on occasions, confirming the findings of Båmstedt et al. (1999) from mesocosm studies that *C. finmarchicus* was capable of feeding effectively during nanophytoplankton blooms and that small algae may be significant in the diet. Gifford et al. (1995), however, reported that the grazing impact of *C. finmarchicus* on cells <20 µm was negligible.

Harris et al. (2000) found that *Calanus finmarchicus* as well as *C. helgolandicus* generally show little selectivity between different food types. Most of the selectivity measured during the study was attributed by the authors to size selectivity. Diatoms formed a major component of the diet of both species of *Calanus* in the Norwegian Sea and the English Channel during the spring bloom. Harris et al. further reported that naupliar growth was significantly influenced by algal food type. They explained it as follows: Lipid storage in *Calanus* is used to fuel egg production after ascent from overwintering. A certain quantity of fresh food also seems necessary to maintain egg production, probably contributing essential molecules. Therefore, the quantity of food necessary to produce an egg probably varies depending on the lipid storage, with consequent seasonal variations in the relation between egg production and food. This fact, incidentally, makes the rate of egg production an inadequate technique to estimate carbon requirements. Equally, in the case of *Calanus*, rate of egg production must be a very poor predictor of the growth rate of copepodites, at least during periods when it is fuelled by lipid storage.

Utilization of *Phaeocystis* spp.: Great attention has been given to the role of *Phaeocystis* in the diet of copepods. This flagellate forms colonies and blooms and has a world wide distribution; and it is able to dominate shallow regions of the North Sea at certain times. Generally, copepods are known to consume this alga but the nutritive value is as yet unclear. The reports on *Phaeocystis* forming part of the diet are equivocal.

In the past it was argued that this kind of phytoplankton cannot be utilized by copepods. Martens (1981) noticed an inverse relationship between the colony-forming gelatinous flagellate *Phaeocystis pouchetii* and copepod numbers. Daro (1986) showed that the feeding rate of *Temora longicornis* was considerably reduced during a *Phaeocystis* bloom in the Southern Bight. Several other authors found a depression in grazing rate of copepods (Hansen & Boekel 1991; Bautista & Harris 1992). Nevertheless, in the German Wadden Sea Weisse (1983) measured experimentally a high uptake of *P. pouchetii* by both *Temora longicornis* and *Acartia clausi*. Tande & Båmstedt (1987) stated that *P. pouchetii* is as suitable as the diatom *Chaetoceros furcellatus* as a food source. Huntley et al. (1987) concluded after having conducted a series of laboratory experiments that a diet of *P. pouchetii* colonies should sustain the metabolic and growth requirements of the large arctic copepod *Calanus hyperboreus*. Post-bloom grazing by *Calanus glacialis*, *C. finmarchicus* and *C. hyperboreus* in the region of the Polar Front, Barents Sea has been studied by Hansen et al. (1990). The colonial algae *P. pouchetii* and *Dinobryon pellucidum* dominated the phytoplankton. It seemed that the copepods, besides detritivorous and carnivorous feeding, could utilize this kind of phytoplankton. In addition to *Phaeocystis* sp., other members of the Prymnesiophyceae, the coccolithophorids, are recorded among stomach contents of copepods (Harris 1994).

Gut pigment contents, ingestion rates and abundances of dominant copepod species were analysed by Bautista et al. (1992) from March to May 1990 before and during a spring bloom dominated by *Phaeocystis* sp. in coastal waters off Plymouth (south-western coast of England). The results showed lower gut pigment contents, ingestion rates and copepod abundances during the *Phaeocystis* bloom when compared with the previous period of diatom dominance.

Hansen (1992) studied zooplankton grazing on *Phaeocystis* spp. with special regard to calanoid copepods. Highest feeding rates were found in *Calanus helgolandicus* and *Temora longicornis*. Copepods fed on all size-classes of *Phaeocystis* offered (generally 4-500 µ ESD), but they preferred the colonies. Female *C. helgolandicus* and female *T. longicornis* preferably fed on larger colonies (ESD>200 µ and ESD>100 µ, respectively). However, a field study, carried out in the Dutch Wadden Sea between 30 March and 11 May 1990, showed phytoplankton grazing by the dominant copepod *T. longicornis* to be negligible during the *Phaeocystis* bloom. *T. longicornis* gut fluorescence was inversely related to *Phaeocystis* dominance. The hypothesis has been put forward that *T. longicornis* preferentially feeds on microzooplankton and by this may enhance rather than depress *Phaeocystis* blooms. That is why microzooplankton (e.g. tintinnids) is utilizing the single-cell stage of *Phaeocystis* spp. (e.g. Admiraal & Venekamp 1986).

Bautista et al. (1994) found that *Phaeocystis*-blooms in coastal waters off Plymouth affected feeding and fecundity of copepods like *Calanus helgolandicus*, *Temora longicornis* and *Pseudocalanus elongatus* in a negative manner. Rousseau et al. (2000) studied the trophic efficiency of the planktonic food web in the Belgian coastal ecosystem dominated by *Phaeocystis* colonies. According to their results they suggested that during spring 1998 most of the *Phaeocystis*-derived production in the Belgian coastal area was remineralised in the water column. Verity (2000) conducted model simulations of the role of zooplankton in *Phaeocystis* food webs. With this it was implied that transitions between life cycle stages of *Phaeocystis* may potentially be important to phytoplankton – zooplankton interactions, and that relative rates of ingestion of *Phaeocystis* by various zooplankton may have significant impacts upon material fluxes through and out of *Phaeocystis* – diatom ecosystems. Indirect effects of trophic interactions appear to be equally significant as direct effects.

Utilization of Cyanophyta: In the past, in many studies have been concluded that cyanobacteria are generally not consumed by copepods because of the bad manageability of the filaments, nutritional inadequacy or toxicity (e.g. Lampert 1981a+b, 1987; Fulton & Pearl 1987; Ahlgren et al. 1990; Guo & Tester 1994). Guo & Tester (1994) found that *Acartia tonsa* only ingests *Trichodesmium* sp. when other food is not available. Heerkloss et al. (1984) estimated assimilation efficiencies of 50 to 80% for *Acartia tonsa* when they fed on the cyanobacteria *Microcystis aeruginosa*, while an assimilation efficiency of 35% was found when they fed on the cyanobacteria *Oscillatoria redeckii*. Schmidt & Jónasdóttir (1997) found from laboratory experiments that small additions of a cyanobacterium *Microcystis* sp. to a diatom diet led to a greater rate of egg production of copepods than on a pure diatom diet. Nevertheless, Schmidt et al. (1998) studying egg production and herbivo-

rous feeding of *Acartia bifilosa* and *Acartia tonsa* in the Pomeranian Bay (Baltic Sea) found that based on the analysis of the phytoplankton composition in summer it is suggested that a high proportion of dinoflagellates was beneficial whereas high proportions of cyanobacterial colonies and filaments had negative effects on egg production of the copepods. However, Meyer-Harms et al (1999) could show that cyanobacteria were utilized by calanoid copepods (*Acartia* sp., *Temora longicornis*) in the Baltic Sea.

Utilization of detritus: The utilization by pelagic and coastal copepods of non-living particles as well as living particles, including bacteria, microzooplankton, and phytoplankton, has been subject to a number of reviewing investigations (e.g. Jørgensen 1966; Darnell 1967; Marshall 1973; Conover 1978; Sorokin 1978). However, the non-algal fraction of organic particles is often considered as a supplementary food source for overwintering and deep-sea copepods (Seki & Kennedy 1969; Corner et al. 1974; Harding 1974) or when primary production is less than the food requirements of the populations (Heinle & Flemer 1975; Sorokin 1978). The non-living fraction has been generally assumed to be a poor food source which cannot be readily metabolized (Jørgensen 1962; Marshall 1973; Heinle et al. 1977).

Experiments on the feeding of *Calanus helgolandicus* females on detrital material were carried out e.g. by Paffenhöfer & Strickland (1970). They found that natural detritus from the ocean was never ingested, whereas dead diatoms were readily eaten. Heinle & Flemer (1975) found out that the production of algae in the Patuxent River estuary (Maryland, U.S.A.) was much less than the carbon requirements of a population of the calanoid copepod *Eurytemora affinis*. Detrital carbon was present in quantities that suggest turnover times of 8 to 83 days for this pool, assuming that all algal production was consumed by *E. affinis*. The authors hypothesized that *E. affinis* must consume detritus to meet a part of its requirements for energy. Chervin (1978) studied assimilation of particulate organic carbon by copepods at two stations in the lower Hudson River Estuary and apex of the New York Bight. Detritus formed between 26 and 44% of the diet in the estuary and 31 to 81% in the apex. The author suggested that detritus is inferior to phytoplankton as a food.

Lenz (1977) measured the amount of organic detritus within the particle size fraction 1 to 150 μm in Kiel Bight (Baltic Sea). The values showed a seasonal variation between 100 and 600 mg m^{-3} , expressed as dry weight of organic matter. Organic detritus comprises more than 40% of total organic matter in the above-mentioned size class, which is the class most easily accessible to the relative small filter-feeders in this area. Proceeding from the assumption that pelagic filter-feeders select their food mainly by size and not by taste, Lenz concluded that organic detritus plays an important role as supplementary food source, being ingested together with phytoplankton and small nonmotile heterotrophs. Lenz stated that the nutritive value of detritus is increased by the adsorption of dissolved organic matter and above all through the subsequent colonization by bacteria, which utilize the dissolved substances.

Poulet (1983) summarized that freshly dead and decomposed phytoplankton cells and faecal material are usually consumed by zooplankton (Pechen-Finenko & Pavlovskaya 1975; Paffenhöfer & Knowles 1979). Natural suspensions of particulate matter, 20 to 80% of which are composed of detritus, are not only ingested and assimilated but also could form a dominant fraction of the copepod's diet (Petipa et al 1970; Gerber & Marshall 1974; Poulet 1976; Roman 1977; Chervin 1978). The index computed for *Pseudocalanus minutus* feeding on both living and non-living particles showed positive selection for detritus in 56% of the experiments, alternating temporally with negative values, apparently without any seasonal pattern (Poulet 1976).

Ingestion, survivorship, and growth experiments were conducted by Roman (1984) with the estuarine calanoid copepod *Acartia tonsa*. Various concentrations of the diatom *Thalassiosira weissflogii*, and detritus derived from the macrophyte, *Thalassia testudinum*, were offered. Ingestion rates of detritus increased with increasing detritus concentration. The instantaneous mortality coefficient of *A. tonsa* was a significant linear (negative) function of the diatom concentration. However, when *T. weissflogii* suspensions were supplemented with detritus, the copepod instantaneous mortality rate decreased, and the growth rate increased. Although *A. tonsa* could not grow from egg to adult on a detrital diet, detritus did supplement algal diets to increase copepod production rates.

Irigoiien et al. (1998) reported that a major proportion of the total particulate carbon in surface waters of the Norwegian Sea was not attributable to phytoplankton or protozooplankton, the implication being that this material was detritus. Although e.g. Paffenhöfer & Strickland (1970) showed that natural detritus was not ingested by *Calanus helgolandicus*, Dilling et al. (1998) recently demonstrated feeding by *Calanus pacificus* on large aggregates known as marine snow, and detrital compounds of the diet may be important under some circumstances.

Utilization of faeces (Coprophagy): According to Poulet (1983) the ecological importance of faecal pellets depends on the further utilization of organic matter from a previously incompletely assimilated food source (Paffenhöfer & Knowles 1979). Normally, most of the pellets produced in the euphotic zone are consumed or degraded in the upper section of the water column, with only 0.2% of the daily production reaching the sea floor (Hofmann et al. 1981). The removal of organic matter by attached bacteria and the reduction in size of particles through disintegration tend to reduce their nutritional value and availability to consumers of higher trophic levels. Thus, some kind of competition for nutrients exists between bacteria and copepods within the detritus food chain. Paffenhöfer and Strickland (1970) could observe that *Calanus helgolandicus* females ingested large amounts of faecal material produced by the same species in other vessels. Paffenhöfer & Knowles (1979) demonstrated that *Eucalanus pileatus* and *Temora stylifera* grazed faecal pellets and cells of the diatom *Rhizosolenia* sp. at similar rates.

Experimentally feeding on faecal pellets was also observed in *Calanus finmarchicus* CIII/CIV copepodites already after 2 h of starvation (Baars & Helling 1985). *Oithona similis*, which is one of the most abundant copepods of the central North Sea (ref. to Nielsen & Sabatini 1996), can effectively clear water off larger faecal pellets at clearance rates of 15 ml d⁻¹ for small *Acartia*-pellets and 1000 ml d⁻¹ for *Calanus*-pellets (ref. to Gonzáles & Smetacek 1994). This is important in flux control, since it directly can determine the amount of pellet material arriving at the seafloor. This special type of feeding is known as flux feeding.

Feeding on faecal pellets was also considered important for nauplii at times when phytoplankton density is declining (Green et al. 1992). Experimentally, *Calanus helgolandicus* NIII, the stage where feeding starts at, were able to incorporate faecal pellets of *Pseudocalanus* spp., but not vice versa.

Carnivorous feeding: Copepods are not only herbivorous. Most of them additionally utilize animal prey. Only a few copepod species such as *Tortanus discaudatus* or *Pareuchaeta norvegica* are exclusively carnivorous. Predatory feeding is still less investigated than filter feeding. First experiments with predatory copepods were carried out e.g. by Ambler & Frost (1974). They found that adult females of *Tortanus discaudatus* can capture nearly all of the developmental stages (nauplius III to copepodite IV) of *Calanus pacificus*, thus being serious competitors of fish. *Tortanus* appears to search at randomly for prey and the capture of prey seems to depend on tactile stimuli. The relationship between ingestion rate of *Tortanus* and prey density is satisfactorily described by an Ivlev-curve, with maximum ingestion rates falling within the range of natural prey densities. Yen (1982, 1983, 1987 1991, 1992) investigated predation by carnivorous marine copepods *Pareuchaeta* sp. in detail.

A variety of marine copepods have been shown to injure or capture and ingest young fish larvae in the laboratory. Several copepod species of the family Pontellidae, common to surface waters, are effective predators of larval fish. One to four anchovy larvae are required per day and individual to satisfy the metabolic needs of *Labidocera* sp., depending on the species and the sex (Lillelund & Lasker 1971). A further laboratory study of predation on fish eggs and larvae by copepods were made by Turner et al. (1985). An interesting aspect of carnivorous feeding was also mentioned by Greve & Parsons (1977). They assumed that large copepods like adult *Calanus* spp. may graze away the young stages of their predators (e.g. ctenophores), thus being able to reduce the predator stock size, whereas adult ctenophores were effective predators on the copepods as well as on the nauplii.

Daan et al. (1988) reviewed predation and cannibalism of calanoid copepods from experimental studies with naturally occurring prey of the North Sea. A further step was made by Conley and Turner (1985), who determined omnivory in two continental shelf copepods by combining an experimental and a field approach. Although it has long been known that most copepods are omnivores (Marshall & Orr 1955), quantitative comparisons of herbivore and carnivore feeding upon naturally occurring food items are rare (Conley & Turner 1985; Fransz et al. 1991a).

In the meanwhile the consumption of microphagous zooplankton e.g. of oligotrichous ciliates by copepods is well established. According to Poulet (1983) it has been shown that protozoa can be an important link between organic detritus and copepods (Porter 1973; Heinle et al. 1977; Berk et al. 1977). Particularly in recent times there is increasing recognition of the importance of omnivory and the role of protozoa in the diet (e.g. Ohman & Runge 1994; Harris 1996). Generally, microzooplankton is increasingly recognised as being important in the diet of copepods (Gifford 1991; Gifford et al. 1995). Predation of microzooplankton has been demonstrated e.g. by Stoecker & Egloff (1987) and Stoecker & Capuzzo (1990) in several species previously presumed to be herbivorous. As the main consumers of bacteria (Fenchel 1982 a,b,c) heterotrophic flagellates can be regarded as natural links between the detritus-bacteria standing stock and higher zooplankton.

Studies such as those of Beers & Stewart (1969) and Berk et al (1977) suggest that ciliates are the principle component of the microzooplankton in seawater (10 to 90% of the biomass) and that copepods both graze and grow on them (Heinle et al. 1977; Berk et al. 1977). The relative frequency of protozooplankton (e.g. in the Skagerrak) reflects a situation in which the small size of algal cells of certain populations occurring in masses enables the protozooplankton to enter into competition with the copepods for food resources (Chester 1978). Beers and Stewart (1967), Parsons & LeBrasseur (1970) and Berk et al. (1977) ascertained that, in general, microzooplankton feed on smaller sized particles which are not utilized efficiently by larger consumers. The microzooplankton may graze away between 6 and 24% of phytoplankton standing biomass and up to 52% of primary production per day (Beers & Stewart 1971; Landry & Hassett 1982). Heinbokel & Beers (1979) have indicated that tintinnids from California Bay consume up to 20% of the daily production. Burkill et al. (1987) found off southwest Britain that microzooplankton grazed 13 – 42% and 30 – 65% of the algal standing stocks in summer and autumn, respectively. Thus the microzooplankton, as an intermediate trophic link, make the considerable production of ultraplankton available to higher order consumers.

Berk et al. (1977) demonstrated that aloricate ciliates (8.9 to 17.3 μm body length) were acceptable as food to the estuarine copepod *Eurytemora affinis*. Marine, loricate ciliates (tintinnids) graze most effectively on particles in the nanoplankton size range (e.g. Spittler 1973; Heinbokel 1978a,b). Further, Beers & Stewart (1967) and Parsons & LeBrasseur (1970) ascertained that, in general, microzooplankton feed on smaller sized particles which are not utilized efficiently by larger consumers. If these protozoans are effectively preyed upon by metazoan zooplankton they could play an important role in the pelagic food web dynamics of estuarine and coastal waters where nanoplankton can seasonally dominate phytoplankton productivity and biomass (e.g. McCarthy et al. 1974; Van Valkenburg & Flemer 1974; Durbin & Durbin 1981).

Laboratory experiments by Robertson (1983) showed that e.g. the estuarine copepod *Acartia tonsa* ingested the ciliates *Tintinnopsis tubulosa* (length 148 μm) at rates linearly proportional to prey density. *Favella panamensis* (length 265 μm) was ingested at even higher rates. When the phytoplankton are dominated by small (diameters <10 μm) species, tintinnids in concentrations exceeding 10^3 organisms l^{-1} can be important items in the diets of *Acartia*. Wiadnyana & Rassoulzadegan (1989) have demonstrated that *Acartia clausi* and *Centropages typicus* preferred ciliates (*Stombodinium sulcatum*) when offered an equi-proportional mixture of ciliates and similar sized dinoflagellates or diatoms. Similar results for *Acartia tonsa* and *Eurytemora affinis* were found by Tackx et al. (1995). On the Dogger Bank, *Oithona similis* was correlated to protozooplankton, whereas *Paracalanus parvus* was correlated to Chl a-maxima (Nielsen & Sabatini 1996).

Admiraal & Venekamp (1986) observed that extremely dense populations of tintinnids (24000 to 118000 dm^{-3}) were found during the spring bloom of the alga *Phaeocystis pouchetii* in the Dutch

Wadden Sea and coastal North Sea. These protozoa obviously grazed on the single-cell stage of the colony-forming algae, and thus prevented further growth of *Phaeocystis*. On the other hand, tintinnids can be utilized by several copepods (e.g. Turner & Anderson 1983; Robertson 1983; Stoecker & Sanders 1985).

Additional dietary compounds from the ingestion of ciliates ranged according to Irigoien et al. (1998) from only 2% to 6% of the phytoplankton, owing to their low abundance. Similarly, south of Iceland, Irigoien et al. (2000a) found that, in June, estimated phytoplankton ingestion was too low to cover egg production requirements. However, microzooplankton probably complemented phytoplankton in the diet to sustain the observed levels of egg production. Harris et al. (2000) found in their mesocosm food web studies significant top-down regulation of not only phytoplankton but also protozoans, when CV *Calanus* sp. dominated. Similar results were found by Nejstgaard et al. (1997), who observed selective predation on microzooplankton.

Cannibalism: Landry (1978) stated that cannibalism may regulate the population size of *Acartia clausi*. Daan et al. (1988) found that *Temora longicornis* became more cannibalistic on its youngest nauplii at low phytoplankton concentrations. Oithonid copepods ingest animal diets and can feed cannibalistically (Marshall & Orr 1966; Schnack 1975). Likewise, Lampitt (1978, 1979) observed cannibalistic behaviour of *Oithona nana*.

Landry (1981) studied the switching between herbivory and carnivory by the planktonic marine copepod *Calanus pacificus* (= *Calanus helgolandicus*). Adult females of the omnivorous copepod fed disproportionately on the prey in greatest relative abundance when given mixtures of diatoms (*Thalassiosira fluviatilis*) and copepod nauplii (*C. pacificus*) as food. This switch from herbivorous to carnivorous behaviour may be significant in nature during the decline of phytoplankton blooms. Landry suggested that the widespread omnivorous habit among pelagic animals may be a responsive and flexible trophic organization which contributes to the resiliency of planktonic communities in a dynamic physical environment.

Utilization of dissolved matter: Poulet (1983) summarized that experiments carried out with several species suggest that zooplankton, especially at the pre-feeding and various developmental stages, may adsorb dissolved organic matter (e.g. Lewis & Ramnarine 1969; Khaylov & Yerokhin 1971; Pavillon 1977; Gyllenberg & Lundquist 1978; Gardner & Miller 1981; Chapman 1981). Soft-bodied invertebrates are capable of absorbing dissolved matter in natural concentrations via wall-cell carrier-transport systems (Stewart 1979).

According to Poulet (1983) a possible additional indirect source of dissolved organic matter depends on the initial formation of particles resulting from the dissolution of bubbles in the water column or their breakage at the sea surface (Baylor et al. 1962; Sutcliffe et al. 1963; Johnson 1976; Johnson & Cooke 1980). Growth of *Artemia* was used as a preliminary test whether such organic particles might constitute a satisfactory food for marine filter feeders (Baylor & Sutcliffe 1963), but these observations have never been confirmed. Johnson & Cooke (1980) showed that the sizes of particles formed were a function of the initial bubble size and of the concentration of organic material that were present. Living particles of small size can also be adsorbed onto bubbles. Weber et al. (1983) have indicated the mechanism (i.e. interception) of scavenging of water-borne bacteria by rising bubbles. Poulet recommended that particles produced by bubbling should be re-examined as a possible food for marine zooplankton.

Mann (1988) suggested that the DOM (dissolved organic matter) pathway driven by the activity of bacteria in freshwater may be ecologically more significant than the POM (particulate organic matter) pathway and that processes analogous to those shown for lakes and rivers probably occur in estuarine and coastal waters. Mann found much circumstantial evidence to suggest that planktonic food webs based on DOM are much more important than previously thought. He argued that the conversion of DOM to POM through the 'microbial loop' and its utilization in higher trophic levels is an urgent topic for further study.

Utilization of bacteria: According to Poulet (1983) the ingestion of bacteria by copepods has been reported several times under laboratory conditions when high cell densities were used (e.g. Petipa et al. 1975; Sorokin et al. 1969; Sorokin 1978). Bacteria probably represent a major pathway whereby fractions of organic matter not normally accessible to zooplankton re-enter the grazing food chain (microbial loop). Protozoan microzooplankton and some larger metazoans like appendicularians feed primarily on bacterioplankton and microflagellates (Fenchel 1984, 1988; Urban et al. 1992). Marshall (1973) argued that in the free state bacteria could not form an important part of the diets of copepods. But flocs of bacterioplankton can be consumed by copepods in amounts similar to diatoms (Sorokin 1971; Reiper 1978). Likewise, Harris (1996) and Mauchline (1996) assumed that bacteria are consumed by copepods when they are particle-bound. But in this connection they found it unclear whether detrital or faecal material is a significant component of such a diet.

In the Humber estuary the copepod *Eurytemora* sp. was observed feeding on bacteria, free and attached (Boak & Goulder 1983). *Eurytemora* sp. individual feeding rates were highly variable and somewhat low; total bacterial biomass eaten represented, on average, only 12% of carbon required to maintain respiration. It was suggested that feeding on attached bacteria was restricted by the large mass of suspended solids relative to the small biomass of attached bacteria, while feeding on free-living bacteria was limited by their small size. Population feeding rates were greater at the more upstream sites, where *Eurytemora* sp. was more abundant.

Grazing effects on phytoplankton stock

Steele (1974) proposed that most primary particulate production in the open sea was consumed by zooplankton. According to Daro (1980) in the northern North Sea (Fladen Ground) up to 100% of the primary production can be grazed away in May/June. Nevertheless, it is evident that this is not always the case. In the central North Sea (Oyster Ground) Baars & Fransz (1984) estimated that only 3.2 – 14.2% of primary production was grazed by calanoid copepods.

Dagg & Turner (1982) calculated the grazing rate of the copepod community on transects of the continental shelf south of Long Island, New York and across Georges Bank during April, July and October 1978. During the spring, when *Calanus* and *Pseudocalanus* dominated, grazing tended to be greatest on the outer shelf and slope regions, and community ingestion rates never exceeded primary production rates; much of the spring bloom was not grazed. During the fall, when *Centropages* and *Oithona* dominated, grazing was greatest in the shallower regions and community ingestion rates were often equivalent to or slightly greater than primary production rates. About 50% of the annual primary production was grazed by the copepod community in both regions. In the estuarine habitats of the Schelde River, Tackx et al. (1990) found daily grazing rates of 6 - 18% of the phytoplankton standing stock and 11 - 18% of the daily primary production. Nielsen et al. (1993) reported that in the stratified areas over the Dogger Bank, 15% of phytoplankton standing stock is utilized daily by copepods, whereas in the frontal zone even up to 30% is grazed away by this zooplankton group. Additionally, copepods have to utilize protozooplankton to satisfy their carbon demands.

Hansen et al. (2000) studied food web interactions in a *Calanus finmarchicus* dominated ecosystem. For this they conducted mesocosm-experiments. They found that *Calanus* nauplii could not control either phytoplankton or protozoan growth in either the control or in the enriched system. Ignoring recycling and sedimentation, the fate of the primary production for the nauplii-dominated community was to be grazed by a diverse and abundant protozooplankton community. In the copepodite-dominated community the copepods grazed >100% of the daily primary production, and also grazed heavily on a protozooplankton community of low biomass and diversity and presumably on detritus. During the 'naupliar' period in March, the phytoplankton was characterized by a diatom bloom while during the 'copepodite' period in April, it was in a post-bloom phase characterized by small-celled species such as *Phaeocystis pouchetii*.

Irigoiien et al. (2000b) have shown in laboratory experiments that small-scale turbulence could play a significant role in the biology of copepods (Alcaraz 1997). Variations in small-scale turbulence can produce effects such as enhancing encounter rates (Rothschild & Osborn 1988), eroding filtra-

tion currents (Kiørboe & Saiz 1995) affecting production (Saiz et al. 1992) and altering metabolic rates (Alcaraz et al. 1994). Based on field data of the Norwegian Sea and the North East Atlantic, Irigoien et al. (2000b) reported that wind speed showed a negative relation with gut fluorescence but not with egg production.

Has diatom or dinoflagellate food inhibition-effects on copepod fertility?

In recent years there has been a lively discussion in the literature regarding whether or not diatoms as well as noflagellates can be detrimental to the fertility and reproduction of copepods. We see this discussion in the context of the growing interest in the chemistry of natural compounds. In the following, an attempt is made to give a brief review of the running discussion and the various standpoints.

It has long been known that many copepod species fed on diatoms in the sea (e.g. Lebour 1922; Marshall & Orr 1955). Thus, the spring diatom bloom was considered to initiate and support the cycle of secondary production. The classic pelagic food web refers to the widely held concept of a trophic linkage between outburst of the diatom-rich phytoplankton spring bloom, copepod production and fish production (Runge 1988; Cushing 1989; Legendre 1990). Traditionally, diatoms have always been associated with a short and effective pelagic food chain that led through suspension-feeding copepods to top consumers and important fisheries. According to e.g. Marshall & Orr (1952, 1955b) egg laying of *Calanus finmarchicus* is dependent on the outburst of the phytoplankton bloom in spring, which in temperate and arctic-boreal seas is, normally, a diatom bloom. Tande & Hopkins (1981) showed that sex differentiation in Stage V of *Calanus finmarchicus* and moulting into adults occurs in Balsfjorden (northern Norway) at least 2 months before spawning in April. Phytoplankton levels are not measurable before the spring diatom increase starts at the end of March, implying that development and maturation of gonads are dependent upon internal energy resources. But the final act of spawning seems to require energy input from phytoplankton, so that spawning can occur as soon as possible after the start of the spring diatom increase, which acts as a kind of trigger for the egg laying of the females.

Paffenhöfer & Harris (1976) cultured the copepod *Pseudocalanus elongatus* over multiple generations at 12.5°C on a diet of the chain forming diatom *Thalassiosira rotula*. Mortality from hatching to adulthood averaged 30.4%. The generation time was 28 days. Growth from copepodite I to copepodite V was exponential at all food concentrations. Hirche (1989) studied egg production of single female *Calanus glacialis* fed with the diatom *Thalassiosira antarctica* at super-abundant concentrations ($>300 \mu\text{g C l}^{-1}$). Egg production was closely related to feeding in all experiments. Additionally, Hirche (1990) studied reproduction of *Calanus finmarchicus* collected in polar and Atlantic waters. Single females were kept at 0°C in the laboratory for 22 d (polar) and 77 d (Atlantic) with superabundant food concentrations ($>400 \mu\text{g C l}^{-1}$) of the diatom *Thalassiosira antarctica*. The mean daily egg production rate of all females from Atlantic water over a 60 d period was $24.4 \text{ female}^{-1} \text{ d}^{-1}$. Maximum values were $53.2 \text{ eggs female}^{-1} \text{ d}^{-1}$. These laboratory experiments revealed no apparent detrimental effects of the diatom diet.

Furthermore, many previous field studies have reported that fecundity in marine suspension-feeding copepods is largely governed by fluctuations in the availability of phytoplankton food, particularly diatoms (e.g. Marshall & Orr 1955; Kiørboe & Nielsen 1994; Plourde & Runge 1993). It is well known that diatoms are prominent in copepod diets, especially in productive ecosystems and during the phytoplankton blooms in temperate and high latitudes (e.g. Marshall & Orr 1955; Urban et al. 1992). However, the significance of diatoms as a high quality food source for copepod reproduction has recently been questioned (Kleppel et al. 1991; Kleppel 1993; Ianora & Poulet 1993; Jónasdóttir 1994; Poulet et al. 1994, 1995; Miralto et al. 1995; Laabir et al. 1995; Ianora et al. 1995, 1996; Uye 1996; Chaudron et al. 1996; Ban et al. 1997).

Kleppel et al. (1991) studied egg production of copepods from California coastal waters and from the Irish Sea and conducted feeding and egg production experiments on *Acartia tonsa* and other copepods. The copepod species studied appeared to feed preferentially on dinoflagellates and microzooplankton rather than on diatoms. Patterns of variability in egg production conformed to

changes in dinoflagellate and microzooplankton biomass, but seemed to be independent of changes in diatom biomass.

Ianora & Poulet (1993) and Ianora et al. (1995) reported that egg viability in *Temora stylifera* is, in fact, strongly dependent on food type. Good quality eggs that developed to hatching were obtained with a dinoflagellate (*Prorocentrum minimum*) and flagellate (*Isochrysis galbana*) diet. The opposite was true with four diatom diets (*Thalassiosira rotula*, *Chaetoceros curvisetum*; *Phaeodactylum tri-cornutum* and *Skeletonema costatum*), with hatching success as low as 20% of total egg production.

Poulet et al. (1994) investigated the arrest of development in copepods through diatoms. According to them the diatom *Thalassiosira rotula* has a harmful impact on the reproductive biology of the copepod *Calanus helgolandicus*. When adult females fed on the diatom, both total egg production and hatching success were significantly lower than with the dinoflagellate *Prorocentrum minimum*. Embryonic development in the copepod was arrested when eggs were exposed to diatom but not to dinoflagellate extracts from the same species of phytoplankton. Embryos underwent strikingly abnormal development. Poulet et al. suggested that low egg viability in *Calanus helgolandicus* was not due to an absence of some specific nutrient essential for egg development but rather to the presence of anti-mitotic agents in diatoms blocking copepod egg embryogenesis.

Ianora et al (1996) reported on fecundity, egg viability and faecal pellet production of *Acartia clausi* females fed either with a diatom (*Thalassiosira rotula*) or a dinoflagellate (*Prorocentrum minimum*) diet, at food saturated conditions. The diatom diet significantly reduced both egg and faecal pellet production as well as hatching success. Blockage of egg development occurred with both axenic and non-axenic cultures of *T. rotula*, suggesting that inhibitors were provided by the diatoms and not by the bacteria associated with diatom cultures. Low hatching success was also artificially induced by exposing newly spawned *A. clausi* eggs to high concentrations of diatom extracts, indicating the presence of deleterious inhibitory compounds within the diatom cells which were blocking copepod embryogenesis.

In response to the results presented above, Jónasdóttir & Kiørboe (1996), in a series of experiments, have fed the copepod *Acartia tonsa* several different diets while egg production and hatching success were monitored. The diet was analysed for fatty acid content as an indicator of food quality. Both egg production and hatching were found to be affected by the nutritional quality of the food. Hatching was also highly dependent on female fertility. Exposing eggs to diatom extracts, negative effects were only evident at high extract concentrations, but disappeared when aeration was supplied to the solution. Oxygen measurements showed that failure to hatch was due to hypoxia in the extracts. No inhibitory or toxic effects of diatom cell components on hatching could be found.

Ban et al. (1997) have put together strong evidence from 15 laboratories located worldwide that diatom diets are in fact inferior for copepod reproduction. When fed to females of 16 copepod species, all but 1 of 17 diatom species examined significantly reduced egg production rates or egg viability compared to non-diatom controls. Ban et al. registered with amazement that, while diatoms may provide a source of energy and materials for copepod growth (Vidal 1980), they often reduce fecundity and/or hatching success. Thus, they called these findings “the paradox of diatom – copepod interactions in the pelagic food web”. According to the results of Ban et al. diatoms could reduce fecundity, on average, by 87% and hatching success by 80% with time. Non-diatom diets in controls induced negligible changes in both fecundity and hatching success. The same diatom species showed considerable intraspecific differences in their impact. For example, *Skeletonema costatum* reduced fecundity and hatching in *Acartia clausi*, fecundity but not hatching in *Calanus helgolandicus*, and neither of the two in *Calanus finmarchicus*. Other diatom species affect reproduction of other copepod species. Ban et al. questioned: “What is it about diatoms that modifies copepod reproduction? Is this effect due to missing essential nutrients or to the presence of inhibitory compounds?” There are hints to a lack in diatoms of lipids, carbohydrates and proteins per cell volume compared to dinoflagellates (Hitchcock 1982). Alternately, a more insidious possibility, for which there is mounting evidence (Poulet et al. 1995; Uye 1996), is that the cells of many diatom species contain an as yet unidentified inhibitory compound that blocks copepod embryogenesis

when ingested by the females. This 'inhibition' may represent a defense mechanism by diatoms against grazing by copepod offspring, thereby prolonging diatom blooms. Therefore, Ban et al. believe that the blocking effect of diatom extracts suggests that inhibition of embryonic development was due to factors other than nutrient deficiency.

Measurements of egg viability in the sea recently indicated that egg hatching success is variable, from 20 to 95%, over the course of the reproductively active season (Ianora et al. 1992; Ianora & Poulet 1993; Laabir et al. 1995, Pond et al. 1996). Ban et al. (1997) recommended that it would be worth examining whether diatom blooms could actually inhibit population growth even if copepod productivity during the spring bloom is apparently high.

Recent studies show that mesozooplankton in temperate oceans are omnivorous, feeding on dinoflagellates and ciliates, especially after the spring diatom bloom is past, and that feeding on dinoflagellates and ciliates can sustain egg production (Kleppel et al. 1991; Sanders & Wickham 1993; Ohman & Runge 1994). Although it is well established that copepods feed on mixed diets at sea, it is also known from faecal pellets analysis that diatoms constitute a large fraction of the diet in certain periods of the year (Urban et al. 1992; Laabir et al. 1995). A close examination of growth periods in fish larvae indicates that copepod recruitment and prey productivity for fish larvae may at times be more favourable in post-bloom conditions (e.g. when the microbial food web is established) than during diatom blooms, as suggested for *Calanus finmarchicus* (and fish larvae feeding on *C. finmarchicus*) in the Gulf of St. Lawrence (Runge & de Lafontaine 1996).

In contrast, Jónasdóttir et al. (1998) raised doubts about whether diatoms contain toxic compounds arresting copepod embryonic development. The authors argued that reduced hatching rates are due to the absence of essential nutritional components in the diet rather than to the presence of toxic compounds affecting embryogenesis. They assumed that diets deficient in essential fatty acids must be the likely cause of low hatching success in copepods, and they suggested that the extract experiments conducted by Ianora et al. (1996) are "a procedure no more realistic than suffocating humans in chocolate syrup and then concluding that chocolate is toxic". Jónasdóttir et al. finally recommended that "such procedures should be discontinued".

Ianora et al. (1999) replied to the criticism of Jónasdóttir et al. (1998) and reasoned that there is mounting evidence that diatoms possess anti-mitotic properties similar to the cytotoxic compounds isolated from numerous benthic marine algae. A considerable literature has developed on the natural marine compounds reported to have cytotoxic and anti-tumor activities. The majority of these have been isolated from algae, coelenterates, echinoderms and sponges, which accounted for 93% of the 5000 new metabolites reported from marine organisms in the last decade. Recent studies of the authors have shown that the diatom *Thalassiosira rotula* can also inhibit cell cleavage in copepod, sea urchin and tunicate embryos whereas control dinoflagellate (*Prorocentrum minimum*) extracts, at the same concentration, have no effect on cell division (Miralto et al. 1999).

Ianora et al. summarized their knowledge about the impact of diatoms on copepod development: Initial studies on diatom-copepod interactions had shown that egg viability decreased dramatically when female copepods were fed on a diatom diet (Ianora & Poulet 1993). The greater the number of cells ingested by females, the lower the hatching success, and vice versa (Chaudron et al. 1996). This inhibition was reversible when a diatom diet was substituted by a dinoflagellate diet (Laabir et al. 1995; Uye 1996). The same type of inhibition was also observed using the 'extract' procedure, whereby freshly spawned copepod eggs were exposed to increasing concentrations of extracts prepared from diatom and non-diatom (control) cells (Poulet et al. 1994, 1995; Ianora et al. 1996; Uye 1996; Lee et al. 1999).

According to Ianora et al. this toxic effect is not due to anoxia, as suggested by Jónasdóttir & Kiørboe (1996) and Jónasdóttir et al. (1998), but comes from 3 aldehydes of low molecular weight, a class of compounds that arrests cell division and induces apoptosis (i.e. programmed cell death) in cultured cell lines (Zimmermann et al. 1995). These aldehydes were recently isolated from *Thalassiosira rotula* and will be described by Miralto et al. in the near future.

Ianora et al. reported that the results show that hatching success of the copepod *Temora stylifera* immediately dropped to <40% within 24h with the addition of the aldehydes from the diatom *Thalassiosira rotula* as opposed to controls which received a diet of the dinoflagellate *Prorocentrum minimum*. Females continued to lay eggs and to swim and feed normally in the presence of aldehydes, showing that these inhibitory compounds were not noxious to the adults. However, they were very toxic for eggs, which rapidly degenerated with time. That means that diatom extracts acted as the 'birth control pill' for female copepods that continued to lay eggs, few of which were viable.

The potential for an adverse influence of diatom diets on the reproductive success of the calanoid copepod *Calanus finmarchicus* was investigated experimentally under laboratory conditions by Starr et al. (1999). A mono-specific diet of the common diatom *Thalassiosira nordenskioldii* significantly reduced the viability of *Calanus* eggs, which either failed to hatch or hatched into deformed nauplii. The production of non-viable eggs increased with increasing *Thalassiosira* concentration and was proportional to the female ingestion rate. Non-viable egg production was also induced by a diatom of the genus *Navicula*, but not by two other diatoms, *Skeletonema costatum* and *Chaetoceros debilis*. Among non-diatom diets, maternal feeding on a dinoflagellate (*Prorocentrum micans*) and two flagellates (*Isochrysis galbana*, *Pavlova lutheri*) at food-saturated conditions resulted in the production of normal eggs, more than 70% of which hatched into healthy nauplii. Starr et al. concluded from these experiments that extended feeding on certain extremely common diatom species, by themselves and apparently also in mixtures where they predominate, could have a negative impact on *C. finmarchicus* recruitment rates.

Adding to the confusion, Ianora et al. (1999) published a further paper in which they expressed the suspicion that a further large group of food particles, namely dinoflagellates, might be detrimental to the fertility of copepods. Particularly, they found first evidence of some dinoflagellates reducing fertilization capacity of *Temora stylifera* males. According to the authors, three dinoflagellate diets, *Prorocentrum micans*, *Gymnodinium sanguinium*, and *Gonyaulax polyedra*, significantly modified spermatophore production and reduced the fertilization capacity of male sperm after 6 – 12 d of continuous feeding. Two other diets, the dinoflagellate *Prorocentrum minimum* and the prymnesiophycean *Isochrysis galbana*, had no effect on hatching success, which remained high (>89%) and stable with time.

Laabir et al. (1999) determined the contents of free amino acid (FAA) and total amino acid (TAA) pools in the eggs, embryos and NI and NII nauplii generated by *Calanus helgolandicus* females fed either the diatom *Phaeodactylum tricornutum* or the dinoflagellate *Prorocentrum minimum* for 3 and 10 d. With both diets, egg production rates increased by a factor of 5 to 10, and free amino acid and total amino acid contents were double those measured in eggs spawned by wild females. Higher levels were measured for almost all amino acids except methionine, taurine, glutamine, glutamic acid, aspartic acid and ornithine. When embryos developed to live nauplii, 50 to 72% of the initial concentration of the FAA content was used. There was no preferential utilization of essential over non-essential amino acids. The TAA pool also varied with development. The mean FAA:TAA ratio remained between 11 and 19. With the *Prorocentrum minimum* diet, hatching success remained constantly >85%, whereas it declined to 0% at the end of the 10 d incubation period with *Phaeodactylum tricornutum*. After 10 d of feeding on this alga, the FAA content of developing embryos increased significantly, indicating liberation of amino acids due to proteolysis. None of these embryos developed to hatching. Thus, according to Laabir et al. inhibition of hatching success related to the ingestion of *P. tricornutum* was not due to a lack of any amino acids. The results indicate that the chemical composition of freshly spawned copepod eggs is sensitive to the maternal diet.

Other authors, however, consider the source of fluctuating spawning success in copepods to be a deficiency in certain essential nutrient components. Kleppel et al. (1998), for example, stated that variations in the nutritional composition of the food supply may be responsible for considerable variability in egg production. In a laboratory study in which the amino and fatty acids in the diet of *Acartia tonsa* in six "food environments" were measured, the authors detected differences in egg production that were apparently associated with amino acid deficiency, differences in the proportions and types of fatty acids in the diet, and differences in the kinds of food organisms taken

from a mixture and in the effort required to capture a ration. Egg production varied systematically with the concentrations of 3 fatty acids (of 18 present in the diet) and 4 amino acids (of 16 present in the diet).

Klein Breteler et al (1999) found that in laboratory experiments copepods could not be raised on a diet of the chlorophycean *Dunaliella* sp., though they readily consumed this alga. *Dunaliella* sp. contained all essential amino acids, but was deficient in highly unsaturated fatty acids and in sterols. In contrast to copepods, the heterotrophic dinoflagellate *Oxyrrhis marina* grew well on *Dunaliella* sp., producing significant amounts of the long-chain fatty acids docosahexaenoic acid and eicosapentaenoic acid, in addition to cholesterol and brassicasterol. Using this *O. marina* grown on *Dunaliella* sp. to feed *Temora longicornis* and *Pseudocalanus elongatus*, both copepod species rapidly developed from young nauplius larvae to maturity on the dinoflagellate diet. Hence, in this experimental food chain the inadequate chlorophycean food was biochemically upgraded by the protozoan to high-quality copepod food. The results indicate that highly unsaturated fatty acids and/or sterols are essential compounds, which can be produced by protozoans.

Kang et al. (2000) studied the effect of non-phytoplankton and phytoplankton diets on fecundity of *Calanus helgolandicus*. A fecundity increase followed ingestion of larvae of the sea urchin *Sphaerechinus granularis* and the oyster *Crassostrea gigas* by copepod females, whereas a decrease followed ingestion of eggs of the copepods *Acartia* spp. and *Temora* spp., as a function of protein concentration in diets.

The statements of the above mentioned papers that certain marine diatoms would be deleterious to copepod egg production and hatching induced Tang & Dam (2001) to conduct five separate egg incubation experiments to test if phytoplankton exudates were harmful to copepod eggs. Exudates produced by 3 reportedly toxic diatoms, plus 2 non-diatom species, had no effects on egg hatching in the copepod *Acartia tonsa*. Thus, Tang & Dam concluded that phytoplankton exudates are not likely to inhibit egg hatching. However, a seasonal relationship was observed between egg production and egg hatching of *A. tonsa* such that a high egg production rate resulted in high egg hatching success (80 to 100%) but a low egg production rate resulted in highly variable egg hatching success (0 to 90%).

In summary, the question as to whether diatoms contain substances which block embryonic development in copepods has not yet been conclusively answered. It appears quite probable, however, that copepods cannot grow optimally on a diet of monocultures in laboratory conditions, because they need a mixed diet. This recognition should be taken into account in future laboratory experiments.

Feeding of zooplankton other than copepods

There is little information on food and feeding in the field by other zooplankton in the North Sea.

Protozoa

Protozoan microzooplankton feed primarily on bacterioplankton (Fenchel 1980; Fenchel 1986) and small-sized phytoplankton (pico- and nanoplankton: e.g. Stoecker et al. 1981), but – as flagellates – also can switch between auto- and heterotrophic feeding habits (= mixotrophy: Thingstad et al. 1996). Protozoan feeding on cyanobacteria was reported e.g. by Christaki et al. (1999). The effect of experimental ciliate predation on the most common autotrophic marine prokaryotes *Prochlorococcus* and *Synechococcus* was higher for the latter. Within the applied ciliates the algivorous *Strombidium sulcatum* yielded better results than the bacterivorous *Uronema* sp.

Effective feeding was shown for tintinnids on dinoflagellates (Beers & Stewart 1967; Stoecker et al. 1981), tintinnids on autotrophic flagellates (Gold 1973), and the ciliate *Strombidinopsis* effectively feeding on *Phaeocystis*. However, these feedings can hardly be generalised since the ciliate *Strombidium* did not feed on *Phaeocystis* (Hansen et al. 1993). An example of heterotrophic

dinoflagellates feeding on mikrophytoplankton is given by *Oxyrrhis* spp. (dinoflagellate) feeding on *Phaeocystis* (Hansen et al. 1993).

Feeding on bacteria was observed for many kinds of protozoa: Examples are tintinnids (Hollibaugh et al. 1980), other ciliates like *Uronema* sp. (Hall et al. 1993; Christaki et al. 1999), heterotrophic flagellates (Hall et al. 1993) and the dinoflagellate *Noctiluca scintillans* (Kirchner et al. 1996). Bacterial dynamics in mesocosms were investigated by Thingstad et al. (1996). They concluded that bacterial biomass was both limited by decrease of inorganic phosphate (P-limitation) and predation by ciliates and heterotrophic dinoflagellates.

Abundance and bacterivory of mixotrophic flagellates were examined in a vertical profile during 1 wk in June 1992 in the Bay of Aarhus, Denmark (Havskum & Riemann 1996). A stable pycnocline separated an upper water mass with low salinity, low inorganic nutrient concentration and low bacterial abundance from a bottom water mass with higher salinity, inorganic nutrient concentration, and bacterial abundance. In the upper layer, bacterivorous, pigmented flagellates (mixotrophs) accounted for 49% of the pigmented biomass. In addition to their function as primary producers, mixotrophic flagellates were responsible for 86% of the entire flagellate bacterivory.

Noctiluca scintillans is a large heterotrophic dinoflagellate which is abundant in many coastal areas and forms conspicuous red tide streaks. Although this species has been investigated in several ecological studies both in the field (Schaumann et al. 1988; Sargunam et al. 1989; Uhlig & Sahling 1990; Porumb 1992; Uhlig & Sahling 1995; Huang & Qi 1997; Elbrechter & Qi 1998; Tiselius & Kiørboe 1998; Murray & Suthers 1999) and in the laboratory (Kirchner et al. 1996; Kiørboe & Titelman 1998; Nakamura 1998), there is a paucity in field observations on the changes in *N. scintillans* populations together with those of potential prey items. It has a wide range of potential diet reaching from bacteria and phytoplankton to copepods typically with different feeding modes: mucoid web feeding and – direct ? – entanglement. In Asian waters a green form of *Noctiluca* is known with symbiotic *Chlorella*-algae. For feeding of tintinnids the filtration rate is independent of temperature but correlated with food size (Capriulo 1982). A log-log relationship between body size of the tintinnids and filtration rate on non-colonial *Phaeocystis* (Prymnesiophyceae) was found by Admiraal & Venekamp (1986).

Coelenterata

Clearance rates of *Obelia* and *Phialella* (Hydromedusae) were positively correlated with bell diameter, but independent of water temperature and prey density, furthermore correlated with prey escape response, daily per capita rates of prey, functional morphology important: small with many tentacles = large with few tentacles, *Obelia* unlikely to feed on adult copepods (Fulton & Wear 1985). Clearance rates are species-specific: E.g. in a comparative study higher specific rates were found for anchovy than for gelatinous predators, offering fish larvae as prey, the combined effect yielded 20 to 40% of total larvae per day (Cowan and Houde 1992).

Average digestion time in *Pleurobrachia* spp. (Ctenophora) at 12 °C is 2 h, the respective clearance rates for *Pleurobrachia* are 6.11 specimen per day for *C. finmarchicus* as only prey. This value can decrease to 29% for *C. finmarchicus* in the presence of smaller prey (Båmstedt 1998). Comparable clearance rates for *Sagitta* spp. on *Calanus* are much smaller and reach 0.1 to 0.2 specimen per day (Øresland 1987). For smaller copepods the rate increases to 1.8 per day (Kuhlmann 1977). The prey reached the gut end in on average 12.5 minutes were the material remained until complete digestion which was measured as 2 h 20 minutes at 15 °C (Kuhlmann 1977). For coelenterates the size of the gastric cavities is important for the number of prey specimens that can be digested simultaneously (Purcell 1985).

Experimentally *Mnemiopsis leidyi* (ctenophora) was forced to feed on large diatoms (Deason & Smayda 1982). Actually, a small portion of the algae were eaten, but the portion was not sufficient to maintain the ctenophores carbon demand. Since only 21% of the daily carbon ration were covered by the algal diet, shrinkage of body size took place in the predator.

Examples for the feeding relationship between *Acartia tonsa* and *Chysaora* sp. are given by Suchman & Sullivan (1998). Generally, medusae are non-selective. The catchability of the prey depends on its escape capabilities. So, *Aurelia aurita* shows this type of selection at bell diameters 0.8 to 7.1 cm, when barnacle nauplii and hydromedusae will be captured (Costello & Colin 1994). *Aurelia* medusae < 12 mm consumed hydromedusan prey, > 30 mm copepod prey (e.g. Sullivan et al. 1994).

For the small-sized hydromedusae *Obelia* the calculated per capita ingestion rate per day reached up to 20% of standing stock of nauplii, for *Phialella* 2 to 5% on *Acartia* spp. were found (Fulton & Wear 1985). The relationship copepods-*Aurelia* also depends on turbulence, i.e. in tidally mixed biotopes on a daily basis up to 100 % of copepod biomass required to maintain scycophomedusan biomass due to increased encounter rates. On an annual basis 9-26% of copepod production are utilized by *Aurelia* sp. (Lucas et al. 1997). The evidence of top-down control for copepods was proven for the effect of *Pleurobrachia pileus* (see also Suthers & Frank 1990; Frid et al. 1994).

Of further interest is the specific feeding relationship between *Beroe* sp. (ctenophore) and its prey, *Pleurobrachia* sp. (Båmstedt 1998). Dynamics have been investigated in the German Bight (Greve & Reiners 1988), but require further studies. In Chesapeake Bay, similarly the interplay between the copepod predator *Mnemiopsis leidyi* and the sea nettle *Chrysaora quinquecirrha* preying on *M. leidyi* have been investigated (Feigenbaum & Kelly 1984). It was suggested that sea nettle predation can significantly reduce the ctenophore predator. For German coastal waters, the influence of inter-gelatinous relationships is discussed by Kopacz (1994). The relatively lower abundance in German coastal waters compared to the central and eastern North Sea is likely to be responsible for a lowered impact of gelatinous zooplankton on the crustacean zooplankton.

Chaetognatha

As carnivorous holoplanktonic *Sagitta* sp. was shown to feed on dinoflagellates in the field (Pearre 1974; Alvarez-Cadena 1993). Generally, chaetognaths have a wide range of diets. Albeit copepods are the main diet, all other taxonomic groups are seemingly also fed on if they were abundant enough (Feigenbaum & Maris 1984). Chaetognaths will 'snap' at anything under crowded conditions and are often preserved with their jaws open. Plankton samples are generally swirled when formalin is added and dying chaetognaths are later found grasping the sides of large salps, medusae and even their own tail (Feigenbaum & Maris 1984). In some cases this led to apparently incorrect reports on the types of prey.

Besides copepods *Sagitta* spp. also feeds on cladocerans (Pearre 1974; Øresland 1987). However, differential food choices exist between *S. setosa* (smaller prey) and *S. elegans*. The relative predation pressure of *Sagitta elegans* is stronger on smaller copepods than for *Calanus*. They also ingest cirripedia larvae (Alvarez-Cadena 1993). For chaetognaths and euphausiids evidence of top-down control on copepods as well as food limitation of predators at times of reduced prey was proven (Roff et al. 1988).

Malacostraca

Despite their abundance at certain times and localities, there is a lack of knowledge of the feeding biology of planktonic malacostraca like euphausiids, mysids, amphipods and decapod larvae. Little field measurements have been made on grazing and predation of these taxa in the North Sea in the last decades, the closest studies being on the trophic role of euphausiids in the Oslo Fjord and the Northeast Atlantic. *Meganyctiphanes norvegica* showed a strongly related herbivorous feeding to abundance of algae increased at night. Feeding on copepods was evident both night and day (Onsrud & Kaartvedt 1998). Båmstedt and Karlson (1998) determined the degree on carnivory quantitatively to indicate the trophic position among the dominating species in the Northeast Atlantic. Feeding behaviour of mysids and euphausiids is summarised in Mauchline (1980), but there is little known about in situ predatory behaviour of these animals in the North Sea. Investigations in the Baltic Sea gave some insights in feeding patterns of *Mysis mixta* and the impact to diel vertical migration (Rudstam et al. 1989; Gorokhova & Hansson 1997) and in selective predation of mysids

(Hansson et al. 1990). Most of the studies dealt with freshwater mysids in lakes (Bowers & Vanderploeg 1982; Grossnickle 1982; Ramcharan et al. 1985; Ramcharan & Sprules 1986; Langeland 1988; Hanazato 1990) and estuaries (Johnston & Lasenby 1981; Webb et al. 1987; Webb et al. 1988; Wooldridge & Webb 1988; Jerling & Wooldridge 1995).

Tunicata

The pelagic tunicates including salps, doliolids, and appendicularians exhibit higher feeding rates, greater retention of bacteria-sized food, and much shorter generation times than other marine planktonic herbivores. Their many unique adaptations enable them to reach high population densities and react with maximum flexibility to the unpredictable and patchy environment of the pelagic ecosystem (Alldredge & Madin 1982). The filtration rate of *Oikopleura dioica* at densities 205 - 4600 n/m³ reached 1.3 to 37% per m³ per day and highest filtering rates occurred at particles size $\leq 2 \mu\text{m}$ (Alldredge 1981).

Cannibalism

Cannibalism was found e.g. in chaetognaths (Pearre 1982; Øresland 1987), hyperiids (von Westernhagen 1976) and within decapods, together with necrophagy (Anger & Nair 1979). Pearre (1982) showed that tendency for cannibalism increases with predator size and is also density dependent. The proportion of cannibalism in ecosystem dynamics is probably great, if copepod feeding on nauplii is also taken into account.

Predation mortality of fish larvae

The predation mortality of fish larvae has been extensively studied and deserves special attention. A general review of larval mortality is given by Hunter (1984).

Copepods on fish larvae: In investigating the larval-starvation hypothesis Turner et al. (1985) alternatively examined the risk of fish larvae of being preyed upon by copepod predators (*Anomalocera ornata* and *Centropages typicus*). Whereas fish eggs often could not be handled by the copepods because of their size, both yolk-sac and first-feeding larvae were highly susceptible to predation by the bigger *A. ornata* and to a lesser degree by *C. typicus*. However, for the copepods the daily ration of ingested carbon from the fish larvae was comparable. Similar results were found by Lillelund & Lasker (1971) for the copepod species *Labidocera jollae*, *L. trispinosa* and *Pontellopsis occidentalis*.

Euphausiids on fish larvae: The predation effect of the euphausiid *Thysanoessa raschi* and the copepod *Euchaeta norvegica* on fish larvae was investigated e.g. by Bailey (1984). Rates for *T. raschi* were lower (1.9 larvae per day and individual) compared to *Aurelia aurita* (5.3) but higher than for the copepod *Euchaeta* (1.1). For *T. raschi* yolksac and first-feeding larvae were slightly more vulnerable to predation, but for *Euchaeta* the youngest larval stages were clearly preferred. Similar results were obtained by Theilacker & Lasker (1974).

Cnidarians and Ctenophores: Based on results from the North Sea-wide Young-Fish-Survey, Hay et al. (1990) presented distribution maps both for scyphomedusae and 0-group gadids. They show that 0-gadids are to some degree positively related to medusae of the genus *Cyanea*. In turn, van der Veer (1985) could show, that in the Wadden Sea *Pleurobrachia pileus* (Ctenophora) and *Aurelia aurita* (Scyphomedusae) exert effective control on larval fish populations. Fortunately (for the larvae), occurrences of both are somewhat temporally uncoupled in the Wadden Sea (van der Veer 1985). The negative effect of *Aurelia aurita* on a larval herring population was shown by Möller (1984) by analysing a 4-yr time series. He could show that pressure was exerted on larvae but not on classes older than age-1.

Predation rates on gobiid larvae by *Mnemiopsis leidyi* (ctenophore) yield 1 larvae per day, *Chrysaora hyoscella* yields (scyphomedusae) 7.8 per day. Comparably, anchovy catch 4 items per day. In general, predation rates are reduced when alternate prey is present (Cowan & Houde 1992, 1993).

Vulnerability is higher for small larvae than for eggs and larger larvae, and the clearance rates higher for anchovy than for gelatinous predators. Combined predation can reach an reduction effect of 20 to 40% of daily fish eggs and larvae in Chesapeake Bay. This is especially important since scyphomedusae and fish predators do temporally overlap (Cowan & Houde 1993).

Chaetognaths on fish larvae: Experimentally chaetognaths did not feed on fish eggs but on larvae, although copepod prey was preferred (Kuhlmann 1977).

Hyperiid on fish larvae: These feeding relationships were inferred from examining the gut contents of field populations of hyperiids (e.g. Sheader & Evans 1975; von Westernhagen & Rosenthal 1976; von Westernhagen et al. 1979). However, some of the results have to be re-interpreted (see chapter Parasitism).

Fish larvae as predators

A large amount of literature is available in this field and still growing (e.g. Mielck 1922; Wyatt 1974; Wosnitza 1975; Last, 1978; Last 1980; Last 1982; Suthers & Frank 1990). Apparently, larval feeding depends on larval size and prey abundance, i.e. it is density dependent. The survival in post-larval fish and early juveniles clearly influences year class strength in fish (Lit. In Suthers & Frank 1990). Usually predation pressure of fish larvae can be estimated less than 10% of copepod standing stock per day (Nielsen & Munk 1998).

Conclusion for Predation

Predation must be considered to be the most important process in pelagic ecosystems. From the wide spectrum of predatory relationships merely the herbivorous section is sufficiently treated yet. Especially the role of switching under natural field conditions requires much more effort.

3.3.3. Excretion and defaecation

Excretion considers release of organic and inorganic dissolved and particulate compounds. Corkett & McLaren (1978) already pointed out that excretion has been extensively studied in zooplankton. Although excretion may be of interest as a phenomenon in its own right, there have been two main foci in such studies:

1. Excretion supplies nutrients to phytoplankton.
2. Ratios of excretion supply one component in the "balance equation" of growth or production.

The elements of interest in excretion are nitrogen and phosphorus. Zooplankton species are generally considered to be ammonotelic. However, the work of Jawed (1969) and Mayzaud (1973) indicates that zooplankton may excrete small but significant amounts of organic nitrogen like urea and amino acids. Corner, Head & Kilvington (1972) found that nearly 90% of the nitrogen excreted by the animals was in the form of ammonia. Therefore, the current view should be that NH_3 is the predominant form of excreted nitrogen in zooplankton. It was shown for the copepod *Acartia tonsa*, that ammonia and urea as well as primary dissolved amino acids are excreted in equal proportions, however with diurnal differences among N-species (Checkley et al. 1992; Miller & Glibert 1998). Taking into account the diurnal migration of plankton and the release of N-species during daytime, a considerable flux of N-species into the deeper waters can be anticipated (Hays et al. 1997). However, the measurement of this process requires careful analysis (Hays et al. 1997) and has not yet been verified in the field. For larger crustacean species (e.g. *Euphausia pacifica* and *Neomysis rayii*) ammonium is the major N-product (Ikeda et al. 2000). Similarly, for phosphorus equal proportions of inorganic and organic excretions are assumed by Pomeroy et al. (1963).

Methods

Excretion measurements were carried out on zooplankton for example by Mayzaud (1976), Båmstedt (1985), Verity (1985) and Huntley & Nordhausen (1995).

In order to determine excretion products (e.g. NH_4^+ , PO_4^{3-}), it is essential to guarantee an experimental procedure completely free of contamination. In order to achieve this, during the

Hamburg KUSTOS project acid-rinsed 1 l experimental containers were used filled with natural sea water which had been filtered over 63 μm gauze. Subsequently the containers received a mixed population of pre-cleaned copepods. The vitality of the experimental organisms was provided for in that they were caught during “gentle” vertical hauls with the WP-2 net and then attracted to a point source of light and pipetted out of the sample. The experiments were carried out over 12 h in complete darkness (exclusion of photosynthesis) and with ventilation using acid-cleaned air.

In order to determine the excretion rate of the mixed copepod population the following experimental design was employed:

- Measurement of the blind value for the medium (natural sea water filtered through a 63 μm gauze, without copepods).
- Measurement of the blind value for the medium (natural sea water filtered through a 63 μm gauze) after 12 h.
- Measurement of the ammonium concentration in the containers with the mixed copepod population after 12 h.
- Determination of the dry weight of the experimental organisms (mixed copepod population) after completion of the experiment.

The determination of the ammonium concentration was carried out photometrically according to Grasshoff et al. (1983). The excretion rates were given in $\mu\text{g NH}_4^+ \text{ mg dw}^{-1} \text{ h}^{-1}$.

Excretion rates

There are many publications which include data about excretion rates (see Tabs. 2, 3, 4). Nevertheless, mainly excretion of copepods was studied. There is a definite need for research on the other taxonomic groups. However, it is also necessary to analyse available excretion data with respect to their experimental backgrounds, i.e. to test their comparability, to discover contradictions and to thereby find new measurement approaches. In the following it is only possible to give a brief and incomplete survey of the knowledge on excretion and defaecation rates:

Marshall & Orr (1955) made some measurements of the excretion of phosphorus by *Calanus finmarchicus* and showed that it was most rapid during the first week after a period of feeding. The very high losses after 2 – 3 weeks of starvation led them to suppose that the ^{32}P they were measuring had not been in equilibrium throughout the animals. Marshall & Orr (1961) showed that equilibrium of ^{32}P throughout the body of *Calanus* is reached only after a feeding period of about a week. The time required to liberate by excretion the amount of P present in *Calanus* is about 20 days. Fed *Calanus* excrete at a higher rate than starved. There are large differences in the total P content of individual *Calanus*. A high percentage, up to 55% of the total P, may be lost by excretion during starvation.

Corner, Cowey & Marshall (1965) have measured nitrogen excretion by *Calanus finmarchicus* and *C. helgolandicus* collected in the Clyde Sea area under various experimental conditions. Adult females feeding on *Brachiomonas submarina*, *Cricosphaera elongata* and *Skeletonema costatum* at cell concentrations corresponding to the mean annual level of particulate nitrogen in Plymouth sound excrete 12.4 -, 9.0 – and 6.4 $\mu\text{g N mg dw}^{-1} \text{ d}^{-1}$, respectively. That converts to 0.664 -, 0.482 – bzw. 0.343 $\mu\text{g NH}_4 \text{ mg dw}^{-1} \text{ h}^{-1}$. When the concentration of food is raised, as might occur during a spring outburst of phytoplankton, there is an increase in the quantity of nitrogen excreted. On the other hand, nitrogen excretion rapidly diminishes in the absence of food. When the ambient tempe-

perature is raised from 5 to 15°C, nitrogen excretion is almost doubled ($Q_{10} = 1.80$), but rises by only a small additional amount when temperature is increased to 25°C. Compared with Stage V and adult female *Calanus*, Copepodite Stage II, III and IV excrete considerably more nitrogen, average values being 7 - (Stage V), 10 - (adult female) and 21 - (mixture of Stages II, III and IV) $\mu\text{g N mg dw}^{-1} \text{ d}^{-1}$. These values, together with a corresponding value of 36.4 by Harris (1959) for the much smaller species *Acartia clausi*, are consistent with the view that the smaller members of the zooplankton excrete larger quantities of nitrogen relative to their size than do larger members. Values of 35.7% for gross efficiency and 59.8% for net efficiency of feeding at food concentrations encountered in off-shore waters have been calculated from the results of experiments, with the younger stages.

Corner & Newell (1967) have made a study of the nitrogenous compounds excreted by *Calanus helgolandicus* collected at Plymouth. They stated that most of the excreted nitrogen is in the form of ammonia, which accounts for 60-100% (average 74.3%) of the total, and some of the remainder may be lost as urea. There is no evidence for the excretion of measurable amounts of amino acids. Whether the animals are starved or fed they are primarily ammonotelic, and the ammonia produced at 10°C is $3.33 \mu\text{g N mg dw}^{-1} \text{ d}^{-1}$, that means $0.178 \mu\text{g NH}_4 \text{ mg dw}^{-1} \text{ h}^{-1}$.

Corner, Cowey & Marshall (1967) have measured nitrogen retained and nitrogen excreted by *Calanus finmarchicus* at all stages of development from egg to adult; and the percentage of food digested by adult females grazing algal diets has been estimated by two separate methods. The data have been used to calculate gross efficiency of growth by the young stages as well as that of egg-production by the adult female. The authors showed that during a life-span of approximately ten weeks the animal uses 24% of the nitrogen it captures as food in order to build new tissue and produce eggs. The remaining larger fraction is lost as faecal pellets, moults and excreted end-products of metabolism.

Hargrave & Geen (1968) investigated the excretion of dissolved inorganic and organic phosphorus by starved and fed marine crustaceans and planktonic rotifera (e.g. *Oithona similis*, *Pseudocalanus minutus*, *Acartia tonsa*, *Asplanchna* sp.). Excretion was directly related to temperature and salinity. Excretion rates were higher in early evening than at other times of day and were furthermore a function of both quantity and quality of food. In laboratory experiments conducted in the presence of bacteria, excretion was one-third to two-thirds of that measured when bacterial activity was inhibited. According to the authors, both situations are artificial. If no antibiotics were added to the experimental container a rapid growth of bacteria on the walls of the vessel and a disproportionately large uptake of DIP would result. That is why bacteria used the excreted phosphorus.

Conover & Corner (1968) tried to examine nitrogen excretion, oxygen consumption and O/N-ratios for copepod species at all seasons. Thus, they measured respiration and nitrogen excretion for freshly caught *Calanus finmarchicus*, *C. hyperboreus*, *Metridia longa* and *Pareuchaeta norvegica*, from the Gulf of Maine at all seasons. Seasonal variation in weight-corrected respiration and nitrogen excretion followed similar pattern for all four species, being high in spring and decreasing gradually through summer and fall to a winter minimum. However, the relative proportions of oxygen utilized to nitrogen excreted (O/N-ratio) were different from season to season for each species, probably indicating different food preferences.

Butler, Corner & Marshall (1969) measured in the Clyde Sea area total phosphorus and total nitrogen excreted by freshly caught *Calanus finmarchicus* and *Calanus helgolandicus* during spring, summer and autumn. During late April, when food was plentiful, *C. finmarchicus* excreted daily 13.4% (females), 15.5% (Stage V) and 11.0% (males) of body nitrogen and 19.7% (females), 26.8% (Stage V) and 15.4% (males) of body phosphorus. During early summer (May-June), *C. helgolandicus* at Plymouth excreted lower levels of these substances, daily excretion of body nitrogen being 8.8% (females), 6.6% (Stage V) and 6.2% (males), and that of body phosphorus 15.0% (females), 10.9% (Stage V) and 9.1% (males). Still lower values were observed taken from the Clyde Sea in late October when little phytoplankton was present and most of the particulate material was detrital. Daily excretion of body nitrogen by these animals was 3.54% (females) and 3.78% (Stage V), the corresponding values for phosphorus excretion being 10.0 and 7.06% respectively. The ra-

tio total nitrogen/total phosphorus in the excretion products was fairly constant throughout spring, summer and autumn and close to the values found for much smaller copepods.

The N/P-ratios in particulate material, *Calanus* and excretion products have been used to calculate the gross growth efficiencies of feeding and growing animals in terms of phosphorus (E_P) and nitrogen (E_N). Values for E_P were within the range 18.9 - 34.6% with a mean of 28.3%; those for E_N were within the range 21.4 - 37.7%, with a mean of 33.1%.

Butler, Corner & Marshall (1970) gave a seasonal survey of nitrogen and phosphorus excretion by *Calanus spp.* in the Clyde Sea area based on shipborne experiments. Levels of plant food and those of both nitrogen and phosphorus excretion by *Calanus spp.* followed the same pattern throughout the year. 77% of the phosphorus and 62.4% of the nitrogen captured by the animals during the spring was assimilated (digested and absorbed). Of the total quantity of nitrogen captured each day by *Calanus* in late April, 35.7% was excreted in soluble form, 37.5% was lost as faecal pellets and 26.8% was invested in growth. Corresponding values in terms of phosphorus were 59.8-, 23.0- and 17.2% respectively. Female and Stage V *Calanus* require 8.4% body nitrogen and 13.6% body phosphorus daily in spring to compensate for metabolic losses and ensure growth. The corresponding values in winter are only 1.93 - 2.80% nitrogen and 6.20 - 7.23% phosphorus. The assimilation efficiencies of the animals are such as to allow them to obtain these daily quantities by sweeping clear 29.0 ml sea water d^{-1} in spring and 37 - 58 ml d^{-1} in winter. Some feeding must take place in winter, although plant food is virtually absent.

Corner, Head & Kilvington (1972) conducted feeding and excretion experiments with *Calanus helgolandicus*. The maximum daily rations consumed by each animal were high, being equivalent to 47.5% of the body nitrogen and 46.4% of the body phosphorus. The number of faecal pellets released by *Calanus* increased with the size of ration captured, but the percentage of the ration lost as faecal pellets was fairly constant. In terms of dietary nitrogen the average value was 65.9% and that for dietary phosphorus 59.6%. The percentage of the daily ration of nitrogen excreted in soluble form was 26.6% and that of phosphorus 41.2%.

Jawed (1973) has determined excretion rates of ammonia for mixed zooplankton off the coasts of Washington and Oregon (USA). Rates varied from 0.16 to 0.60 μg -at NH_4^+ -N $mg\ dw^{-1}\ d^{-1}$ for most planktonic animals ($= 0.120$ to $0.450\ \mu g\ NH_4\ mg\ dw^{-1}\ h^{-1}$), and from 0.02 to 0.06 NH_4^+ -N $mg\ dw^{-1}\ d^{-1}$ for jellyfishes.

Mayzaud (1973) carried out respiration and nitrogen excretion studies on *Meganyctiphanes norvegica*, *Phronima sedentaria*, *Acartia clausi* and *Sagitta setosa* under starvation. Although all the species were mainly ammonotelic, apparently a significant amount of organic nitrogen was excreted. The effect of duration of starvation showed for *M. norvegica* and *A. clausi* two different patterns of behaviour, which were chiefly a function of the rate of biomass turnover of the species studied. The rates of metabolism, chemical composition, and reaction to starvation varied with season in *M. norvegica*.

Conover & Mayzaud (1975) studied respiration and nitrogen excretion of neritic zooplankton (*Pseudocalanus minutus*, *Acartia clausi*, *Temora longicornis*, *Eurytemora herdmanni*) in relation to potential food supply. Respiration rate was controlled largely by temperature and size of the respiring animals. Rates of ammonia excretion were strongly correlated with parameters related to the food supply. Body size of the animals did not appear to be very important.

Mayzaud (1976) studied changes in the respiration, ammonia excretion and biochemical composition for three species of starving zooplankton (*Calanus finmarchicus*, *Sagitta elegans*, *Acartia clausi*). Respiration rate of all three species decreased followed by a more or less constant level. A similar pattern was observed for the ammonia excretion rate of *S. elegans* and *Acartia clausi*, where *C. finmarchicus* excretion appeared to oscillate between high and low levels of protein catabolism. Study of the biochemical changes showed that *C. finmarchicus* consumed primarily lipids, and at times proteins, to meet its energy requirements, whereas *S. elegans* and *A. clausi* primarily used protein. *C. finmarchicus* alternated between periods of protein-dominant catabolism and lipid-domi-

nant catabolism during starvation. No similar change in catabolism was observed in the two other species. The question here is whether the metabolic behaviour observed by Mayzaud for *C. finmarchicus* might be causally related to the diurnal vertical migrations of this species, since the periodic alternation between lipid and protein metabolism could have caused fluctuations in the specific weight of the animals (see section on vertical migrations).

Corner, Head, Kilvington & Pennycuik (1976) found that all forms of nitrogen excreted increased with size of ration ingested. Total nitrogen excreted increased from 7.68 to 11.46% body nitrogen for a seven-fold increase in size of ration ingested. Assimilation efficiency varied in the range 79.5 – 99.9% and although there was evidence of a fall in value with higher rations, the effect was slight.

Benson & Aldrich (1981) measured the respiration and nitrogen excretion of the marine copepod *Temora longicornis* and calculated from this O/N-ratios. A mean respiration rate of $1.05 \mu\text{l O}_2 \text{ mg wet weight}^{-1} \text{ h}^{-1}$ was found at an incubation temperature of 10°C . In respect of total nitrogen excretion there is a significant difference between mean measurements made in late spring and those made in early summer. The main nitrogen product was ammonia with $0.41 \mu\text{g NH}_3 \text{ mg wet weight}^{-1} \text{ h}^{-1}$ excreted in the spring rising to $1.72 \mu\text{g NH}_3 \text{ mg wet weight}^{-1} \text{ h}^{-1}$ during the summer measurements. This represents 70% of total nitrogen excretion in the spring and 84% during the summer. The mean value for total body nitrogen represents 1.3% of the wet weight of *Temora*. The mean value of $13.8 \mu\text{g N mg wet weight}^{-1}$ was not significantly different between the spring and the summer measurements. The seasonal variation in nitrogen excretion is expected considering the changes which occur in temperature and food level during the year.

Vidal & Whitley (1982) re-evaluated the effects of body weight and temperature of habitat on the metabolic rate of marine zooplankton, presented new measurements of the rates of oxygen consumption and ammonium excretion of planktonic crustaceans from boreal and subtropical regions, and showed that the weight exponent of the allometric equation for zooplankton, like that of equations obtained for nonplanktonic poikilotherms (Scholander et al 1953), is independent of temperature of habitat. However, the intercept of the equation is strongly influenced by temperature of habitat and the lipid content of the animals. The relation between the rates of oxygen consumption and ammonium excretion of planktonic crustaceans and their body weight, as expressed by the allometric equation ($M = aW^b$) (M = metabolism; W = body weight), was established for animals collected from two habitats of different temperature.

The relationship between food ingested and NH_4^+ excretion was investigated by Miller & Landry (1984) for female *Calanus pacificus* collected in August 1982 from the San Juan Archipelago, Washington State USA. Although ingestion rates of *C. pacificus* varied from 0 to over 20% of body N d^{-1} at the different food levels, excretion was a constant $6.6 \text{ nmol NH}_4^+ \text{ copepod}^{-1} \text{ h}^{-1}$ or about 10% of body N d^{-1} .

Paffenhöfer & Gardner (1984) determined release rates of ammonium by nauplii, copepodite stages (CII, CIV) and adult females of the marine copepod *Eucalanus pileatus* at 0.1 and $3.0 \text{ mm}^3 \text{ l}^{-1}$ of the diatom *Thalassiosira weissflogii* at 20°C . When food was abundant, animals of all stages released ammonium at similar rates per unit ash-free dry weight ($24\text{--}35 \text{ nmol NH}_4 \text{ mg AFDW}^{-1} \text{ h}^{-1}$ on average). At low food levels, CIV's and adult females released ammonium significantly more slowly than did the nauplii or CII's (28 and 24 versus 51 and $50 \text{ nmol NH}_4 \text{ mg AFDW}^{-1} \text{ h}^{-1}$). Because they weighed less (50%), low-food nauplii and CII's had higher calculated weight-specific excretion rates, than high-food ones of the same stage but release rates per copepod were similar in the two food regimens. In contrast to the early life stages, the CIV's and adult females released less ammonium per copepod in the low-food than in the high-food environment.

Off the west coast of Sweden weight-specific excretion rates of ammonium, urea, inorganic phosphate and total dissolved phosphorus from 19 zooplankton-species were measured by Båmstedt (1985) during March–October 1981. Excretion rates of most species were highest in spring and relatively low during summer. The high excretion rates in spring corresponded with the spring phytoplankton bloom, but later blooms did not affect the excretion rates of the zooplankton. The ave-

rage excretion rates varied considerably between species: ammonium from 3.2 to 68.1 urea from 0.9 to 6.3, inorganic phosphate from 0.3 to 8.2, and organic phosphorus from 0 to 3.5 nmol excreted per mg of body protein per hour.

Båmstedt (1985) found for *Calanus finmarchicus* 0.100 to 0.150 $\mu\text{g NH}_4 \text{ mg dw}^{-1} \text{ h}^{-1}$ and for *Metridia longa* 0.270 to 0.340 $\mu\text{g NH}_4 \text{ mg protein}^{-1} \text{ h}^{-1}$. Båmstedt & Tande (1985) worked in Arctic waters of the Barents Sea and measured in shipboard experiments respiration and excretion rates of *Calanus glacialis* during the period from 27 May to 13 June 1983. The phytoplankton biomass and abundance varied considerably between localities, but these variations were not generally reflected in the respiration and excretion rates of the copepod. Measurements were performed at the ambient temperature of -1.8°C . Average respiration rates were 0.95, 0.73, 0.57 and 0.60 $\mu\text{l O}_2 \text{ mg dw}^{-1} \text{ h}^{-1}$ for Copepodite Stage III, IV, V and adult females, respectively. The measurements revealed excretion rates of ammonium ranging between 2.9 and 16.8 for CIII, 3.7 and 21.1 for CIV, 1.3 and 28.4 for CV and 1.6 and 18.7 for adult females, all expressed as $\text{nmol mg dw}^{-1} \text{ h}^{-1}$. In all experiments, excretion rates of inorganic phosphate varied between 0.7 and 1.5 (CIII), 0.5 and 1.1 (CIV), 0.2 and 0.8 (CV), and 0.3 and 1.0 (adult females) $\text{nmol mg dw}^{-1} \text{ h}^{-1}$. Ratios of O/N, O/P, and N/P indicated that much of the metabolic energy was derived from catabolism of proteins. Comparison of the turnover rate of carbon and nitrogen showed, however, that nitrogen turnover was between 2.6 and 8.9 times higher than that of carbon. This may indicate that the copepods deaminate ingested protein, with the carbon skeleton of the amino acids subsequently being used in the synthesis of lipid compounds, possibly wax esters.

Ammonia excretion rates of oceanic copepods were measured on three cruises of the Sargasso Sea in Aug./Sept. '80, Aug./Sept. '81, and March/April '82 by Verity (1985). Twenty experiments were conducted using species representing genera abundant in the tropical and subtropical North-west Atlantic, e.g. *Calanus sp.*, *Clausocalanus sp.*, *Undinula sp.*, *Microsetella sp.*, *Macrosetella sp.*, *Oncaea sp.*, *Farranula sp.*, *Candacia sp.*, and *Pleuromamma sp.* Excretion rates were significantly related to body dry weight, with small copepods releasing more NH_4 for their size than large species. The small harpacticoid and cyclopoid copepods excreted NH_4 at rates equivalent to their entire body nitrogen every three days.

Harris & Malej (1986) investigated the diel patterns of ammonium excretion and grazing rhythms in *Calanus helgolandicus* in surface stratified waters. Samples of adult females were collected at mid-day and midnight from the upper 20 m of the stratified water column in the western English Channel over three days in July 1983. Pronounced diel vertical migrations through the thermocline occurred. Weight-specific ammonium excretion showed highly significant diel differences: night-time ammonium excretion being 1.7 times that observed at midday, indicating a marked nocturnal feeding behaviour.

Respiration – and excretion rates of *Calanus finmarchicus* and *Metridia longa* are given by Båmstedt & Tande (1988) for March and April. The overwintering stages of the two marine copepods displayed large differences in metabolic activity and behaviour. *C. finmarchicus* overwintered as Stage V copepodites in deep water and began to metamorphose to adults by the time the phytoplankton spring bloom started. Stage V copepodites did not feed, had low rates of respiration and excretion and low digestive enzyme activities, and remained in the deep water throughout the day and night. *M. longa* overwintered as adults, performed diurnal vertical migration, and had relatively high respiration and excretion rates and high digestive enzyme activities. *M. longa* fed throughout the entire water column. Adult females *C. finmarchicus* and *M. longa* responded rapidly to the onset of the spring phytoplankton bloom by increasing metabolic activities. In arctic-boreal waters the herbivorous copepod *Calanus finmarchicus* spends the overwintering period in diapause until January or early February, when sexual differentiation occurs in Copepodite Stage V, and this is immediately followed by moulting to adult stage, insemination and the onset of ovary development. On the other hand, the omnivorous copepod *M. longa* overwinters as physiologically active adult males and females and displays diurnal vertical migrations.

Ikeda & Skjoldal (1989) measured rates of oxygen consumption, ammonia excretion on a hydro-medusa (*Aglantha digitale*), pteropods (*Limacina helicina*, *Clione limacina*), copepods (*Calanus fin-*

marchicus, *C. glacialis*, *C. hyperboreus*, *Metridia longa*), an amphipod (*Parathemisto libellula*), a euphausiid (*Thysanoessa inermis*) and a chaetognath (*Sagitta elegans*). Respiration rates ranged from 0.33 to 13.8 $\mu\text{l O}_2 \text{ individual}^{-1} \text{ h}^{-1}$, ammonia excretion rates from 0.0072 to 0.885 $\mu\text{g N individual}^{-1} \text{ h}^{-1}$. In general, higher rates were associated with larger species, but considerable differences were also seen between species. From the results of metabolic rate measurements and elemental analyses, daily losses of body carbon and nitrogen were estimated to be 0.50 to 4.15% and 0.084 to 1.87%, respectively, showing faster turnover rates of carbon than of nitrogen.

Schneider (1990) gave a comparison of carbon based ammonia excretion rates between gelatinous and non-gelatinous zooplankton. For that about 560 literature data on weight-specific ammonia excretion rates of gelatinous zooplankton (cnidarians, ctenophores and salps) and non-gelatinous zooplankton (mainly crustacea) were converted to carbon based units to enable a better comparison between both groups. If carbon is used as body-mass unit, ammonia excretion rates of gelatinous zooplankton are in the same range as values obtained for other zooplankton taxa, indicating a similar nitrogen output per unit of organic matter in both groups. These results suggest nutrient regeneration potential to be the same in gelatinous and non-gelatinous zooplankton, and that nutrient regeneration within the pelagic system depends more upon the carbon biomass ratio between gelatinous and other zooplankton than on physiological differences.

Saiz & Alcaraz (1992) studied enhanced excretion rates induced by small-scale turbulence in *Acartia* spp. Both inorganic nitrogen and phosphorus excretion rates significantly increased about 60% under turbulent versus non-turbulent conditions.

Drits et al. (1994) presented in their study data on feeding, respiration and excretion rates as well as biochemical body composition for the dominant antarctic copepod *Calanoides acutus*. Weight-specific respiration and excretion rate of the animals inhabiting the 500 – 1000 m layer was 10 to 25% of the copepods living in the surface layer: In the 0-100 m layer *C. acutus* (Stage V) respired $33.8 \pm 5.7 \mu\text{l O}_2 \text{ mg dw}^{-1} \text{ d}^{-1}$ and excreted $0.57 \pm 0.28 \mu\text{g N mg dw}^{-1} \text{ d}^{-1}$. In the 500-1000 m layer *C. acutus* (Stage V) respired $3.0 \pm 0.02 \mu\text{l O}_2 \text{ mg dw}^{-1} \text{ d}^{-1}$ and excreted $0.15 \pm 0.05 \mu\text{g N mg dw}^{-1} \text{ d}^{-1}$.

O/N-ratios

Harris (1959), investigating the nitrogen cycle in Long Island Sound (USA), first showed the importance of the simultaneous measurements of respiration and nitrogen excretion in the definition of the metabolic characteristics of zooplankton. The O/N-ratio should be a good indicator of the state of general metabolism, reflecting the level of activity of the oxidative and protein metabolism of the animal studied. Indeed, the value of the atomic O/N-ratio shows what biochemical fraction of the body is used as an energy source, and what main metabolic pathways are involved. Harris found O/N-ratios ranging from 4 to 15.8 with a mean of 7.7 in experiments with natural plankton populations. Redfield, Ketchum & Richards (1963) found that an average sample of particulate organic matter in the sea contains a C/N/P-ratio of 106/16/1 and that it requires about 276 atoms of oxygen to oxidize it completely. Thus, during respiration about 1 atom of nitrogen should be excreted for ever 17 oxygen atoms combined in respiration.

Eighty to ninety per cent of the nitrogen excreted by copepods and other zooplankters is in the form of ammonium. Urea accounts for less than 10% of the total nitrogen excretion (Conover 1978). The small remainder consists of amino acids. That is the reason why ammonium excretion is a good indicator for protein metabolism (Corner & Newell 1967; Mayzaud 1973; Benson & Aldrich 1981; Kiørboe et al. 1985). The substrate mainly used by the organism group investigated (protein or lipid or carbohydrate) can be ascertained by determining the O/N ratio empirically (the atomic ratio of respired oxygen and excreted nitrogen). Examination of the O/N-ratio can provide information about the nature of the substrate being oxidized by the organisms, that means about their metabolic state. A high O/N-ratio (>17) implies that fat or carbohydrate are being oxidized to provide energy (herbivory). A lowering in the value of the ratio suggests a shift from fat or carbohydrate breakdown to the oxidation of protein (carnivory). For a purely protein metabolism the quotient lies between 6.5 and 8, whereas it is above 400 for pure lipid degradation and would theoretic-

call be infinite for pure carbohydrate metabolism (e.g. Ikeda 1977c; Schneider - manuscript). Mayzaud (1973) proposed a minimum O/N-ratio of 4 for zooplankton oxidizing a strictly protein substrate.

Corner, Cowey & Marshall (1965) found an average O/N-ratio of 13.5 for several experiments with *Calanus finmarchicus*. Mayzaud (1973) reported about an O/N-ratio of only 1.34 in the copepod *Acartia clausi* considering that this low value was due to the effect of starvation upon the copepod. Kiørboe et al. (1985) determined for *Acartia tonsa* an O/N-ratio of 8.2 for all food concentrations. Conover & Mayzaud (1975), investigating respiration and nitrogen excretion of neritic zooplankton like *Pseudocalanus minutus*, *Acartia clausi*, *Temora longicornis* and *Eurytemora herdmanni*, showed that the atomic O/N-ratio was quite uniform over most of the year ranging from 25 to 40, although several periods of depressed values, when the zooplankton appeared to be oxidizing above normal amounts of protein, were observed in the winter months. The O/N-ratio was just significantly and positively correlated with chlorophyll but no other measure of potential food supply. Benson & Aldrich (1981) presented for *Temora longicornis* a total O/N-ratio of 3.16 in the spring and of 1.0 during the summer measurements. Ikeda & Skjoldal (1989) having measured respiration rates and ammonia excretion on *Aglantha digitale*, *Limacina helicina*, *Clione limacina*, *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia longa*, *Parathemisto libellula*, *Thysanoessa inermis* and *Sagitta elegans* found that the ratios between the rates (O/N, N/P, O/P) exhibited a wide species-specific variation, indicating differences in dominant metabolic substrates. Nevertheless, typical protein orientated metabolism was identified only in *S. elegans*.

Measurements of ammonia excretion rates during the KUSTOS experiments

During the field investigations in the German Bight, ammonium excretion of the copepod mix was measured in adaptation of the method described by Verity (1985). For the measurements the animals were separated from the rest of the sample in the same way as described for respiration measurements, namely by attraction to a point source of light. The copepod mix was held in the complete dark in a thermolaboratory for 12 hours in a natural sea water medium (filtered through a 200 μm gauze) under NH_4 -free ventilation. The temperature of the laboratory was adjusted to the ambient temperature of the mixed layer in the field. The concentrations of dissolved excretion products were compared to those in the natural medium without copepods.

The average ammonium excretion during the experiments carried out during the drift phases was $0.281 \mu\text{g NH}_4 \text{ mg dw}^{-1} \text{ h}^{-1}$ (var. coeff. 18.4) in summer of '94 and $0.418 \mu\text{g NH}_4 \text{ mg dw}^{-1} \text{ h}^{-1}$ (var. coeff. 20.2) in spring of '95, whereby the variability was relatively low in each case. On the other hand, the excretion measurements gained over the station grid in the German Bight showed considerable variability. The average excretion rate in August of '95 was $0.776 \mu\text{g NH}_4 \text{ mg dw}^{-1} \text{ h}^{-1}$ (var. coeff. 41.4). Particularly the measurements at the stations near the coast showed relatively high excretion rates ($1.14\text{--}1.17 \mu\text{g NH}_4 \text{ mg dw}^{-1} \text{ h}^{-1}$). Based on the field investigations in summer of '94, the experimentally determined rate of $0.281 \mu\text{g NH}_4 \text{ mg dw}^{-1} \text{ h}^{-1}$ was related to the biomass of the copepods in the German Bight. This resulted in a calculated mean excretion of $0.531 \text{ mg NH}_4 \text{ m}^{-2} \text{ h}^{-1}$ for the copepoda group. Using the mean respiration and excretion data from the shipboard experiments during the KUSTOS project, it was possible to calculate the O/N ratios of the copepod mix during the individual measurement phases. The results are given in Table 8. From these results it can be concluded that the investigated animals at no time showed a purely protein metabolism (Krause et al. in prep.).

Defaecation

The observation that copepods produce a larger number of faecal pellets with increasing feeding is the opinion of several authors. Because its automatic filtration behaviour (Marshall & Orr 1955; Gauld 1966), *Calanus finmarchicus* shows a larger ingestion rate with greater food availability, and this rate asymptotically approaches a maximum value (Mullin 1963; Haq 1967; Frost 1972; Gamble 1978). This leads to a higher production of faecal pellets by these copepods (Butler et al. 1970; Corner et al. 1972; Gaudy 1974). By so doing, the nutritional efficiency is most probably reduced because of the faster passage through the alimentary canal.

average NH ₄ -excretion of the copepods in the German Bight				
Season	temperature [°C]		Copepoda-mix [µgNH ₄ /mg dw x h]	position
26 Feb. - 05 March '96	1.4	MIN MAX MEAN st. deviation var. coeff. n	--- --- 0.180 --- --- 1	one position
28 April - 07 May '95	8.0	MIN MAX MEAN st. deviation var. coeff. n	0.300 0.561 0.418 0.084 20.18 7	drift station
29 May - 01 June '95 and 29 May - 01 June '96	10.0	MIN MAX MEAN st. deviation var. coeffizient n	0.206 0.345 0.257 0.077 29.96 3	different positions
29 July - 10 August '94	16.0	MIN MAX MEAN st. deviation var. coeff. n	0.206 0.364 0.281 0.052 18.45 10	drift station
15 - 22 August '95	17.5	MIN MAX MEAN st. deviation var. coeff. n	0.384 1.168 0.776 0.322 41.42 6	different positions
01 - 05 October '96	12.0	MIN MAX MEAN st. deviation var. coeff. n	0.259 0.505 0.385 0.100 25.90 5	different positions

Tab. 7: average NH₄-excretion rates of the copepod-mix in the German Bight during different temperatures (seasons) from Krause et al. (in prep.)

O/N-ratios of the copepods in the German Bight				
Season	temperature [°C]	O ₂ -consumption [µg O ₂ /mg dw x h]	NH ₄ -excretion [µg NH ₄ /mg dw x h]	O/N-ratio atomic ratio
26 Feb. - 05 March '96	1.4	2.912	0.180	18.20
28 April - 07 May '95	8.0	4.457	0.418	12.00
29 May - 01 June '96	10.0	5.075	0.257	22.22
29 July - 10 August '94	16.0	7.491	0.281	30.03
15 - 22 August '95	17.5	8.256	0.776	11.97
01 - 05 October '96	12.0	5.778	0.385	16.90

Tab. 8: O/N-ratios of the copepod-mix in the German Bight during different seasons.

Marshall & Orr (1955) found a defaecation rate for *C. finmarchicus* of 6-12 faecal pellets h⁻¹. Gaudy (1974) established a defaecation rate for copepods of 200 faecal pellets individual⁻¹ d⁻¹. According to Petipa et al. (1970) faecal pellet production led to a daily defecation rate of 14.8% of the body weight of *Calanus finmarchicus* or *Pseudocalanus elongatus*. That would mean that an amount of organic material equivalent to about 15% of the standing stock of copepods in the trophogenic layer is being lost every day, if the experimentally determined high sinking rates of faecal pellets (e.g. Smayda 1969, 1971; Fowler & Small 1972; Wiebe et al. 1976; Turner 1977; Honjo & Roman 1978) are true.

Nevertheless, the retention of faeces in the surface layer, or, at least, a reduced release of faeces into deeper water layers, would certainly be of great importance of the nutrient availability in the euphotic zone of the water column. Krause (1981) studied the vertical distribution of faecal pellets of *Calanus finmarchicus* from water bottle samples in the Fladen Ground area. Generally, the faecal pellets showed a clearly defined maximum above the main thermocline within a depth of 0 - 30 m. Only in a period of storms was the faeces maximum lowered to the main thermocline, which occurred at 50-60 m depth. The maximum numbers of *Calanus finmarchicus* initially occupied the same level as the faeces maximum. However, from the middle of May, the *C. finmarchicus* population started a diel vertical migration, during which the copepods migrated away from the surface region into deeper waters. On this occasion, the faecal pellet maximum did not break up but remained in the uppermost layer of the water column, indicating very small sinking rates. In Fig. 18 some of altogether 78 examples of vertical profiles of faecal pellets and *Calanus* distribution in the Fladen Ground are given. Based on investigations in the framework of the ZISCH-Project Martens & Krause (1990) stated that the length of the faecal pellets was negatively correlated with water depth, indicating a degradation during sinking. Hardly any formed faecal material was detectable below 100 m water depth. It was assumed that in summer most of the planktonic faecal material is disintegrated in the upper water layer and the role of faeces in sedimentation is minor. According to Porter (1976), Colebrook (1982) and others grazing activity (superfluous feeding) and nutrient release e.g. in form of faecal pellets may enhance and extend phytoplankton blooms in the euphotic zone.

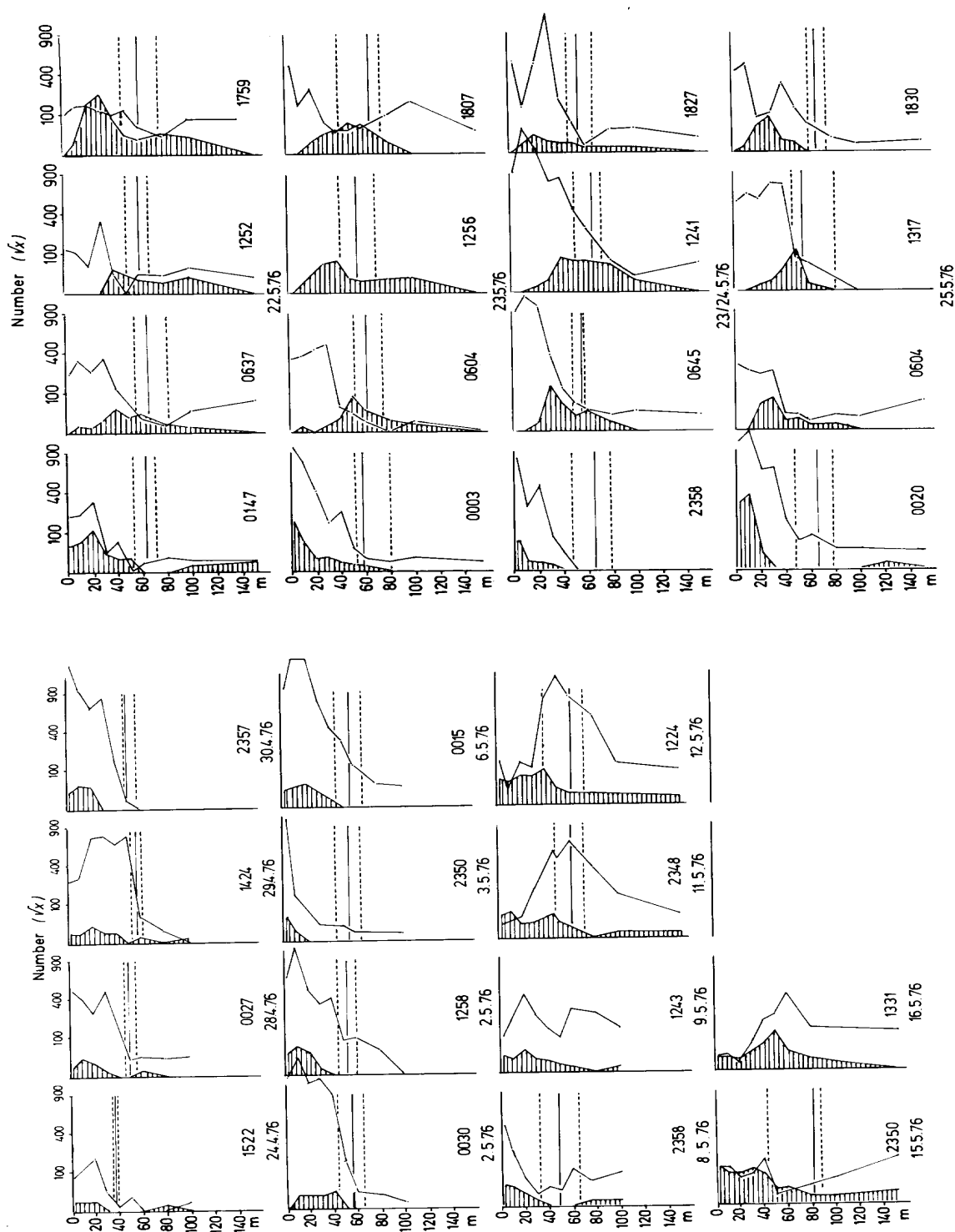


Fig. 18: Examples of vertical profiles of *Calanus finmarchicus* (CI-CVI) (hatched curves) and faecal pellets of these copepods (full lines) expressed in numbers per 10 l. The x-axis has been reduced in proportion to \sqrt{x} . The upper and lower limits (broken horizontal lines) and the centre (full horizontal lines) of the main thermocline during the sampling period have been drawn in the diagrams as lines (from Krause 1981).

Excretion effects on phytoplankton stock

The return of plant nutrients to sea water has been already investigated by Cooper (1935), Gardner (1937), and Harris (1959). The first two authors showed experimentally that living zooplankton organisms rapidly increased the concentration of phosphorus in sea water, and Harris showed that excretion was important in supplying nitrogen to the phytoplankton of Long Island Sound (USA). He estimated that at least 50% of the nitrogen regeneration was accomplished by zooplankton. Ketchum (1962) indicated in his paper on the regeneration of nutrients by zooplankton that the excretion of phosphate and nitrogen by zooplankton played a substantial part in the cycle of nutrients in the sea. Martin (1965) stated that the zooplankton of Narragansett Bay must have an important role in the production of nutrients, especially during the late summer and fall. Corner (1973) studied the importance of zooplankton in the marine phosphorus cycle with particular reference to the calanoid copepods. According to the author these animals are of central importance to the marine food web in several sea areas. In laboratory and field studies the rates have been measured at which zooplankton release soluble forms of phosphorus in relation to species, body size, food availability and season.

It was calculated by Jawed (1973) from historic data that, in the Columbia River plume, ammonia excreted by zooplankton provides about 90% of the nitrogen requirements of observed primary productivity. For ambient oceanic water this value is 36%, whereas in inshore waters nitrogenous excretion by zooplankton is relatively unimportant. Replenishment of nitrogen sources in surface layers of inshore waters is greatly enhanced by river-induced entrainment and wind-induced upwelling of deeper water. Båmstedt (1985) reported that estimations of the regenerative importance of nitrogen and phosphorus from macrozooplankton excretion indicated that between 4 and 50% of the phytoplankton nitrogen demands could be fulfilled, with highest percentage demand being met during autumn. For phosphorus the range was 14 – 102% of the phytoplankton requirements.

Banse (1995) revealed the pivotal role of zooplankton in the control of production of the nutrient-depleted areas of the oceans. Under oligotrophic conditions, the rate of phytoplankton cell division in the light-saturated part of the euphotic zone depends directly on the rate of nutrient regeneration by zooplankton; indirectly it depends on the liberation of dissolved organic matter that provides the bacterial substrate, mainly from “sloppy” feeding of the zooplankton, excretion, and release from faeces, as well as a small contribution from exudation by phytoplankton. Banse discussed the possibility that, via nutrient regeneration, temperature-controlled zooplankton physiology largely controls the rate of phytoplankton production.

Summarizing, it can be assumed that at least in surface stratified waters, turnover of plankton carbon is rapid compared to that in the light-limited, mixed water system and, under certain conditions, the phytoplankton may obtain between 43% (Alcaraz et al. 1994) and > 50% (Holligan 1984) of their nitrogen requirement from ammonium excretion by zooplankton.

Generally, direct (DOM) excretion is small compared to microbial regeneration (app. less than 10%, see Båmstedt et al. 1990; Glibert et al. 1992; Miller & Glibert 1998), a fact that is consistent with the high degree of contribution of feeding features like sloppy feeding and pellet production to regeneration of nutrients thus leading to enhanced bacterial production.

3.3.4. Reproduction

Copepods

The study of reproduction comprises several aspects from seasonality in breeding, mating behaviour, spawning to the impact of food availability to egg production. In our latitudes species of copepods usually show seasonality in breeding especially in copepods which produce resting eggs. The occurrence of a resting egg phase in the life cycle of marine planktonic copepods is well documented and receiving increasing attention by investigators. Recent studies have focused on the conditions that promote the occurrence of resting eggs, the factors that affect their survival and

hatching from sediments, the existence of egg banks in sediments and the impact of resting eggs on plankton community structure. Marcus (1996) and Marcus & Lutz (1998) summarized the understanding of embryonic dormancy in marine copepods.

Within the breeding season some copepods like *Acartia* and *Calanus* produce eggs continuously (Conover 1967; Rodriguez et al. 1995). Others, for example *Eurytemora* and *Pseudocalanus*, lay their eggs in distinct clutches attached to the genital somite until the nauplii hatch out (Bautista et al. 1994; Viitasalo et al. 1994; Gómez-Gutiérrez & Peterson 1999). Gonad maturation and egg production rate are key parameters for studying reproductive strategy, which plays an important role in adaptation to highly variable environments. Different stages of maturation could be detected by determining the developmental state of the ovaries in females (Razouls et al. 1991; Norbin 1994), and the presence of spermatophores within the male gonoduct indicates the potential for mating (Tande & Hopkins 1981; Tande 1982). In natural environments female dimorphism was found in *C. finmarchicus*. This phenomenon was described earlier by Fleminger (1985) in most of the copepods in the family Calanidae. It will be an advantage to switch sex for CV males into females because they probably end up with a higher reproductive success during a narrow time window when males are found to be in majority (Svenson & Tande 1999). This phenomenon could be explained by the size-advantage-model formulated by Ghiselin (1974).

One area of interest is the possibility that egg-laying is timed to take advantage of phytoplankton increases or blooms (Mauchline 1985). The results, however, are partly equivocal. Whereas during the Fladenground Experiment a temporal link of 2 to 3 days was found between peak primary production and peak in copepod eggs and 10.8 days for primary production and nauplii, respectively (Krause & Trahms 1983; Radach et al. 1984), on the other hand it was shown that the egg-production of *C. finmarchicus* in the Norwegian Sea can be partly decoupled from the spring bloom (Niehoff et al. 1999). At the US west coast, egg-production of larger copepods (*Calanus*, *Centropages*) was positively related to upwelling with high Chlorophyll a-rates, in contrast to rates of smaller copepods (*Paracalanus parvus*, *Acartia longiremis*, *Pseudocalanus* spp.). Their hatching success was only about 20-40% (Gómez-Gutiérrez & Peterson 1999). Thus, a great lack of knowledge of the environmental factors controlling reproduction is present.

Egg-carrying cyclopoid copepods have lower fecundity and feeding rates, and longer egg hatching times, than free-spawning calanoid copepods. Simple demographic considerations suggest that the lower feeding and fecundity of egg-carrying cyclopoids are adaptations to the potentially elevated mortality of ovigerous females, while the shorter egg hatching time and higher feeding and fecundity rates found in free-spawning calanoid copepods might be adaptations to the very high mortality rates experienced by suspended eggs (Kiørboe & Sabatini 1994). There are a lot of laboratory studies on the fecundity of different species of calanoids (Katona 1975; Gaudy & Pagano 1987; Gaudy 1989; Hirche 1989; Hirche 1990; Ianora & Bouttino 1990; Hirche 1992; Ianora & Poulet 1993; Hirche 1996) but nearly a total lack in field estimates. One exception is a study on the reproductive biology of *C. finmarchicus* in the Norwegian Sea. It was obvious from feeding experiments that food quality limited egg production prior to the phytoplankton bloom, while presumably food quality was not sufficient during the post bloom. Due to high abundance of females prior to the bloom the total egg production in this time was the same as during the bloom. This implies that the reproduction is to some extent de-coupled from the phytoplankton bloom. (Niehoff et al. 1999). Size as well as the protein-, carbohydrate-, and lipid-content of the eggs laid by the females of *C. helgolandicus* varied with time and were positively correlated with the amount of food available (Guisande & Harris 1995).

The role of dinoflagellate-diet is shown for two different copepods. The effect of dinoflagellate-diet on male copepod fertilization capacity of *Temora* sp. was negative, while the egg viability of *Calanus* was not influenced. Ianora et al. (1999a) suggested that insemination played an important role. Actually, mating seemingly is essential for the viability and amount of eggs produced by the females. Although virgin females can produce eggs (Carlotti et al. 1997), these eggs are morphologically different from viable eggs. High and continuous egg production requires several matings. Even after mating, hatching success is not complete.

For many copepods the development of resting eggs and benthic overwintering stages is known. For the shallow southern North Sea this is a promising strategy to survive adverse living conditions. Examples are known for the calanoid copepods *Labidocera* sp. and *Centropages* spp. (Grice & Marcus 1981; Grice & Gibson 1982; Lindley & Hunt 1989; Lindley 1990; Marcus et al. 1997; Marcus & Lutz 1998). To some degree these features are monitored within the CPR framework.

Fransz et al. (1991a) summarised the knowledge of reproduction of copepods of the North Sea and showed that the significance and stimulation of diurnal and seasonal vertical migration patterns related to reproduction are not well understood.

Other zooplankton

Seasonal changes in the abundance, size and occurrence of furciliae of *Euphausia krohni*, *Nematoscelis megalops* and *T. gregaria* were described by Lindley (1982b) from samples taken at 10 m depth with the Continuous Plankton Recorder (CPR) in the North Atlantic Ocean over a period of 2 years (January 1966 to December 1967). *E. krohni* and *T. gregaria* were found to breed through most of the year but *N. megalops* bred only in spring and summer. An overview of seasonal timing, which to some degree also serves as a calendar of reproduction in the German Bight for several species, was given by Greve and Reiners (1995).

Metabolic state of copepods

In preparation of egg production storage lipids were found in a great amount in *C. finmarchicus* sampled at Georges Bank and the Gulf of Maine in February and March. Pure wax ester out of the oil sac was transformed to triacylglycerols elsewhere in the body (Miller et al. 1998). At the highest egg production rates of *Acartia tonsa* in Mobile Bay, the amount of the storage lipid triacylglycerol (TAG) in adult females was greatly diminished, to <50 ng female⁻¹. Therefore McManus and Foster (1998) suggested that lipids in the diet can be very tightly coupled to egg production. Hirche and Kattner (1993) found an indication of a food-dependent and food-independent reproductive mode in *C. glacialis*. In fed females food provided most of the energy, whereas in starved females the lipid content strongly decreased when spawning took place. Lipid concentration in *Pseudocalanus* increased with food concentration and temperature until 15°C while at 20°C the lipid concentration was on a lower level (Klein Breteler & Gonzalez 1988).

Effects of feeding: In addition, fatty acids in the lipids of copepods originated from dietary input may be used as trophic markers for herbivorous feeding (Kattner & Hagen 1995). Furthermore, fatty acid analysis helps to characterize the degree of herbivorous or omnivorous feeding behaviour (Ward et al. 1996). This is consistent with a study of lipid biochemistry of Sargent and Petersen (1988), which shows that *C. finmarchicus*, mainly herbivorous, accumulates higher stores of neutral lipid and has more of that lipid as wax esters than *Metridia longa*, which is more of an omnivore.

Effects of seasons: In the Fladen Ground area and in the eastern North Sea the seasonal variations of lipids (wax esters, fatty acids and alcohols) in calanoid copepods, *Calanus finmarchicus*, *C. helgolandicus* and *Pseudocalanus elongatus* were investigated by Kattner & Krause (1989). Wax esters were generally the main lipid class, with up to 88% in Copepodite Stage V. The wax ester proportion of the females was much more variable than that of the copepodite stages, ranging from 2.6 to 79% of total lipid, probably indicating phases of egg production. The fatty acid compositions showed a high variability and diversity throughout the seasons. So, e.g. during spring, the fatty acid composition reflected the diatom food by increasing levels of the 20:5 acid. When food became scarce, e.g. during winter or even in summer, the fatty acid compositions were nearly reduced to the three main acids: 16:0, 20:5 and 22:6. Changes in lipids during the development of *Calanus finmarchicus* from Copepodite I to adults in the North Sea were studied by Kattner & Krause (1987). Total lipid and the wax ester proportion increased exponentially until Copepodite Stage V. The females were sometimes lower in lipids than Stage V, indicating again egg production phases. The wax ester proportion reached about 90% of total lipids in males and Copepodite V and up to 40%

in Copepodite I. The investigations also showed that fatty acids of the diet are incorporated mostly unchanged into the lipids of the copepods.

Specific differences: In comparing *C. finmarchicus*, *Acartia clausi* and *Pseudocalanus* sp. Båmstedt et al. (1990) stated that the three species represented different development stages concerning the degree of dependence on food supply and overwintering strategy: The non-diapausing *Acartia clausi* mainly contained TAG as a relatively short-term storage product, whereas the diapausing *C. finmarchicus* contained large portions of wax esters, a long-term storage product. *Pseudocalanus* sp. showed intermediate levels for both lipid classes.

3.3.5. Growth and production

Growth is the increase in size or biomass (somatic growth), production is growth integrated over time. In particular for mature individuals, growth is no longer expressed in terms of somatic growth but in terms of production of offspring.

Methods

Among others van Beusekom & Diel-Christiansen (1993) summarized the problems in measuring secondary production. Estimation of secondary and tertiary production of zooplankton population in the sea are more difficult to carry out than measurements of primary production. There is unfortunately no equivalent to the ^{14}C method for zooplankton.

There are several approaches to production estimates, each with its own advantages and disadvantages:

- Assessments of one and the same stock, i.e. in the same water body, over a longer period of time can be used to estimate production. The growth of the stock (minus predation and natural mortality) can be estimated from the time series of the numbers of individuals of species and developmental stages, which can be calculated as biomass using conversion factors. Since it is necessary to ensure that the same body of water (i.e. the same population) is being sampled the whole time, the results are subject to large error.
- A further possibility is the determination of stock size in the field and parallel experimental determination of growth rates in order to extrapolate the production in the area of investigation from the stock sizes found. A disadvantage is the fact that the estimates are only valid for individual taxa, that the laboratory experiments must be carried out over several days and that they probably do not produce exactly the same rates as in the natural milieu.
- Van Beusekom & Diel-Christiansen (1993) also pointed out that the carbon invested into eggs by the non-growing female (as carbon produced per female carbon weight per unit time, or specific egg production) can be used as an approach of the daily P/B ratios (corresponding to growth rates) of the copepodite stages (Sekiguchi et al. 1980). Egg production is either determined in laboratory experiments or simply figures as female/egg ratio in the water column, divided by the temperature dependent hatching time (=residence time in the water). Also with this method it is only possible to estimate the production of a part of the zooplankton spectrum.

Nevertheless, based on their study Campbell et al. (2001) recommended that secondary production rates of *Calanus finmarchicus* and possibly other lipid-storing copepods should not be estimated from egg production measurements alone, because growth, including structural growth, is not equivalent for all stages. Likewise Harris (2000) explained: lipid storage in *Calanus* spp. is used to fuel egg production after ascent from overwintering. A certain quantity of fresh food also seems necessary to maintain egg production, probably contributing essential molecules. Therefore, the quantity of food necessary to produce an egg probably varies depending on the lipid storage, with consequent seasonal variations in the relation between egg production and food. This makes the rate of egg production an inadequate technique to estimate

carbon requirements. Equally, in the case of *Calanus*, rate of egg production must be a very poor predictor of the growth rate of copepodites, at least during periods when it is fuelled by lipid storage.

- Finally, production can be estimated by measuring stock biomass in the field in connection with the experimentally determined respiration rates. For the calculation of the production, however, some physiological standard values are necessary which can be obtained from the literature.

Growth of copepods

Copepods, like other crustaceans, increase their body size by moulting. The first nauplius stage hatches from the egg and develops through five moults to the sixth nauplius. The following first copepodite stage passes through five successive moults to become the sixth copepodite, which is the adult stage (male or female).

Growth is one of the important characteristics which determine the life history trait. Growth has been studied in controlled laboratory experiments as well as by time series sampling of field populations and identification of the nauplii, copepodids and sequential cohorts and generations. Recent studies of growth address particular questions or hypotheses that have a broad implications for the understanding of how pelagic populations and ecosystems function and respond to environmental variability and stress. Food and temperature are the most investigated factors which influence growth to a certain degree. Generally, increased food level enhances growth (Klein-Breteler & González 1982). The effect of temperature on the development of eggs in *Pseudocalanus minutus* was more obvious than an effect of salinity (McLaren et al. 1968). In *Acartia* spp. the same negligible effect of salinity in relation to temperature was found (Uye 1980). The temperature affects also the hatching success of eggs. Coastal species like *Paracalanus* sp. show a hatching success better than 60% between 7.5 and 21.3 °C but less than 30% at temperatures higher than 22.6 °C (Uye 1991). Less eurythermic species of the oceanic regions may have a restricted temperature window for successful hatching (Mauchline 1996). Differences in developmental times of eggs occur between free-spawned eggs of *Paracalanus*, *Calanoides* and *Calanus* species and clutched- spawned eggs of *Pseudocalanus* and *Eurytemora* species. The former take only half the time as the latter, 24 h as opposed to 2 d.

Developmental sequence of the copepod through the naupliar and copepodite stages was investigated by observing stage duration in laboratory (Klein-Breteler et al. 1982; Runge 1985). Growth patterns of calanoid copepods were divided up in four different patterns of development. Species of the genus *Calanus* and *Centropages* were found to have an equi-proportional development (Corkett et al. 1986; Fryd et al. 1991), which was introduced by Corkett (1984). *Acartia* species in contrast can be described in terms of isochronal development, that is characterised by the same duration of all stages (Corkett & McLaren 1970; Katona 1971; Uye 1980; Klein-Breteler et al. 1982; Davis & Alatalo 1992; Klein-Breteler & Schogt 1994; Klein-Breteler et al. 1994; Klein-Breteler et al. 1995). Sigmoidal development was found only in *Calanus marshallae* by Peterson (1986). The fourth category summarises all developmental pattern which do not fit into the other ones. The stage duration vary somewhat irregularly in investigations of *Acartia clausi* (Christou & Verriopoulos 1993) and of *Calanus* species (Tande 1988; Peterson & Painting 1990; Fryd et al. 1991; Uye 1991).

For *Centropages typicus* moulting rates were determined experimentally and in the field (Carlotti & Nival 1992): Experimentally successive moulting took place at the 2nd day within a given stage, during the 1st in this given stage survival usually was high. In the field slightly slower rates were observed, which were stage specific : 0.1 day⁻¹ for females, 0.27 day⁻¹ for juveniles. This probably supports the hypothesis, that juvenile growth contrasting adult growth is not food limited. Derived from energy budgets for field populations, Båmstedt et al. (1990) obtained growth rates of 1-2% of body weight per day for *Acartia clausi* and *Pseudocalanus* sp., whereas *Calanus finmarchicus* had an increase of 4.1 to 8.5% per day.

Some attention has to be paid on the difficulties of moulting studies. The individual variation in stage duration within a batch culture presents problems in determining the true duration. Therefore a standardisation was suggested by Peterson and Painting (1990) and Klein-Breteler et al. (1994) to use the "median development time (MDS)". A further problem are the constant conditions in laboratory experiments while the developmental stages of copepods will experience changing conditions in their natural environment. Combining stage duration data with comparable data on the increment at each successive moult is crucial to an understanding of the processes involved in growth and development of the copepods (Mauchline 1996). For example, Bosch & Gabriel (1994) developed a model that predicts isochronal and equiproportional development.

To get a better understanding of the variation in zooplankton populations, recent studies of the dynamics of copepod populations, either in the field (Peterson et al. 1991; Peterson & Kimmerer 1994) or by modelling (Miller & Tande 1993) illustrate the importance of quantitative growth rate measurements. The study of Klein-Breteler & Gonzalez (1988) demonstrated that body size of copepods is determined both by temperature and food concentration. The effect of temperature seems to be somewhat larger than the effect of food concentration in *Temora*, but in *Pseudocalanus* both factors contribute equally to the final size reached in the adult stage. The condition factor increases with temperature especially for *Temora* until 20 °C, but less in *Pseudocalanus* (until 15 °C) (Klein-Breteler & Gonzalez 1988). High temperatures enhance a small body size and early reproduction and low temperatures extend the development in each stage and start breeding at large size. *C. helgolandicus* in the Celtic Sea showed a decreased length with temperature (Williams & Robins 1982).

A general concept of growth of calanoids is proposed to describe the intermoult periods of successive stages of development. But there are only few accurate descriptions of development in very few species. Ivanova (1973) and Bosch & Gabriel (1994) started an approach to develop models which describe body length of each stage and its stage duration and predict isochronal and equiproportional development respectively. An other way to examine growth is to observe changes in body weight during development. The body of a copepod can be conceived as consisting of two compartments, the structural and the storage compartment (Harris 1983). Body dry weight and body length fluctuates seasonally and is related to environmental temperature. Body length and body dry weight seems to be independent and their relation have initiated the approach of the concept of a condition factor (Durbin & Durbin 1978). The increase of body weight is measured as a weight specific growth rate which is related to generation time, so that longer-lived copepods grow at slower rates (Mauchline 1996). In further studies growth should be investigated with respect to describing rates of approach to sexual maturity. There are still open questions to the connection of the processes of the formation and maturation of the gonads and growth with respect to temperature.

Growth of other zooplankton

Growth in gelatinous zooplankton (*Aurelia aurita*) is determined by the allocation of food: Scarcity in food reduces the growth rate, but also changes the energy allocation towards reproduction, which thus occurs at a smaller size than for well-fed medusae (Ishii & Båmstedt 1998). At insufficient diets (Deason & Smayda 1982) and periods of starvation (Båmstedt 1998) gelatinous zooplankton can shrink again. For estuarine mysids an extensive growth study was presented by Winkler (2000).

For growth, though not complete and mainly focussed on copepods, the extent of knowledge in this field has far developed. For metabolic state, research on storage products, lipids etc. and their role in influencing fecundity needs to be intensified.

Estimation of copepod-production during the Hamburg KUSTOS-Project

In the frame work of the Hamburg KUSTOS-Project Sabine Diel-Christiansen made an attempt to estimate the production of the copepods in the German Bight using the stock-data of the copepods

and the experimentally determined respiration rates of the copepod-mix (Krause et al. in prep.). In the following a short description of her calculations is given.

Basis for calculation: For the calculation of a range which can be seen as probable for actual copepod production, in addition to the stock biomass and the corresponding weight specific respiration rates, additional physiological orientation values are necessary, which can be taken from the literature:

The respiratory quotient (RQ) gives the efficiency with which a substrate (=protein, carbohydrate or lipid part of the assimilated food) is metabolized. The RQ can have a value between 0.7 and 1.0, depending on whether mainly fats or proteins are digested. If one mole of O_2 is taken up to produce one mole of CO_2 , then the $RQ=1$. For marine, mainly herbivorous plankton, a RQ of 0.97 is recommended (Omori & Ikeda 1984), and this has been used in the present calculations. The relatively high RQ indicates a primarily protein metabolism of the copepods, which has been confirmed by our own respiration and excretion measurements during KUSTOS, comparing the ratio of consumed O_2 to excreted NH_4 (see chapter: Excretion and defaecation; O/N-ratios).

The RQ, together with the biomass dependent O_2 consumption ($\mu g O_2 m^{-3} h^{-1}$), is used to calculate the respiratory carbon demand (RK). This specifies the minimum amount of carbon an organism must take up with its food in order to maintain its metabolism. On the other hand, it is also a measure for the amount of primary production that has at minimum to be consumed by the copepod plankton.

$$RK = \text{biomass} \times \text{respiration rate} \times 12/32 \times RQ$$

The **net growth efficiency (NGE)** corresponds to the proportion of the assimilated energy (production + respiration) which is invested in production (growth of the stages, energy depots, reproduction).

$$NGE = E_{\text{Production}}/E_{\text{Assimilation}}$$

NGE is species, size, food and – to a lesser degree – temperature dependent. From experimentally determined published data a minimum NGE of 0.5 (Vidal 1980) and a maximum NGE of 0.75 (Kiørboe et al. 1985) was derived for the production calculations of the copepod-mix.

The range of potential production (growth, reproduction) is determined by multiplying the assumed minimal or maximal net growth efficiency with the respiratory carbon demand of the copepod stock and converting it to the corresponding dimension ($mg C m^{-3} d^{-1}$).

The production/biomass relation (P/B) is an indicator for the change in biomass over time (dimension: d^{-1}) and corresponds to the growth rate. When growth is not limited by food, the P/B relation is a function of temperature (Rijswijk et al. 1989).

The growth rate (G) is calculated from the developmental rate (D), i.e. the daily change in the median of the stage distribution of the species and the increase in weight according to

$$D = s_t - s_0/t$$

$$G = D * \ln W_t/W_0$$

The stage duration is $1/D$.

The production during the summer drift in '94 in the German Bight, which was calculated and averaged over a drift phase, was of a range between $MIN = 9.45 mg C m^{-3} d^{-1}$ and $MAX = 28.34 mg C m^{-3} d^{-1}$. The daily growth rate calculated from this was $P/B-MIN = 0.15$ and $P/B-MAX = 0.46$. That means that the daily growth of the copepod stocks was between 15% and 46%. During the spring drift in '95 there was a mean production of copepods of $MIN = 1.01 mg C m^{-3} d^{-1}$ and $MAX = 3.04 mg C m^{-3} d^{-1}$. From this a daily growth rate $P/B-MIN = 0.09$ and $P/B-MAX = 0.27$ can be calculated. Hence, the daily growth of the copepod stocks during this time was between 9% and 27%.

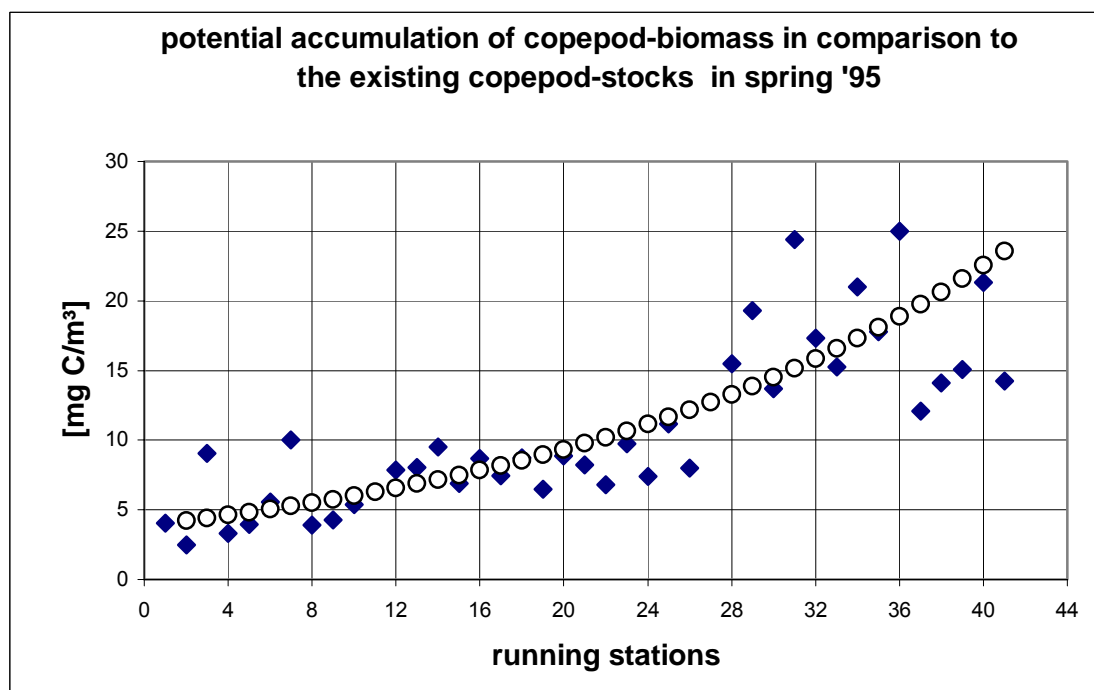
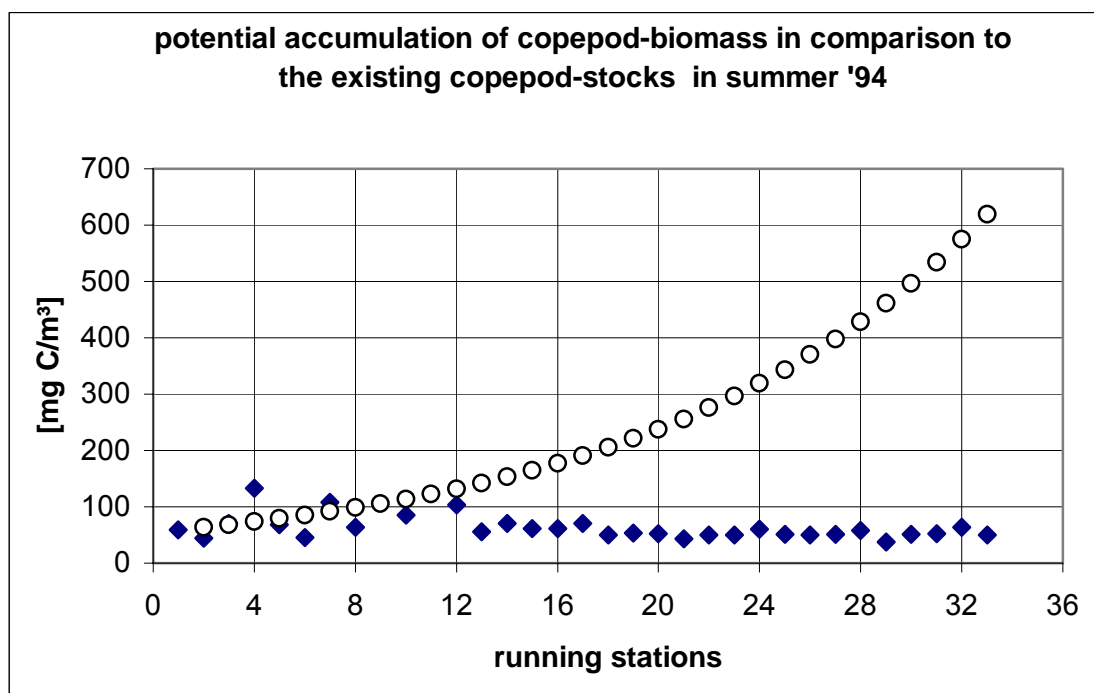


Fig. 19: Calculation of the potential accumulation of copepod biomass (open circles) in comparison to the existing copepod stock at (black diamonds) two drift phases in the German Bight during the KUSTOS-project (Krause et al. in prep.).

From the averaged (from MIN and MAX) daily production rates, the potentially possible biomass accumulation of the copepod stocks during both drift phases was calculated and is shown as a function of time in Fig. 19 (open circles). For comparison, the found copepod stock sizes derived from the net hauls are also shown (black diamonds). From this it can be seen that during the summer drift the copepod stocks were stagnated, in spite of a high production rate (mean: 0.305). On the other hand, during the spring drift the measured stock sizes, which had a smaller production rate (mean: 0.180), showed a development which truly oscillated but was similar to the calculated stock accumulation. In spring, the potential production seems to have been reflected in growth, while in summer it may have gone into increased reproduction (e.g. gonad development, egg production), which did not manifest itself in an increase in stock size. Moreover, it can be presumed that the copepod stocks in summer of '94 were subject to a strong predatory pressure, which is plausible considering the large populations of small hydromedusae and *Sagitta* sp. (Krause et al. in prep.).

3.4. Parasitism

In the pelagic realm little is known about the impact of parasitism and degree of host mortality related to parasitism. For copepods parasitism is a phylogenetically modern adaptive strategy to changing unstable environmental conditions (Hairston & Bohonak 1998) and has been developed several times between and within different taxa, e.g. within the cyclopoid copepods (Ho 1994). Three major complexes can be discerned within this field, of which the parasitism complex of the gelatinous plankton is probably the best known: Parasitism on copepods, parasitism on gelatinous plankton, and parasitism on fish.

Parasitism on copepods: A very early description with drawings of worm-like parasites on copepods was given by Apstein (1911). He discerned 3 groups of parasites: intestinal, extra-intestinal and epizoic. At some locations in the North Sea he assessed parasites to be common on copepods. Copepod-bacteria relationships were investigated for Tokyo Bay and Woods Hole (Nagasawa 1986). It was found that up to 100% of copepods were colonised by bacteria, often generating excessive slime on the host. At times these bacteria infested the intestinal track and were therefore regarded to be parasites. Other common parasites are protozoans (Al-Yamani & Fahmi 1995), certain diatoms (Hiromi et al. 1985), dinoflagellates (Kimmerer & McKinnon 1990) and even other crustaceans (Uye & Murase 1997). Still little is known for the North Sea.

Parasitism on gelatinous plankton: Of quantitative importance for the North Sea is the association of amphipods, e.g. hyperiids, with medusae. A review of medusan parasites was presented by Thiel (1976). It can be seen from this compilation, that the common North Sea scyphomedusae *Chrysaora hyoscella*, *Cyanea capillata*, *Rhizostoma* sp. and *Aurelia aurita* all are subject to parasitism by the hyperiids *Hyperia galba* and *H. medusarum*. *Parathemisto gaudichaudii* was found to be associated with salps (review in: Laval 1980). Juvenile *P. gaudichaudii* experimentally attached themselves to hydromedusae. Laval discusses the case of hyperiids to be free living predators and concludes, that this is rather unlikely due to morphological and ontogenetical constraints. Laval argues for the statement of Harbison (in Laval 1980) "that it may well be that all hyperiid amphipods spend some portion of their lives in association with gelatinous plankton". Laval also discusses the aforementioned interactions between hyperiid amphipods and fish larvae and emphasises that they were derived from unnatural in situ experimental constellations. Observing hyperiids with SCUBA-divers revealed a clear association to gelatinous hosts even for those species that were assumed to be free living. Laval (1980) argues that the free living phase might be restricted to the times the amphipods change their host due to exhaustion of the host. Therefore, predatory impact of hyperiid amphipods as calculated from laboratory feeding experiments (e.g. von Westernhagen & Rosenthal 1976; Frid et al. 1994) might be overestimated. However, von Westernhagen (1976) could show that field collected *Hyperoche medusarum* to some degree had fed on crustaceans, so that the impact of hyperiid amphipods remains an open question.

3.5. Processes at the interface to hydrophysics

Currents

The effect of currents was analysed for meroplankton distributions along the coast of the southern North Sea (Belgrano et al. 1995). It appeared that wind direction and associated currents were most responsible for the distribution of coastal plankton.

Frontal systems

Fish larvae are feeding more intensively in frontal zones. This was found e.g. by Rissik & Suthers (1996) in Australian waters and by Munk & Nielsen (1994) and Munk et al. (1995) in the North Sea (Dogger Bank). It is assumed that fronts concentrate plankton by means of convective currents and thus provide better feeding conditions. Additionally, an increase of turbulent motion can be expected (see next section). Effects on feeding were investigated for the copepod *Centropages typicus* in the western Mediterranean with equivocal results (Saiz et al. 1992). Population density at the frontal station was highest for the copepod, paralleled by a maximum for primary production. However, relative and absolute feeding activity was higher in the non-frontal stations. Micro-scale turbulence and change in algal chemical and taxonomical composition were discussed as possible causes.

The effects of eddy formation on oceanic zooplankton has been widely described (e.g. Piontkovski et al. 1995). In this context injection of nutrient enriched deep water into the euphotic zone plays an important role for increased primary production and subsequently increased zooplankton biomass. Effects of this kind can only be anticipated where nutrient enriched Atlantic water enters the northern North Sea. For all other parts energy dissipation, i.e. increase of motion due to turbulence, must be seen as primary effects of eddies in relation to zooplankton.

Turbulence

Data and models on turbulence

Turbulence measurements were carried out for the southern North Sea (Veth 1990). A comparison of these measurements with model results derived from wind speed and vertical mixing indicated a high degree of reliability of the model results. In a similar way turbulence was applied in a 3-D model for the North West European shelf (Delhez 1998). The simulation emphasized the strong influence of the local depth and of water column stability and by this turbulence, on the whole annual plankton cycle.

Turbulence and its effects

Turbulence is a key process in the sea. It determines diffusion and encounter processes for all kinds of matter. Turbulence is usually described by its dissipation rate of energy (in $\text{cm}^2 \text{s}^{-3}$), or by its intensity (in cm s^{-1}), i.e. motion, from larger to smaller eddies. During dissipation of energy, the kinetic energy lost is transferred to the ambient environment and absorbed by means of heat. For turbulence two scales can be distinguished: the inner and outer scale. The dynamic margin between these two types of scale is determined by the Kolmogorov minimum length scale. In Kiørboe et al. (1999) boundary layers of 0.1 cm are calculated in which shear decelerates flow (deviation more than 1% from free-stream velocity - compare to Kolmogorov scale in Appendix - Table 5. Usually smallest length scales for turbulent eddies are app. 6 mm (the Kolmogorov scale) and for temperature fluctuations app. 2 mm (Batchelor scale). For nitrate minimum fluctuations are app. 0.2 mm.

Turbulence, i.e. random non-linear motion of water, only occurs within the range of the outer scale, whereas laminar flow occurs within the range of the inner scale, i.e. the viscous environment, experienced by organisms as shear flow. However, such a linear downscaling from large turbulent to increasingly smaller eddies in the outer scale actually does not occur. In turn, the distribution of kinetic energy shows variance maxima at certain length- and frequency scales, i.e. a inhomogeneous distribution. This phenomenon is known as intermittency (Seuront et al. 1999). The intermittent structure can be understood as a series of parent and daughter structures, for which certain scale ratios are constant. In such a way turbulent structures can be analysed as multifractal structures, which has been successfully achieved for phytoplankton (Seuront et al. 1999).

For phytoplankton mainly diffusion gradients are affected. For zoo- and ichthyoplankton turbulence acts in two different ways. Firstly, contact rates are increased by turbulence. Secondly, physiological rates also change in a way that turbulence is experienced as stress. In comparing field and experimental designs, it is evident that contact rates in the field due to turbulent motion are considerably higher than in experiments (Rothschild & Osborn 1988), which are hampered by design constraints. The dynamics of contact rates and by this the change in encounter probabilities for prey and predator have been investigated by means of models. A work by Gerritsen & Strickler (1977) suggests that successful zooplankton has two different strategies according to turbulent motion: The first strategy is that of cruisers feeding on slowly swimming prey. The second successful strategy is to act as ambush predator on fast swimming prey. In practice two different processes are concerned by this model: the one is the process of perception of changes in the flow field essential to detect prey (or the predator) beyond the range of chemical sensory organs. The second is the enhanced mixing. Turbulence as meant by shear is used to detect predators and the reactions to shear can be investigated. Generally, the shear necessary to elicit escape reactions is higher than ambient shear (velocity). Secondly differences between species (*Labidocera* needed much higher shear stress than *Oithona* and *Acartia tonsa*) and developmental stages (nauplii require higher shear to elicit same degree of reaction than adults) exist. Conclusively, high mortalities of nauplii can result from being relatively insensible to shear and thus be easily captured (Fields & Yen 1997). Kiørboe et al. (1999) confirm this with experimental findings for the copepod *Acartia tonsa*: Nauplii react at higher levels of acceleration and by this approach closer to the predators than adult copepods. From a literature review Kiørboe et al. (1999) discuss that threshold reaction levels (by means of deformation rates: 0.5 to 6 s^{-1}) are in the same range as deformation rates observed in the ocean due to turbulence (1 to 10 s^{-1}). However, copepods can escape high turbulent conditions by migrating into deeper water (as observed by Williams 1996). But, vertical distribution of *Oithona similis* and *Microsetella* sp. are seemingly unaffected by turbulence, whereas *Temora* sp. and *Pseudocalanus* sp. are affected and show a deeper distribution than under calm conditions (Lagadeuc et al. 1997). In turn, the measured sensibilities are lower than deformation rates exerted by the feeding currents (app. 15 s^{-1} acc. to Kiørboe et al. 1999), so that escape from current fields of predatory copepods is possible (question remains: if predatory copepods overcome escape distances by jumping or pursuing (?), can they get the prey?).

For phytoplankton feeding copepods using feeding currents, an alternative conceptual model of the process is that the food particles are diffusing towards the predators. Their feeding currents trap the prey (even though they are well beyond the range of either visual or chemical detection) and entrain them towards their waiting arms. The predators thus benefit from the turbulent motion and diffusion, even though much of it is due to motions with scales significantly larger than their body's size. The feeding currents serve to dramatically increase the flux for food (Osborn 1996). For ambush predators without feeding currents the perception of the prey by the predators depends on the motility and by this velocity of the prey much more than on the movement of the predator. *Oithona* waiting for prey perceives motile prey (size range $4.6\text{ }\mu\text{m}$) at 0.013 cm s^{-1} . Since swimming speed increases with size, larger prey are effectively perceived, whereas small prey with slow swimming speed is not recognised since its speed does not exceed that of the ambient water. For immotile prey sinking speed needs to exert the trigger. For *Oithona* sinking only is effective to elicit capture reactions for calcula-

ted sizes > 80 μm . Faecal pellets with their relatively high density of 1.15 g/cm³ sink faster than diatoms and are perceived at a size of app. 6 μm - and bigger pellets are perceived better and utilised at much higher clearance rates than smaller ones (Kiørboe & Visser 1999). The diffusion aspect has already been mentioned for phytoplankton, but is also important for particle sieving zooplankton. Diffusion is enhanced due to turbulence and by this more particles entrain the area where feeding currents are effective (Osborn 1996).

However, another aspect has to be considered, the handling time. This means, that increasing turbulence not only increases contact rates and encounter probability, but also decreases time to utilise and handle the prey. This has been investigated by a model of MacKenzie et al. (1994). As result a dome shaped curve between turbulence and feeding rate (i.e. encounter rate * successful catch) is obtained: At high deformation rates there is no time left to handle the prey. These results were further confirmed by theoretical studies (Jenkinson 1995). Field studies indicate that turbulence actually has detrimental effect on plankton and thus supports this view. Low biomass and low production rates are typical of copepods in So-lent, an eutrophic area with high tidal exchange rates (Hirst et al. 1999).

Changes of physiological rates in relation to turbulence have been described for crustacean zooplankton, albeit these changes often are regarded as indirect changes depending on the direct changes of motility (Alcaraz & Saiz 1992; Alcaraz 1997). As an indicator of metabolic activity heart beat rate was found to increase under turbulent conditions (Alcaraz et al. 1994). In a validated model run Caparroy & Carlotti (1996) discovered that turbulence increased ingestion rates and gut contents of the copepod *Acartia tonsa* but in turn reduced gut passage time and thus assimilation efficiency.

Turbulence in models has not been considered extensively in models. An example was given by Delhez (1998). Intensive work has been carried out by Baird and co-workers: Turbulence was treated as part of the transport formula $J = \psi \cdot D \cdot \text{Sh} \cdot (\text{grad of conc.})$ in modifying Sherwood number, depending on shape of body and dissipation energy and relative velocity respectively (Appendix: table 1 and eq. 7-9 in Baird & Emsley 1999). Furthermore, handling time was considered in ERSEM.

Zooplankton field work on turbulence effects are rare. Most examples for the North Sea originate from the working group of Thomas Kiørboe. One of the first field studies was carried out at a permanent station the Skagerrak (Kiørboe & Nielsen 1990). Subsequent to a storm event, primary production increased followed by an increase in copepod egg production. A similar increase of copepod production after a storm event was recorded for the American west coast (Mullin et al. 1985).

Conclusion: The understanding of turbulence effects is regarded as a central issue of future marine studies and underemphasised in present work. Field studies are scarce, incorporation into models is weak and at present most work on turbulence effects is done by means of experiments. As a consequence sometimes contrasting results are presented.

3.6. Model development

Models of biological-physical interactions in the sea must take into account both physical transports and biological-chemical processes. Whereas models of physical transports always try to conserve the total amount of the variables (biogeochemical models after Tett & Wilson 2000), models of biological and chemical processes are non-conservative in the way that certain features are eliminated during time (ecological models after Tett & Wilson 2000). The development of computing power has in the present decade begun to allow the coupling of models of biological processes (see below: models of biological processes) with increasingly realistic three-dimensional physical models.

The evaluation of North Sea ecosystem models by Fransz et al. (1991b) for representation of higher trophic levels, i.e. those trophic levels including zooplankton with more than one item, indicates that until 1990 only a few North Sea relevant models attempted to resemble dynamics of complex interactions between different herbivores and carnivores. These interactions in turn are important for the dynamics of the lower trophic levels, which is usually represented by phytoplankton. Thus, fluctuations of the herbivores caused by predatory effects can release corresponding fluctuations in the phytoplankton irrespective of nutrient availability and therefore create alternative regulation phytoplankton regulation patterns. A model by Greve (1981) for the German Bight shows that in times of copepod control by ctenophore predation phytoplankton is controlled by nutrients, whereas when ctenophore predation is attenuated phytoplankton becomes controlled by copepod grazing.

The relevant processes in model formulation for higher trophic levels are: Grazing and ingestion, assimilation, respiration, mortality, nutrient regeneration, and phytoplankton regulation. From this set of processes only the first group, grazing and ingestion, is considered in more detail in this section.

Model construction

Biomass vs. production: The scope of modelling complexity is essential for accurate resolution of annual cycles. Davis (1987) shows in a comparison of different models, that models following the paradigm that biomass and production cycles coincide (referred to as 'trophic level models') fail to precisely predict production cycles. Results of research on Georges Bank indicate periods of high production under high predation pressure paralleled by low zooplankton biomass content especially in autumn, which is in contrast to the aforementioned paradigm of coinciding trends. This high autumn production is attributed to small-sized copepods with low biomass but high turnover. Size (as a compromise between species specific and trophic level models) and species specific models are better (sometimes referred to as 'individually based models' (Broekhuizen 1995), whereas Steele & Clark (1998) define individual-based models as models with individual, behavioural aspects and species and size specific models as population-based models.

For North Sea zooplankton, the most recent ERSEM model is a trophic level, biomass model considering two mesozooplankton components (omni- and carnivorous mesozooplankton, microzooplankton is a separate submodel) (Broekhuizen 1995). For this model the same comments have to be made as for the Georges Bank model, since a comparable decline in copepod biomass during autumn (August-September) due to high mortality was found in the Kattegat and presumably other parts of the North Sea. This decline would likely mask a significant production phase at that time of year (indicated by Kiørboe & Nielsen 1994).

The end of the model: Of great importance is the end mortality of the model, the so-called closure term of the model. The closure term indicates the mortality conditions for the top predator. The way the closure term is constructed (density dependent or density independent) influences cyclic and chaotic behaviour of the model (Caswell & Neubert 1998). In accordance to Steele & Henderson (1992a; 1995) they recommend to use density dependent mortality terms M in the form $M = EZ^\alpha$, where α denotes the higher order effect on the level Z . Varying values for α from 0 to 1 creates a sort of Holling type II functional response for higher order predators.

Models of biological processes

Growth in copepods has attained much attraction and attempts were undertaken to summarize the results into global models. Two different approaches can be discerned: (1) models based solely on temperature (e.g. Huntley & Lopez 1992), (2) models based on temperature and weight (e.g. Hirst & Sheader 1997).

The temperature dependent growth model assumes exponential growth and is based on adult and egg weight. The daily weight specific growth rate g is:

$$g = 0.0445e^{0.111T}$$

where T is temperature.

The weight and temperature dependent approach was based on respiration measurements. While converting O_2 -requirements into carbon equivalents and assuming certain assimilation and growth efficiency rates, daily growth rates were determined as:

$$g = 7.714 \cdot 10^{0.025T - 0.1259 \cdot W^{-0.01089T + 0.8918 \cdot W_C^{-1}}}$$

where W_C is the individual weight in carbon μg .

The results of Hirst & Sheader (1997) generally indicate, that growth and egg production of adult females can be better explained if body weight is taken into account as an additional variable. Furthermore, growth and fecundity rates tend to decrease with size.

In a further refinement Hirst & Lampitt (1998) analysed growth rates for different spawning types: (1) for broadcast spawners, permanently releasing eggs into the water, adult female fecundity was negatively related to body weight; (2) for sac-spawners a significant positive relationship was found to temperature. (3) For juvenile growth a similar relationship was found for sac-spawning species, while for broadcast spawner juveniles a relationship both to temperature and body weight was apparent. In situ rates for adults were in the range of 25% to 40% of rates obtained under food saturation, indicating that adults are food limited. This was not indicated for juveniles, for which growth was much less food limited. Thus, in model development (1) biological typus, and (2) food effects must be taken into account.

Models with changing feeding modes

Models on omnivory and mixotrophy were presented by Tett & Wilson (2000) and Thingstad et al. (1996), respectively. However, both models deal with microplankton and protozoan feeding. The omnivory of metazoans is not well understood yet, except for copepods in some cases (e.g. *Calanus helgolandicus*: Corner et al. 1976; *C. finmarchicus*: Ohman & Runge 1994).

Tett & Wilson (ibid.) could significantly improve a trophic microzooplankton model when protozoan grazers were allowed to switch between bacterial and phytoplankton diet. The functional response was formulated as Holling type II with a threshold. Thingstad et al. (ibid.) explained that a model of a mixotrophic gradient can be applied to protozoan ecology, albeit early observations from marine environments demonstrated low or insignificant phagotrophy among pigmented, i.e. autotroph flagellates. But recently it has been demonstrated (1) that a large number of flagellates are mixotrophic, (2) that mixotrophic are abundant and are important bacterivores. In the mixotroph-bacteria relationship, somewhat paradoxically, high predatory abilities will reduce the quantitative importance of predation in the mixotrophs nutrition. The reason is a strong reduction in prey abundance, allowing the mixotroph to survive as a photoautotrophic despite its low competitive ability taking advantage of then unexploited dissolved nutrients.

Grazing models

Grazing models intend to formulate mathematically the relationship between phytoplankton concentration and the grazing of zooplankton. Roughly two different approaches can be discerned. The first approach takes into account the measurement of decline of food in ambient water, the second approach measures gut contents and/or related physiological measures related to food already taken up. Methods taking into account the decline of food resources include e.g. the direct measurement of ambient chlorophyll and phytoplankton cell counting

with Coulter counters. Indirect measures are provided by the dilution method (Landry & Hassett 1982), where reduction/filtration rates are inferred from phytoplankton growth rates at different concentrations of predators, with the reference growth rate obtained at zero concentration for the predators. Physiological measures include egg production (Kiørboe et al. 1985; Kiørboe et al. 1988a), gut contents by gut fluorescence or short term radioactive labelling and concentrations of digestive enzymes in the gut. Baars and co-workers mainly developed the labelling technique (Baars & Fransz 1984; Baars & Oosterhuis 1984; Baars & Helling 1985; Baars & Oosterhuis 1985). The measurement of gut contents additionally requires an estimate of gut passage time to derive a rate estimate. For gadoid larvae an estimate of 4 h to clear the gut was given (Lough & Mountain 1996).

Depending on the approach chosen, for *Temora longicornis* 31% to 3% of body weight $C\ d^{-1}$ were ingested, whereas estimates for *Calanus finmarchicus* range between 40 to 90% during spring (pure numerical modelling, Radach et al. 1984) and *Calanus spp.* of 8 to 10% (lab measurements in Fransz et al. 1991a).

For most species the filtration rates saturate at higher food concentrations and thus can be described by means of a Michaelis-Menten-kinetic (Holling Type II response) (Carlotti et al. 2000):

$$I = I_m * (c/(c+a))$$

Where c is food concentration, a is half saturation constant, I is ingestion rate, I_m is maximum ingestion rate. Often this approximated by the Ivlev-formulation $I_m(1-e^{-bc})$. As has been experimentally proven, ingestion rates below a threshold value c' drops to zero, so that I becomes (Holling Type III response)

$$I = I_m * ((c-c')/(c+a))$$

Threshold values can be anticipated for copepod genera *Temora*, *Calanus* and small copepods in general, all in the range of $50\ \mu g\ C\ l^{-1}$ (Fransz et al. 1991a). For *Pseudocalanus* and *Centropages hamatus* no threshold values were found. The application of type III response functions is recommended.

Radach et al. (1984) apply a grazing algorithm to diurnal feeding by multiplying an ingestion function with a cosine function of time. Next to time size spectra and food particle quality and multiple preys have to be – but seldom are considered in grazing models. In the case of multiple prey, also switching has to be taken into account, i.e. to change they the preferred prey item after it declined to a certain lower concentration. Carlotti et al. (2000) provide examples have to deal with these aspects mathematically. However to find parameter values for the different preference levels appears to be difficult.

Predation models

The interception of prey and predator: The encounter rate (e) between prey and predator is essential for analysing the predatory relationship:

$$e = \sum \beta_i C$$

where β_i is the weighting factor (kernel) for the encounter processes of the prey item with concentration C . Visser & MacKenzie (1998) proposed a different encounter model based on the reactive distance of the predator, which first of all must recognise the prey. They could show that if the reactive distance of the predator is much smaller than the distance between two prey items, contact rates are smaller than suggested by the aforementioned encounter model.

Interception predators filter the water and get into contact with their prey by modest filtering with a flagellum, e.g. the dinoflagellate *Noctiluca scintillans* (Kiørboe & Titelman 1998). Due to their small size these species all have low Reynolds-numbers indicating that they strictly depend on the viscosity of the water. For these organisms encounter rate can be considered as an estimate of the clearance rate (Kiørboe & Titelman 1998). Several approaches have been made to describe the clearance rate: The approach by Fenchel (1984) take the dependence on both prey N and predator P into account:

$$\beta \sim 2\alpha r_N r_P v$$

where v is the local fluid velocity between N and P and r describes the different spherical sizes of the particles. Coagulation theory as the second approach considers a stronger role for the prey as the particle to meet and determines the contact rate solely by prey size and velocity difference:

$$\beta \sim 0.5\alpha r_N^2 U$$

where U is the velocity difference between the moving predator and its prey. For *N. scintillans* model calculations based on the coagulation model were insufficient as long as it was treated as a spherical predator. If actually a cylindrical model was applied taking into account that only the flagellum of the dinoflagellate is the active part to catch prey, realistic clearance rates were obtained (Kiørboe & Titelman 1998).

Cruisers and ambush-predators. Cruisers feed on slowly swimming prey, ambush-predators feed on fast swimming prey (Gerritsen & Strickler 1977).

Fish (age-0 and larvae as predators): Working with Leslie-projection matrices to model the development of the prey populations as well as predation on them (prey), whereas exponential growth, respiration and mortality terms are taken for fish larvae (predator). Results of the model are sensitive to changes of population parameters of both components. Test runs with ichthyoplankton data indicate that fish larvae can have a significant effect on zooplankton (copepods) (Bollens 1988). Leads to application of bioenergetics models, in which consumption is calculated on the basis of temperature dependent physiological functions (i.e.: Mehner 1996). Mehner (1996) compares two models: the Kitchell model - which is sensitive to incorrect allometric coefficients for C and R

$$C=(R+S) + (F+U) + (\Delta B);$$

$$\text{with } C=C_{\max} * P * f(T) \text{ and } C_{\max}=a * W^b; R=\alpha * W^\beta * f(T) * A; S=SDA * (C-F)$$

C=consumption; R=respiration; S=energy for specific dynamic action (SDA); F=egestion; U=excretion; ΔB =somatic growth; T=ambient temperature; W=weight of fish larvae; A=proportionality factor for activity

and the Vinberg model, which is sensitive to the activity multiplier A:

$$C=1.25*(A*SMR+\Delta B)$$

SMR = standard metabolic rate, taken from experimental data for different species and temperature.

The Vinberg model tends to overestimate the daily consumption and consumption rates of zooplankton by fish larvae (see very simple equation). Results indicate that daily rations of 0.2 - 0.3 (weight zooplankton / weight fish larvae d^{-1}) can be reached for herring larvae.

In a modelling study on the growth of North Sea herring, Heath et al. (1997) complain that no relevant data on mesozooplankton are available, since the CPR-samples operate with a too

large mesh size (first feeding larvae consume eggs and naupliar stages of copepods, later on copepodites are fed, here *Pseudocalanus* and *Temora* are preferred, *Acartia* and *Calanus* rejected). Heath *et al.* (1997) argue, that on a larger scale temperature accounts for most of the stock variability and therefore apply temperature dependent growth functions. Hence, zooplankton data are incorporated as a forcing function by means of temporally and spatially resolved CPR-data and not dynamically modelled, leading to unprecise results especially for the southern North Sea herring populations (Downs). Predation dynamics of fish on zooplankton modelled in Bryant *et al.* (1995).

Stoichiometric models

In marine ecology, stoichiometric models (models considering changes related to shifts in C:N:P relationships) are often considered in connection with the development of phytoplankton, especially the evolution of nuisance algal blooms. For zooplankton, a comparable relationship between nutrients in general and zooplankton community was hypothesised, as a follow up to a ratio-dependent change in phytoplankton community (Greve & Parsons 1977). This hypothesis was related to the food chain perspective in zooplankton ecology as presented by Landry (1977), which forecasts a bifurcate development under high (large diatoms and large copepods) and low (microphytoplankton and small mesozooplankton associated with gelatinous predators) nutrient conditions. Thus, due to the availability of larger zooplankton the high nutrient conditions are considered favourable for fish production. The hypothesis of Greve and Parsons (1977) suggests a similar bifurcation in relation to the changing phytoplankton community due to pollution effects and climate change. This hypothesis still warrants further evaluation. Generally, stoichiometric modelling in marine zooplankton ecology is less developed than in limnetic zooplankton ecology.

In limnetic environments stoichiometrically influences are presumed to be an important factor for zooplankton community development (references in Elser & Urabe 1999). The shift from the copepod *Acanthodiaptomus pacificus* (240:48:1 C:N:P) towards the cladocerans *Bosmina longirostris* (151:26:1) and *Daphnia similis* (80:14:1) likely is driven by the nutritional element ratio. For marine zooplankton elemental ratios were indirectly applied to determine the nutritional status of individuals. Anger & Nair (1979) applied C:N ratios to identify the degree of starvation in decapod larvae. In a bioenergetic model Anderson (1992) divided assimilated food into two groups: nitrogenous (proteins) and non-nitrogenous (carbohydrates, lipids), and made assumptions to determine how each group is utilised for growth and respiration. Zooplankton growth is predicted to be carbon-limited, in contrast to existing experimental evidence which suggests to some degree nitrogen limitation. Excretion of nitrogen increases with the nitrogen content of food, and quantities of food consumed. A dissolved organic matter carbon to nitrogen ratio of 10.2:1 was predicted below which bacteria remineralise nitrogen, and above which ammonium is taken up from the environment and used as a growth substrate (Anderson 1992). For zooplankton, further the ratio of excreted elements is regarded important for the recycling of nutrients. In limnetic environments in general, the cladocera have higher P:DW and P:C-ratios compared to copepods (see aforementioned example), while copepods have a higher N:P-ratio. This implies that different zooplankton species or taxa have different demands for P and N, and that a corresponding variable proportion of ingested minerals will be released. The ratio of recycled elements (C:N:P) thus depends not only on sestonic concentrations or ratios of elements, but also on the composition of the zooplankton community respiration and C:N and discussion (Hessen 1992). This context has been discussed up to present only for marine protozoa, but not for higher taxa (Caron & Goldman 1993; and references herein).

The role of silica was investigated by Turner *et al.* (1998). Marine diatoms require dissolved silicate to form an external shell, and their growth becomes Si-limited when the atomic ratio of silicate to dissolved inorganic nitrogen (Si:DIN) approaches 1:1, also known as the "Red-field ratio." Fundamental changes in the diatom-to-zooplankton-to-higher trophic level food web should occur when this ratio falls below 1:1 and the proportion of diatoms in the phyto-

plankton community is reduced. These predictions were investigated by using a variety of data from the Mississippi River continental shelf, a system in which the Si:DIN loading ratio has declined from around 3:1 to 1:1 during this century because of land-use practices in the watershed. It was suggested that, on this shelf, when the Si:DIN ratio in the river decreases to less than 1:1, then (i) copepod abundance changes from >75% to <30% of the total mesozooplankton, (ii) zooplankton faecal pellets become a minor component of the in situ primary production consumed, and (iii) bottom-water oxygen consumption rates become less dependent on relatively fast-sinking (diatom-rich) organic matter packaged mostly as zooplankton faecal pellets. This coastal ecosystem appears to be a pelagic food web dynamically poised to be either a food web composed of diatoms and copepods or one with potentially disruptive harmful algal blooms. The system is directed between these two ecosystem states by Mississippi River water quality, which is determined by land-use practices far inland.

Allometric models

The assumption of allometric relationships implies a general size dependence for biological processes. This contrasts the view of each species bearing specific features in terms of life-cycle strategy and individual adaptation to its ambient environment. Thus, where attempts have been undertaken to scale biological processes solely to size and/or weight (e.g. Kiørboe & Sabatini 1995; Hansen & Bjørnsen 1997; Blanco et al. 1998; Banse 1982; Huntley & Lopez 1992), the resulting average relationships must be regarded as features of an ideal though not existent species, and that in turn the real species deviate from this average scheme depending on individual requirements and adaptations. For example, the temperature dependence of copepod growth as postulated by Huntley and Lopez (1992) turns to be a temperature and weight specific relationship for which also spawning dynamics have to be considered (e.g. Hirst & Lampitt 1998). Thus, to the authors opinion applying allometric relationships to dynamics of larger ensembles of species is reasonable in terms of conducting experiments to test the sensitivity of models in relation to different scenarios rather than to expect its perfect simulation. In turn, the application of models with a multitude of state variables is not feasible (see below: Limits to expectations on 3-D modeling). Further reading on size-dependent models can be made in Carlotti et al. (2000).

Model comparison

A few authors attempted to apply different model constructions and philosophies to the same biological data set. Two examples are presented here, because the results are partially Tett and Wilson (2000) applied four types of models for the same mesocosm data set: (1) A Riley model in two different versions (see Appendix: Table 4, #4) which is a simple grazing model, (2) a microplankton model with grazing and recycling of nitrogen, (3) an autotroph-heterotroph model with Lotka-Volterra grazing impacts on several levels, (4) a microbial loop model with bacterial remineralisation. Models increase in complexity from (1) to (4).

3-D structured ecosystem models with zooplankton

Overview

The general frame of these models is

$$\frac{\delta n}{\delta t} + \nabla \cdot (nv) = \gamma,$$

with ∇ being the gradient operator describing advection and diffusion processes, γ being the sum of biological processes (Donaghay & Osborn 1997). This is consistent with slightly different formulations (Dubois 1976) i.e. using the summation function Σ instead of the inte-

gral function \int which allows more than one approach to the analysis of the problem, in this case a discrete approach with statistical interpretation of data.

Models exist with integration of diel/tidal effects to describe distribution of meroplankton larvae. It can be shown that larvae select tidal phases (Manuel & O'Dor 1997; Manuel et al. 1997). This behavioural aspect is not included in most models but certainly important for the North Sea dynamics.

The gradient operator, the diffusion (mixing) and advection term, can be expressed in terms of a diffusion coefficient (eddy diffusivity coefficient K in direction z) (Donaghay & Osborn 1997; Baird & Emsley 1999)

$$\frac{\delta n}{\delta t} = \frac{\delta}{\delta z} \left(K_n \frac{\delta n}{\delta z} \right) + \frac{dn}{dt} = K_n \frac{\delta^2 n}{\delta z^2} + \frac{dn}{dt}$$

Differences between models mostly occur according to representation of biological interactions (Appendix – Table 4).

Conclusion: Limits to expectations on 3-D modelling

(1) The models presented in the Appendix - Table are all different in the way the complexity of the zooplankton community is described and concerning the chosen mathematical tools. Fransz and Radach (in Fransz et al. 1991b) state that this variety is not surprising since all the models were made for different purposes, usually to elucidate the significance of a limited number of aspects of ecosystem structures and processes. In fact, the complexity in algorithms and amounts of data needed to simulate a complex community could be compared with the 'Schrödinger's equation' problem in physics: Although the solution in principle is achievable, capacity to do so is so immense that the task cannot be executed. As argued by other modellers like Nihoul in Tett & Wilson (2000) it is neither possible nor desirable to capture the entire complexity of marine pelagic ecosystems in one model. In addition to computational limitations, uncertainty in parameter values would propagate through simulations, making the results unreliable.

(2) However, a tentative evaluation can be made in a way that models which treat zooplankton as a bulk without resembling the species structure are less effective in reproducing near-reality conditions (e.g. model #6 in Appendix: Table 4). Whereas were multiple species with one target species (#8, #11) or multiple stages for one species (#9, #10) are considered in detail, the concordance with field conditions is relatively good. At present, models are still unable to resolve the complex pelagic interactions as to become general ecosystem models. Admittedly this is not only a failure on the model side, but also depends on a lack of published data for validation and development of models, since successful applications always require data sets for the situations being modelled. For the German zooplankton modellers this means that the only larger public data sources are the FLEX data and data from the English CPR as far as they have been published. In turn, data from the Helgoland Roads series mainly remain unpublished yet.

Population models

Population models are discussed separately because the focus in population models is concentrated on one species, for which complexity can be resolved much better than on the ecosystem level. Two different approaches can be seen for population models, using linear and non-linear models. Furthermore, population models do not implicitly need the input of physics and usually treat their objects in terms of numbers instead of carbon or nitrogen units, which are transferred to other part of the ecosystem. A detailed guide through population models is given in Carloti et al. (2000).

Some stage structured growth models are summarised in Table 9. As a prerequisite for stage structured models, rates for mortality etc. have to be anticipated constant within one stage otherwise the parameters (named a in Table 9) cannot be estimated. In contrast to stage structured models individual based models (IBM's), which simulate a multitude of individuals separately, can take account of individually specific changes in parameters between members of the same population.

Table 9 Selected Examples of zooplankton population models

Name/Type	Zooplankton term	ref. and comments
linear / Leslie-Matrix	Generally, $N_{i,t+1} = a_1 N_{i,t} + a_2 N_{i-1,t} - a_3 N_{i,t}$, which is $N_{t+1} = N_t a$ in matrix notation, where N is the number at stage i at time $t+1$, depending on those that stay, those that descend from stage $i-1$ and those that leave stage i .	(see Bollens 1988), model used to investigate predation effects of larval fishes.
non-linear / Ordinary Differential Equation	ODE do not anticipate conjoint changes of variables, i.e. the development of partial differential equations is dispensable. ODE do not calculate the size of the population at the next time step but the change of population at the current time step : $\dot{N} = \frac{dN}{dt} = aN$	(Rothschild et al. 1997), focus laid on optimisation procedures for parameter estimation.
non-linear / Manly model	$N_i(t) = M_i \int_{t-a}^t f_{i(x)} * mort \, dx$ with $N_i(t)$ numbers of stage i at day t , $f(x)$ is the normal probability function, $mort$ is the mortality function.	(Aksnes and Magesen 1988), the normal distribution function and the GAMMA function do not differ much for the bulk population. The normal distribution function yields comparably good results. Model applied to <i>Centropages</i> sp., <i>Temora</i> sp., <i>Pseudocalanus</i> sp. and <i>Paracalanus</i> sp for a Norwegian Fjord.
non-linear / Gamma Distribution Function	also applying a distribution function, i.e. the asymmetrical GAMMA function in a simplified modus : $\tau(t) = t^a e^{(-bt+c)}$, where τ is the moulting rate per day, a is the shape parameter and b the inverse scale parameter of the GAMMA-distribution.	(Souissi et al. 1997), a and b are food and temperature dependent and fitted to experimental data.

Individual based models

Individual based models (IBM) calculate the i -state for each individual instead of its number, which actually is 1 (Carlotti et al. 2000). The i -state describes the size, weight, metabolic state etc. of an individual, and depending on certain threshold values, changes in behaviour can be accomplished, i.e. moulting, spawning etc. The application of IBM's can be very promising where this individual approach can be linked to particle tracking models, i.e. Lagrangian models in oceanography. Individual effects within stage structured populations models were investigated by Carlotti & Nival (1992a+b). They could show that physiological rates change with age within stage. Individuals remaining for too long in one stage loose the capability to moult and must die.

Model based on statistics: Network analysis techniques

The reason to include this paragraph into this chapter is that the network analysis approach provides an alternative view to diversity in community ecology. Instead of analysing only numerical properties of components of a system, these are understood to be linked to each other by flows of matter, and that flows and components together determine the final compo-

ment structure of the system. The direction of the flows is indicated by the trophic status of each component. In this line a series of diversity indices of systems organisation have been developed (Kay et al. 1989). In contrast to this holistic perspective, species diversity measures only describe structure within the components of a system. Thus, the organisation indices deliver a better refined measure of the realised and ultimate status of a system, compared to species diversity indices. It shows, that the 'development capacity' has no counterpart in terms of species diversity.

Instruments to calculate the flows of matter are given by steady state models and inverse models. Both model types analyse a system of linear equations, in which biomass data and specific flow rates are used to calculate flows between components. Whereas the steady state models use a priori information on flows to calculate the indices, the inverse approach calculates flow parameters from existing biomass data by means of matrix algebra with inverse matrices (thereby 'inverse' approach) (for details see Ducklow et al. 1989; Vezina 1989). Recent literature on network analysis considering the ECOPATH software presents a mixing of both approaches in such a way, that already known rates are presented to the model and remaining blanks are calculated by the inverse method (Pauly and Christensen 1993; Monaco & Ulanowicz 1997; Niquil et al., 1998).

Table 10: Comparison of network and species diversity measures and the levels of systems performance to which they address. Since the network measures are based on information theory, the Shannon-Wiener index is compared to them. For reasons of comparisons, all indices have the logarithm based on 10. The maximum values are calculated for T_i and p being equal for all components. Network indices after Ulanowicz and Goldman (1988) and Kay et al. (1989).

Level of performance	Network diversity	Species diversity
realised in a system	$A = T \sum_i^n \sum_j^{n+2} \frac{T_{ij}}{T} \log \frac{T_{ij} T}{T_i T_j}$ <p>A = ascendancy, T_i = flows leaving i, T_j = flows reaching j, T_{ij} = flows leaving i and reaching j, T = total flows</p>	$H_{SW} = - \sum_{OS} p \ln p$ <p>OS = number of observed species</p>
ultimate value	$C = -T \sum \frac{T_i}{T} \log \frac{T_i}{T}$ <p>C = Development capacity</p>	
maximum value	$C_{max} = -T \log \frac{T_i}{T} = T \log OC$ <p>OC = no. of observed components</p>	$H_{max} = -\log p = -\log \frac{1}{OS}$ $= -\log 1 + \log OS = \log OS$

4. Process understanding – Ecosystem dynamics

4.1. Ecosystem dynamics

According to actual observations in the North Sea and Northeast Atlantic all components declined during recent decades in concert with phytoplankton, which points to a general food limitation. The removal by fishing of many predators from the North Sea did not increase the density of their prey. Most probably, the North Sea ecosystems are not ruled by a sequence of stabilised predator-prey interactions, but rather derive structure and stability from a seasonal sequence of food pulses enabling production, growth and survival of a limited number of individuals in each developmental stage of the many species. (Fransz et al. 1991b).

The relationship between copepods and primary production in the Oysterground (central North Sea) revealed that copepod distribution vertically followed Chl a in the water column (Fransz & Gieskes 1984). At that time hydromedusae were the most abundant predators. Summer production of copepods over Oysterground was estimated 9 g ADW m⁻².

For the northern North Sea near-Atlantic conditions can be anticipated. The follow-up of a microbial community after silicate depletion and sedimentation of the diatom bloom led to reduced flux to the ground and intensive recycling within the upper water column (Sieracki et al. 1993). Post-bloom microbial food webs can be anticipated to be general follow-ups (Thingstad et al. 1999), spatially resolved over the Doggerbank (Richardson et al. 1998). For phytoplankton development besides nutrient availability the structure of the water body is essential. The role of stratification for the blooming of *Ceratium* sp. was discussed by Dickson et al. (1992). *Ceratium* sp. is common during summer in the Kiel Bight (Smetacek et al. 1984). The latter discussed ratios (see Richardson et al.) and found that metazooplankton biomass (note meta- not copepods) was still high during summer with high meta- to protozooplankton-ratios. Similar data can be found in Fransz et al. (1998). It has to be noted, that these differences are probably due to averaging temporarily (Smetacek) or spatially (Fransz), whereas Richardson et al. resolved to patches and did not average anything at all.

Mixotrophic feeding strategies bring advantage under nutrient limitation, i.e. for members of the microbial food web (see also: Nygaard & Tobiesen 1996; Thingstad et al. 1996).

A bloom has possibly selflimiting properties, so that coagulation and the formation of marine snow by bloom members leads to the end of the bloom (Tiselius & Kuylenskierna 1996). After the bloom had then decreased by sedimentation, grazing by the heterotrophic dinoflagellate *Gyrodinium cf. spirale* increased exponentially after the peak of the bloom with maximum (temperature-adjusted) growth rates. After the rapid aggregation and sedimentation of the bloom, they were able to control any further growth of diatoms. Nitrate and silicate were never depleted, but phosphate may have been limiting by the end of the study period. The authors concluded that mass aggregation during a gale marked the end of the bloom, and that intense grazing by heterotrophic dinoflagellates prevented any subsequent increase of diatoms (Tiselius & Kuylenskierna 1996). Generally, phytoplankton aggregation and sedimentation as sink for blooms makes them unavailable to grazing (further reading in Hansen et al. 1995).

The role of diatom diet for copepods is equivocal: new experiments needed to really test toxicity hypothesis, otherwise the results are rather a case of insufficient nutrient supply and different grazing rates (Jonasdottir et al. 1998). So deleterious effects after several days of diatom feeding were found: accumulation of inhibitory compounds or exhausting stored essential substances (Chaudron et al. 1996). In a reply to Jonasdottir et al. the role of secondary metabolites especially aldehydes as inhibitory substances, anti-mitotic etc. was stressed (Iannora et al. 1999b). In turn, the general perception of diatom diet is that diatom based food chains lead to better condition of fish larvae than dinoflagellate-based food chains (St. John & Lund 1996). The diet component is known for lipid storage, and essential fatty acids are potentially limiting in the field for copepod hatching success (Pond et al. 1996).

4.2. Food web control

Preponderance of Predation: Ever since the last century and tentatively finalized in (Hardy 1924) for the herring predation is known as a major biological interaction in marine ecosystems. However, according to Parsons (1991), a lack of knowledge for trophodynamics of fish and jellyfish still prevents marine scientists from developing an appropriate view of top-down control in marine ecosystems. This discrepancy is due to a division of working fields (fisheries researchers vs. biological oceanographers), the focus on bottom-up control (Verity &

Smetacek 1996) and the mere visibility of the subject: You usually don't see what you're working at, except where scuba diving is applied.

Furthermore, it has to be recognized that predation (sensu feeding) usually occurs on more than one trophic level: Most marine species are omnivorous (as for *Nereis*) for zooplankton (e.g. Conley & Turner 1985), often including cannibalism. Omnivory helps stabilizing stressed ecosystems (Fagan 1997). The structuring effect of predation on the dynamics of estuarine copepods was shown by Lonsdale (1981) in the Chesapeake Bay. The spring occurring copepod *Scottolana canadensis* and the autumn occurring copepod *Oithona colcarva* could not develop summer populations due to predation by the copepod *Acartia tonsa* and the lobate ctenophore *Mnemiopsis leidyi*.

The predation risk is reduced with size: size of fish larvae reduces vulnerability to predation by coelenterates - large larvae (herring) may be immune to smaller predators, highest vulnerability for yolk-sac and early post-yolk-sac as well as starved larvae (Purcell 1985). In copepods the strategy to reduce predation risk is by reducing visibility: reduced grazing activity was found (Cieri & Stearns 1999). Data on visual thresholds by means of light intensity in Blaxter (1968), more references in Cieri and Stearns (1999).

Peculiarities: Copepods feeding on bacterioplankton (Boak & Goulder 1983) and ctenophores feeding on diatoms (Deason & Smayda 1982).

Trends for phyto-, zooplankton and fish: Cushing (1995) analysed long-term trends for North Sea herring and zooplankton. Residuals from the stock biomass-recruitment relationship were negatively correlated to zooplankton abundance, especially for *Pseudocalanus/Paracalanus*, for a time window 6 months after hatching. This indicates a relationship between late larvae and zooplankton. The relationship was persistent regardless of spatial aggregation of data. Cushing interpreted this negative relationship in the following way: Positive residuals were found at low food levels, as if the herring larvae had eaten the zooplankton, and negative residuals were found at high food levels, as if there were not enough larvae to reduce the plankton abundance. Taking into account the results for 6 more fish species, Cushing (1995) found positive as well as negative relationships to food, postulating a parabolic relationship between zooplankton concentration and fish recruitment residuals. Additionally, he argues that climate is an important factor.

Long-term changes for the Baltic herring were also related to zooplankton, i.e. food quality and taxonomic composition (Flinkbaum et al. 1998). Weight-at-age for the herring declined parallel to a change in zooplankton size spectrum, i.e. while smaller species increased. The food content of the smaller species was less so that ingestion and assimilation by the herring also declined.

4.3. Strategies

Forwarded maturation

For gelatinous zooplankton, scarcity of food reduces the growth rate, but also changes the energy allocation towards reproduction, which thus occurs at a smaller size than for well-fed medusae (Lucas et al. 1997; Ishii & Båmstedt 1998).

Size dependence of pelagic grazing and predation and the role of sedimentation

In early spring microzooplankton grazing on algae $> 5 \mu\text{m}$ is 0.23 d^{-1} , whereas in a bloom forming area over the doggerbank the rate increased to 0.5 d^{-1} . In algae $< 5 \mu\text{m}$ grazing rates were 0.25 d^{-1} to 0.31 d^{-1} . In summer grazing was 0.25 d^{-1} for $< 5 \mu\text{m}$ algae, whereas no results were obtained for algae $> 5 \mu\text{m}$ (Kuipers & Witte 1999). For mesozooplankton similar

relationships exist. In a cross-system comparison, the highest phytoplankton biomass, dominated by chain-forming diatoms, occurred in the oceanic zone associated with low primary production rates. Copepod feeding had a low effect on oceanic phytoplankton; up to 0.2% of carbon stock and <3% of carbon production was consumed daily (For comparable value see Razouls et al. 1998). In contrast, medium-sized and large copepods removed 3% of carbon stock and 12% of primary production daily near the coast, where phytoplankton were dominated by small flagellates in active growth. The highest variability in both plankton composition and ingestion rates was found in the shelf-break zone, probably due to displacements of the front. Copepods exerted a moderate predation pressure on phytoplankton in coastal waters. Meanwhile, the impact of copepods on the offshore bloom was negligible and the fate of the accumulated particulate carbon would be mostly determined by sedimentation and water dynamics (Barquero et al. 1998).

The vulnerability of fish larvae is also size-dependent: For slow swimming predators (*Aurelia aurita*) and small ciliates relationships between larval size and escape capability for fish larvae exist, whereas for larger predators (*Thysanoessa raschi*) the escape capability of the prey is of lesser importance.

Physiological state and vulnerability

Vulnerability of fish larvae is considerably increased, when larvae are starved (Bailey 1984). Food limited copepods can change their diurnal vertical migration behaviour and by this get susceptible to day-feeding predators (Huntley & Brooks 1982; Roman et al. 1988; Tande 1988; Calbet et al. 1999).

Density dependence

Both densities of predators and prey are important (Veer 1985). With high abundant predators, mostly consisting of *Clytia* sp. (Hydzoa = gelatinous predator), rations of up to 400% (potential consumption fourfold higher than abundance of nauplii, the preferred prey item) are reached in the central Georges Bank area, whereas in low predator but high copepod regions merely 5% (Madin et al. 1997).

Chemical selectivity and food quality

In the presence of phytotoxins grazing by omnivorous copepods is reduced. Species of the genera *Acartia*, *Eurytemora* and *Centropages* refused the uptake of *Alexandrium* sp. algae on basis of chemosensory detection of toxins cells prior to ingestion. *Centropages* and *Eurytemora* maintained daily rations due to increased and selective uptake of non-toxic prey, whereas *Acartia* reduced its daily ration (Teegarden 1999).

4.4. Temporal relationships

Temporal organization: Phasing

The relationship between phytoplankton and zooplankton can be seen as a transfer of matter. However, concepts of transfer efficiency are rather inappropriate to describe transfer processes, since pelagic material is fastly removed from the water column and lost (e.g. Brussard et al. 1996). In contrast, the onset of a bloom initiates a complementary development on higher trophic levels. This relationship has been described as phasing (Parsons 1989). The portion of phytoplankton captured by first order predators (herbivores) is then incorporated into recycling processes, which allow to distinguish between 'new' and 'regenerated' production in the water column. The regenerated production drives part of the microbial loop. Subsequent community stages then thrive on new and regenerated production, but not solely on the amount of matter initially transferred. Thus, communities can alternatively be described by

means of temporal relationships than by transfer of matter alone. This phenological perspective was applied by Greve and Reiners (1995). The role of phasing is indirectly mirrored in a publication by Verity and Smetacek (1996). They advocate that predation and resource availability act through morphologies and life history strategies of organisms to structure pelagic ecosystems, and hence to drive biogeochemical cycles.

Phasing: 2 weeks to transfer material (Blight et al. 1995). The observations were consistent with routes via a slowly cycling pool, such as polymeric organic material. This pool would function as a reservoir and result in microheterotrophic respiration persisting after the decline of photosynthesis, and causing a positive to negative temporal sequence in net community production.

Seasonal compensation

Microbial O₂ fluxes exhibited seasonal patterns linked to the seasonal cycle of water column stratification and mixing, with positive NCP during the spring, negative throughout the summer and close to zero in winter (Serret et al. 1999). This pattern was altered at coastal regions, where productive periods were linked to coastal upwelling, whereas in winter persistent net heterotrophy was measured, presumably in relation to increases in organic matter discharge of continental origin. The maintenance of summer heterotrophy in the region was based upon the consumption of the surplus of organic matter produced in spring. The uncoupling in the microbial auto- and heterotrophic metabolisms, based on the accumulation and delayed consumption of dissolved organic matter as a consequence of the processes controlling phytoplankton growth and microbial heterotrophic activity in temperate seas, would explain such a pattern. It is concluded that the seasonal compensation of production and respiration processes is a characteristic of the dynamics of the pelagic ecosystem, at least in coastal temperate seas. The implications of this conclusion are of great relevance for the interpretation of new production and the estimation of the trophic status of the ocean from direct measurements of plankton net production.

4.5. Physical-physiological impacts

Frontal zones

It is assumed that fronts concentrate plankton by means of convective currents and thus provide better feeding conditions. This is paralleled by an increase in phytoplankton and persistent chlorophyll maxima (van Haren & Joordens 1990).

Ice winters and copepod growth

In the icewinter 1995/96 a large bloom of *Coscinodiscus wailesii* and *C. concinnus* (cold adapted species) occurred. *C. concinnus* produced oil droplets during the bloom phase. Copepods feeding on *C. concinnus* showed incorporated droplets at the beginning of the plankton bloom, which is normally observed at the beginning of autumn. Correspondingly early reproduction took place in copepods. However, oil droplets in *C. concinnus* were not recorded for the whole area covered by the bloom but only in the southern German Bight (Günther & Nissel 1999).

Turbulence

In comparing two coastal ecosystems, Lucas *et al.* (1997) found a considerably higher transfer efficiency of 73% of secondary copepod production to the level of coelenterate predators in sheltered areas compared to 9 to 26% in tidally mixed areas. This supports the view of a dome-shaped relationship between turbulence and predation rate. Indications of increased zooplankton productivity after storm exist: However, the increase can be due to post-turbu-

lence effects such as upwelling and better nutrient supply, not necessarily related to increased contact rates (Kiørboe 1993).

Multiple stressors effects

Especially in estuaries: Trace metal effects are proportionally greater when nutrients are added. In turn, nutrient effects (eutrophication) can be masked under certain elevated trace metal concentrations. For copepods nutrient addition leads to increased density, whereas in trace metal plus nutrient treatment abundance is decreased (Breitburg et al. 1999).

4.6. Specific fluxes

copepod production

In the southern Kattegat three production events (measured by egg production) related to three plankton blooms (net phytoplankton !! with algae measured as chl $a > 11 \mu m$) were found but unrelated to nanoplankton, dinoflagellates, nauplii and ciliates (other components too dilute to contribute considerably), whereas egg production rates were related to these during the 'poor' periods of year (see ciliates below) - although on a low level of production. Annual biomass distribution was unimodal. The autumn production was masked by a decline in biomass due to high mortality (Kiørboe & Nielsen 1994).

Ciliate production

In the southern Kattegat ciliate temperature corrected growth rates always were near to maximum rates indicating no or low influence of food limitation for these bacterivorous species. Biomass distribution with two peaks in spring and autumn (latter smaller), whereas production is temperature dependent with a maximum in summer. Community clearance rates of copepods are sufficient to control ciliate abundance throughout the whole year (Nielsen & Kiørboe 1994).

Jellyfish predation

Daily rations for ephyrae can reach $> 100\%$ (Båmstedt et al. 1994), for medusae of *Aurelia aurita* for larger zooplankton and fish can reach 150 to 250%. An analysis of Baird & Ulano-wicz (1989) for the summer Chesapeake Bay indicates that 35% of zooplankton ingested carbon can be exported to other system compartments, of which 50% and another 17% are utilized by ctenophores and sea-nettles resp., whereas ca. 10% are utilized by fish and fish larvae. In the Wadden Sea ctenophores (*Pleurobrachia pileus*) and scyphomedusae (*Aurelia aurita*) are supposed to break down effectively low abundant populations of fish larvae by means of their high number (Veer 1985). This underlines the importance of considering jellyfish predation as an effective factor for at least the southern and central North Sea.

Benthic-pelagic coupling

Not only for the flux of matter (e.g. Graf 1992; faecal pellets, larvacean housings e.g. Hansen et al. 1996), but also for long-term parallel trends benthic-pelagic coupling is evident. CPR-series indicate a change in plankton community structure from the 70's to the 80's, which was followed by a parallel change in benthic community structure. In the plankton, central North Sea mesozooplankton has changed from being numerically dominated by holoplanktonic calanoid copepod species from 1958 to the late 1970s to a situation where pluteus larvae of echinoid and ophiuroid echinoderms have been more abundant than any single holoplanktonic species in the 1980s and early 1990s. The abundance of the echinoderm larvae as a proportion of the zooplankton taken in the samples has followed a continuous increasing trend over the Dogger Bank, but off the eastern coast of northern England and southern

Scotland the increase did not become obvious until the 1980s. This trend is consistent with reported increases in abundance of the macrobenthos. It is proposed that changes in the benthos have influenced the composition of the plankton. ABC-plots (abundance-biomass-comparison plots) for the benthos revealed an undisturbed benthic state in the 60's and early 70's, whereas after then a little disturbance was indicated for a benthic series in the Skagerrak (Austen et al. 1991). However, the results were not all statistically significant. This common ecosystem change at the end of the 70's was emphasized by Lindeboom et al. (1995). They suggested a change in nutrient dynamics from a benthic-orientated to a pelagic-orientated system.

Further aspects of benthic-pelagic coupling are diurnal feeding migrations of benthic-pelagic species, for example of mysids in coastal waters, and the deposition of resting eggs. Mero-plankton ascends from the benthos. However, although close relationships are apparent, a quantitative relationship between benthic population size and structure for example for mero-plankton populations has not been extensively studied. One attempt has been made for *Phoronis muelleri* in the German Bight (Niermann 1996) and small medusae (Werner 1961).

Case study : The Dogger Bank

The Dogger Bank serves as an example for a transition, i.e. frontal zone between isothermal and stratified zones.

- The tightly interlaced relationships between nutrients - microbial food web – mesozooplankton was shown (Richardson et al. 1998).
- In the shallow microbial part of the Dogger Bank the cyclopoid *Oithona similis* can contribute 70% of mesozooplankton biomass. Under stratified conditions small nanoflagellates dominate associated with bacteria and concentrated near the pycnocline.
- *Oithona* has a wide prey spectrum : Diatoms - faecal pellets - protozoans – mesozooplankton - fish larvae.
- Peaks of mesozooplankton occurred within frontal areas (tidal fronts across the Dogger Bank), also for the northern North Sea (Kiørboe et al. 1988b) and the eastern North Sea (Munk et al. 1995), larval fish populations tend to retain within these frontal areas.
- In the stratified area 15% of PP are utilized by copepods, whereas in the frontal zone up to 30% is utilized by copepods. Additionally, copepods need to utilize the protozooplankton to satisfy carbon demands (Nielsen et al. 1993).
- Fish larvae utilize 3-4% day⁻¹, replenished from zooplankton production with 3-7% day⁻¹. Another 3% are eaten by scyphomedusae and chaetognaths (Munk & Nielsen 1994). Decreasing zooplankton abundance might lead to competition among predators (Munk & Nielsen 1994).
- *Oithona similis* was correlated to protozooplankton, whereas *Paracalanus parvus* was correlated to chl a-maxima (Nielsen & Sabatini 1996).

4.7. Climatological forcing

Climatological forcing can affect the temporal organization, the advection of certain populations via currents or influence abundance directly.

Temporal organization

Climatic impacts can be seen in changes of developmental speed for certain key species, which then enter the food web earlier or later (see phasing). This can be for phytoplankton,

for which attempts have been made to relate the onset of the spring bloom to northerly winds (Dickson et al. 1988), the latter delaying the start of the spring bloom leading lower levels of zooplankton. They found a long-term increase in northerly wind component over the eastern North Atlantic and European Seaboard between 1950 and 1980 associated both with a decline of phytoplankton and zooplankton biomass in sea-areas around the British Isles, and with an increase in upwelling intensity along the Iberian west coast. They also found implications for certain pelagic fish stocks in the area. For gelatinous zooplankton, in models (Parson & Kessler 1987) as well as in time-series analysis (Heyen et al. 1998) temperature-dependent earlier development of ctenophore populations was found to be a key factor for the development of certain prey species (e.g. fish or mesozooplankton).

In a seasonal analysis for the copepod species *Acartia clausi* and *Pseudocalanus elongatus* the CPR-team (CPR-Survey Team 1992) showed that seasonal differentiation was greater in the period 1948-1974 than in the period after 1975, i.e. seasonal dynamics were uncorrelated in the former period reflecting their different biologies. *P. elongatus* is a relatively slow growing copepod. Its abundance are determined to a large extent by the range and size of the overwintering stocks. On the other hand, *A. clausi* achieves faster growth so that the summer populations can develop fast enough to gain independence from the overwintering stocks. A temperature increase in the second period after 1975 synchronised both the winter population size and summer growing success for the both species.

North Atlantic Oscillation index

Aebischer et al. (1990) traced the presumed effects of changes in westerly weather through four trophic levels of northwest European biota including CPR-zooplankton. For all trophic levels a parallel downward trend through the 70's and 80's was found. For crustacean zooplankton, recent publications indicate a relationship between NAOI and abundance of zooplankton by means of temperature and wind effects (Fromentin & Planque 1996; Planque & Fromentin 1996) as well as import of Atlantic water to the North Sea (Stephens et al. 1998). For the relationship between *Calanus finmarchicus* and the NAOI a wind-based mixing hypothesis was developed to explain the data (Fromentin & Planque 1996). An alternative hypothesis on the connection between *C. finmarchicus* and climate was then further investigated by Backhaus et al. (1994). They assumed that the North Sea resident standing stock over winter was not large enough to sufficiently build up the North Sea stock of the successive year, so that the populations dynamics depended upon invaders from deeper shelf edge water. Model calculations and field work were effective to prove this hypothesis. A high degree of congruence with CPR-data was reached (Heath et al. 1997b). Their work provides a meaningful mechanism for the fluctuations of the copepods abundance in relation to climate since the overwintering capacity and thus the number of invaders depends on the thickness of the overwintering water layer which in turn depends on the general circulation pattern in the North Atlantic which in turn is connected on the atmospheric regime.

Gulf Stream index (GSI)

The Gulf Stream Index (Taylor et al. 1992; Taylor 1995; Taylor 1996) describes the departure of the Gulf Stream from the North American coast. According to Taylor (1996) the direct effect of GSI works through a teleconnection, which reduces the number of storm tracks over north western Europe. Furthermore, the GSI probably also influences the hydrographical system of the whole North Atlantic with a reasonable time lag of one year for the North Sea. However, these influences do not affect the performance of zooplankton community states. For a Northumberland series on zooplankton, Frid & Huliselan (1996) found a significant negative correlation for zooplankton and GSI, the same as for the limnetic Lake Windermere data series (in Frid & Huliselan 1996). It was suggested that the reduction of storm impact leads to an earlier onset of the spring bloom, so that the match between phyto- and zooplankton is decreased.

Planque and Taylor (1998) emphasized the dual regime of NAOI and GSI who both follow different pathways to affect plankton dynamics. This view can be supported in the analysis presented here, where the impacts of both effectors were analyzed simultaneously and the different pathways became evident.

Advection

Further aspects of advection besides the possible impact on the dynamics of *C. finmarchicus* can be seen due to advection of warm southerly waters into the southern North Sea through the English Channel and the intrusion of Lusitanian species (e.g. doliolids, see Lindley et al. 1990; e.g. siphonophores, see Greve 1994). In turn, cold periods were characterised by the presence of Atlantic indicator species, e.g. the copepods *Metridia lucens* and *Corycaeus anglicus* and the chaetognath *Sagitta elegans* (CPR-Survey Team 1992; Frid & Huliselan 1996).

Direct effects

A relationship between the size of the overwintering stocks of zooplankton and the winter temperatures was suggested by Colebrook (1986a). The size of the overwintering stocks is a key factor for the development of the subsequent summer populations. Furthermore, a strong link between phytoplankton production and zooplankton grazing was implied, with grazing fuelling production by means of recycled inorganic nutrients.

Element turnover in ecosystems

In pelagic systems the elemental turnover is more rapid than in benthic systems, indicating high respiration for microzooplankton and high potential of mineralization by means of applying the Redfield –ratio for the O:C:N relationship (Fourqurean et al. 1997), esp. for the North Sea (Iriarte et al. 1991). Under a changed temperature regime this unbalance can increase, which approaches the idea expressed by Lindeboom et al. (1995) of a more intensified pelagic turnover since 1979. Additionally, under a changing nutrient regime potential scarcity of food can reduce the growth rate for medusae, e.g. *Aurelia aurita*, but also can change the energy allocation towards earlier reproduction, which then occurs at a smaller size than for well-fed medusae (Ishii & Båmstedt 1998).

4.8. Managemental implications

Methods for the study of effects of habitat fragmentation were introduced by Dettki et al. (1988). Although applied to terrestrial lichens, applications in the course of this paper can presumably be promising for marine habitats, too. Basically, their analysis investigates whether a species' response to fragmentation only relates to habitat loss or also bears true fragmentation effects. In the case of the random sample hypothesis, a reduction by half for habitat would result in reduction by half for the population. A steeper slope, i.e. more sharp decrease of population size, would indicate a decrease due to fragmentation effects. These aspects could be of great managemental importance for meroplanktic populations and benthic-pelagic coupling under the aspect of undisturbed benthic habitat.

Actually, habitat protection is one tool of marine ecosystem management (Fogarty & Murawski 1998). For groundfish and lobsters habitat protection is already achieved. In the Wadden Sea preference of enclosed areas is discussed and being implemented. Tools for site selection are available (e.g. Fogarty & Murawski 1998).

However, prior to any kind of ecosystem management assessment of the status is indispensable. At present, no sound indicators for ecosystem state or indices have been developed for zooplankton (for possible applications see Done & Reichelt 1998).

5. Instruments and Methods

5.1 Zooplankton abundance and species identification

Historical background

Ships, nets and microscopes - these three terms outline the frame which influenced our understanding of zooplankton in the past from the beginning of the 20th century until the seventies. And these terms certainly biased our understanding in such a way, that at that time – and even nowadays - we still have no proper imagination of what is going on in the sea.

Data were only collected there where a ship made its course, ambient conditions left or right from the course were not recognised. This is a real disadvantage in an environment that depicts small scale phenomena such as patches, eddies and gyres over and over. Second sampling with plankton nets was the standard protocol for nearly most of the past century. As Reeve (1988) stated, the reality of the samples was the reality of the net designs. Nets were usually towed in a manner which gave ample warning to all but the old and infirm that they should move out of the way. Only the tiniest individual, whose absolute ability to move through the water is severely limited, could be captured with any degree of certainty. Unfortunately, the capture success itself is limited by the mesh size used, so that usually this tiny individual was first caught, but afterwards swept through the net again, and not recognised at all. Third, even if the very juvenile stages were successfully caught, they usually were hard to distinguish with the most common technique, the microscope, for several reasons. At the one side, they probably all looked very much alike. Next, due to netsampling, most of the sample material usually is awfully distorted and hard to describe on the basis of their morphology, especially for soft-bodied individuals. Last but not least, there is still no adequate taxonomic literature covering the whole zooplankton spectrum. Although this is not necessarily the case for the taxonomic-morphological description of adult organisms, for the juvenile stages (e.g. nauplii and copepodite stages of copepods) the necessary identification is quite sparse and incomplete.

Traditional methods

Marine zooplankton research has been rich and diverse at least over the last three or four decades. While earliest studies had more taxonomic and morphologic character as in describing the species found in the investigated sea areas, later papers dealt with the horizontal and vertical distribution of these organisms involving abiotic (e.g. temperature, salinity, currents) and biotic (e.g. food supply, predation stress) environmental parameters. Meanwhile approximately 1300 papers investigate the standing stock and the variability of zooplankton in the North Sea and adjacent areas. It must be remarked here, however, that the methods of investigation have usually been highly variable, which means that the comparability of the various results is only possible to a limited degree. The Continuous Plankton Recorder Surveys represent one of the very few standardised collection methods which have been used area wide for over fifty years and whose results can be used for long-term trends. Nevertheless, this method also presents many points worthy of criticism. Its limits need to be clearly defined and published so that the data is not interpreted unsuitably (see chapter: Stock data; methods).

Nevertheless, advancements in technology have enabled major accomplishments in marine zooplankton research (life cycles/history, production; organism level research, modeling) over the last years. New culturing methods were developed which enhanced the lab measurements of feeding, excretion, respiration, egg production and growth rates to a great extent. To evaluate the importance of nutritional substances (e.g. fatty acids, dissolved organic matter) also new methods were applied. Biochemical methodologies, gut pigment analysis and fertility indices were developed and applied both in the field and the laboratory. Food web relationships have been elucidated with the help of immunological probes, which identified

species composition in the stomach of zooplankters. Inverse modeling gave some insights to mortality rates in the field. New molecular biological methods helped to differentiate between morphologically similar species and life stages and thus gave better information on the species community structure.

The application of cinematography and video microscopy gave new insights into the behaviour of individuals. Zooplankton organisms turned out to be not just passive filter feeders but most have the possibility to accept or reject individual food particles. Swimming and mating were found to be highly complex behaviours. Advances in computer technology and modeling gave progress in the development of more realistic coupled biological/physical models. Recent concentration based models integrate among vertical migration, population growth and physical transport in describing plankton distribution. Individual-based model approaches include organism processes into population dynamics. At the moment these models are coupled to physical transport models. A lot of modeling research over the last years has focused on micro scale turbulence affecting encounter rates (Butman & Davis 1998).

Only during the last two or three decades explorations were made more process orientated. Some studies used theoretical approaches lent from terrestrial ecology or from results of limnic investigations as a conceptual framework to explain e.g. species distribution patterns and patchiness. Besides integrative concepts as trophodynamic theory involving energy transfer in the food web were applied to analyse marine zooplankton dynamics.

5.2. New methods in marine zooplanktology

Taxonomic identification: distribution and abundance – with a special emphasis on the North Sea

Introduction, question

Society places at least two major expectations on marine zooplanktology today. The first topic “zooplankton as food for fish” was already part of the agenda of ICES at its commencement in 1900 (Gran and Ogilvie, 1915). The global human population has been increasing dramatically over the past 100 years and so has our demand for food including marine food resources especially fish. Therefore, gaining knowledge about the availability of zooplankton as a food resource for fish is still a pressing issue. Zooplankton populations develop and parish much faster than we are able to produce numbers that describe what happens. Thus, we need new, fast survey methods.

The second expectation of society is to provide knowledge about “global climate change”. This topic is not specific to zooplanktology of course. Society asks all natural sciences to provide analysis as to where we are now and where we might go in the future. Time is running out. Therefore, funding agencies give money to fields of science that promise fast answers. However, zooplankton ecology is immensely complex and zooplankton research is laborious and slow. Consequentially, zooplanktology has been trailing behind while satellite surveys and rapid in-situ measurements have pushed physical and chemical oceanography and to some extend phytoplanktology to the forefront of international marine research programs (Dickey 1991, 2000). Zooplanktology has not been able to provide the huge amounts of data necessary to develop, test and finally run ocean biology models (Culverhouse et al., 1996). Thus developing rapid survey methods comparable to other ocean sciences is of utmost importance.

In addition to the specific expectations - applied science - of the public, zooplanktologists study all aspects - basic science - of marine zooplankton. The scarcity of data and huge time lag involved (months to years) until survey data become available have made it difficult to distinguish signal from noise respectively the specific from the common. In turn general con-

cepts remain vague. The basic problem is the difference in scale between the organisms (μm to cm) and their environment (m to 1000's of km). Thus, only automatic, in-situ devices will be able to provide the data needed.

In order to amend the situation zooplanktologists have in fact been developing new methods throughout the 20th century (table 1). The question to be answered in this chapter is whether the latest developments in the acoustic, optic and genetic field will be able to substitute and even be better than the old methods in the foreseeable future or not. Technical development is one of the grand challenges of zooplanktology.

History

Taxonomic identification and biogeographic surveys have laid the groundwork for research in the field of marine zooplanktology (Schulze et al., 1992) such as physiology, ecology, and biodiversity issues.

Traditionally research programs have been utilizing a variety of nets, pumps, bottles, and traps to take zooplankton samples. Nets can be distinguished as single, double, multiple, and continuous nets (plankton recorder). Some nets have opening and/or closing mechanisms. Nets can achieve high sample volumes. Pumps are either onboard or submersible and the seawater is filtered through a net, too. With pumps, spatial resolution can be high (**Donaghay et al., 1992**). **Bottles contain only small sample volumes but treat organisms** much more gently than either nets or pumps. Traps collect sinking detritus and marine snow including dead zooplankton and fecal pellets. Nets have been taking a lead role over pumps, bottles and traps for meso- and macrozooplankton. The new ICES zooplankton methodology manual contains detailed technical descriptions of these methods (Harris et al. 2000b).

Early investigations in the 19th century concentrated on qualitative descriptions of samples only. Nevertheless, researchers did use some relative terms to state the abundance of taxonomic categories present in the samples thus indicating the need for quantitative information even back then. Eventually researchers started with counting samples under the microscope (Müller, 1846; Hensen, 1887).

Practical considerations have been determining counting strategies. Since manual labor involved has been the main limiting-factor, zooplanktologists were coming up with ideas to automate the process at the beginning of the 20th century already (table 11). Scientists have been spinning down plankton samples to fractionate the organisms by density or have been using a combination of nets with different mesh sizes to divide the samples by particle size. Later the Coulter Counter originally developed to count red blood cells, found use to automatically count particles within several size categories. But there are technical problems involved with organisms that are not smooth, round and separate from each other like red blood cells and thus the utility of the Coulter Counter for zooplankton has always been limited. None of these methods has been able to substitute manual taxonomic identification and enumeration of zooplankton by highly trained people.

Current situation North Sea field research

A zooplankton literature database with app. 7800 records (Krause, per. com.) contained about 1300 papers dealing with North Sea field studies. A thorough keyword search revealed that none of those studies implemented any new optical, acoustic, or genetic methods for zooplankton abundance measurements or species identification. Thus producing such data depends on massive manual labor up to this day.

Current situation of scientists

Through the grant selection, researchers compete not only for excellence but also against each other. Zooplanktologists feel that the difficulty in obtaining data in combination with the uncertainty of financial resources might force many of them to cling to their own data and use ideas of others in order to stay ahead of competitors. There have been attempts to remedy

<ul style="list-style-type: none"> • Method • Raw data • Dimension of zooplankton organism* 		References	
<ul style="list-style-type: none"> • centrifuge (separation of densities) • density groups • 0D 		Gran & Ogilvie, 1915	
<ul style="list-style-type: none"> • Coulter Counter (measurement of conductivity) • abundance, size classes • 1D 		Coulter, 1956 Maddux & Kanwisher, 1965 Sheldon et al., 1972	Boyd, 1973 Herman & Dauphinee, 1980 Herman & Mitchell, 1981
<ul style="list-style-type: none"> • silhouettes, photo sensor, scattered light • distribution, abundance, size classes • 1D bis 2D 		Parrish et al., 1960 Mitson, 1963 Cooke et al., 1970 Ortner et al., 1979, 1981 Lough & Potter, 1983 Jeffries et al., 1984 Lutter, 1987	Herman, 1988, 1992 Sprules et al., 1992 Freimann, 1993 Vessey, 1996 Zavala-Hamz et al., 1996 Beaulieu et al., 1999 Samson et al., 2000
<ul style="list-style-type: none"> • video pictures, photos • distribution, abundance, size classes, coarse taxa • 2D 		Liacopoulos, 1983 Latrous, 1984 Rolke & Lenz, 1984 Rolke, 1987 Berman et al., 1990 Froese et al., 1990 Paffenhöfer et al., 1991 Welsch et al. 1991	Bergström et al., 1992 Davis et al., 1992 Schulze et al., 1992a, b Simpson et al., 1992 Culverhouse et al., 1994 Williams et al., 1994 Petersen, 1996 Davis et al., 1996 Benfield et al., 1996
<ul style="list-style-type: none"> • holography • small scaled distribution, density in a patch, sizes or size classes, coarse taxa • 3D (from one direction) 		Krantz et al., 1996 Foster & Watson, 1997	Hobson et al., 1997 Watson et al., 1998
<ul style="list-style-type: none"> • Sonar (underwater acoustics) • biomass, distribution, maximum diameter • 1D 		Machlup, 1952 Beamish, 1971 Samovol'kin, 1974 Greenlaw, 1977, 1979 Pieper, 1979 Artemov, 1983 Greenlaw & Johnson, 1983 Kristensen & Dalen, 1986	Holliday et al., 1989 Greene & Wiebe, 1990 Pieper et al., 1990 Smith et al., 1992 Holliday & Pieper, 1995 Greene et al., 1991, 1994, 1996, 1998a,b,c David et al., 1999
<ul style="list-style-type: none"> • gene tests • screening of a few taxa • 0D 		Miller, 1976 Bucklin et al., 1989 Olson & Hood, 1994	
<ul style="list-style-type: none"> • combinations (optics, acoustics) • biomass, distribution, abundance, size, coarse taxa, screening of conspicuous taxa • 2D 		Schröder, 1961 Johnson et al., 1983	Benfield et al., 1998 Culverhouse & Williams, 2000
reviews		UNESCO, 1968 Schulze et al., 1992 GLOBEC, 1993	Freimann, 1993 Culverhouse et al., 1996 Harris et al. 2000b

Table 11: Partial automation of taxonomic identification/sorting of zooplankton.

this situation in the past. However, creativity is at the heart of science and thus scientists have circumvented any measures taken.

Zooplanktologists divide into many small groups. The economic pressure on such small units is high and their knowledge base limited, just as their ability to lobby for themselves. Project-to-project survival entangles them and leads to an adverse scientific climate. If zooplanktology is to fulfill the expectations placed on it by society it will take an international concerted effort to build the research base that will allow researchers and their ideas to flourish.

Past reviews

The literature contains mainly comparisons between two or three zooplankton sampling/counting methods each. There are three general reviews on non-traditional methods: one in 1968 (UNESCO), another in 1992 (Schulze et al.) and one in 1993 (GLOBEC) resulting from a workshop. Schulze et al. (1992) conclude that studies of zooplankton behavior are already profiting from new in-situ instruments. In contrast, zooplankton surveys are still largely dependent on semi-automatic catch and manual species identification/counting. Only bulk measurements (particle counts, sizing) with the OPC (optical plankton counter) are reliable and easy to handle.

Science Criteria

In order to tackle the question of this chapter (see above) in a systematic way, the first step should be to gain an overview by which criteria old and new zooplankton identification and abundance methods can be evaluated. Table 12 is a list of criteria for comparison. Please note "samples taken" is different from "samples analyzed". The order of appearance in the table is of no avail.

Producing data always takes a certain amount of work. Optimizing the process for one criterion usually encompasses worsening the level of another. For example if we want to decrease statistical error, we might choose to increase the total sample size but on the down side, this raises workload and time needed to complete the project. Generally, the goal is to balance advantages and disadvantages for each specific scientific question. For traditional zooplankton identification and enumeration methods, this it is very difficult. Usually workload and time exceed project capabilities, including human endurance of boredom before statistical validity of the data reaches a reliable level.

Therefore, how do we get more and better data without increasing workload? We do not. The solution industrial culture usually attempts is to shift workload from manual labor to automation in order to save time and peoples nerves in spite of high workloads. The value of automation depends on the circumstances; it is not intrinsically good or bad. In this case, the drawbacks are higher costs and sophistication necessary but it is the only means to eventually increase productivity beyond human limitations.

Taxonomic detail and taxonomic categories

Evaluating old and new methods, taxonomic ability is the crucial factor to look at. If new methods provide too little information, it will be meaningless whether they do so easily and unbiased or not. Schulze et al. (1992) state that the ultimate success of video instruments is largely dependent on the limitations of image processing. Taxonomic information is described by two criteria taxonomic detail and taxonomic categories (table 12).

How can we compare taxonomic ability of different methods? We need to quantify the parameters. The number of taxonomic categories can be used directly but there seems to be no index for taxonomic detail in the literature. Therefore, for the purpose of this review here is a newly defined "level of identification" (lid) index (table 13).

Criteria	Explanation	Better	Worse
time	duration of completing one project (i.e. 50 to 500 samples), e.g. 1 hour, 6 months, 3 years	short	long
temporal resolution	number of samples taken per unit time at one station, e.g. 4 sample/day, 1sample/month, 2sample/season	high	low
temporal continuity	ability to repeat (regularly) sampling over time, e.g. a time series over the past 10 years	long	short
synoptic ability	taking samples at different places (a, b) at the same time t, therefore $t_a = t_b$ and $\Delta t = t_a - t_b $, e.g. by using several ships or steaming between sampling	$\Delta t=0$	$\Delta t>0$
speed = duration ⁻¹	number of samples taken and analyzed per unit time, e.g. 100 samples / 1 year	high	low
single sample size	volume or number of organisms of one sample, e.g. 2 ml, 1 l, 10 l, 100 m ³ , or 3 organisms, 100 organ., 2000 organ.	depends	
total sample size	total volume of water sampled or numbers of organisms at one station, e.g. 10 l at 5 depths = 50 l	large	small
minimum spatial resolution	small to large scale, e.g. μm to cm to km	small	large
maximum spatial resolution	small to large scale e.g. m to km to global	large	small
taxonomic detail	amount of information per organism, e.g. biomass, numbers, groups, genus, species, stage, sex	fine	coarse
taxonomic categories	number of "parameters" looked at, e.g. 5 key species, 200 species/stage/sex overview	many	few
statistical error	error evolving from the fact that we count a sample and not the whole ocean, sources of error: e.g. sample size vs. water column volume, patchiness, sub sampling	low	high
mechanical error	error evolving from the practical implementation, sources of error: e.g. avoidance, clogging, turbulence, mesh size, water pressure, towing speed, total mesh area, porosity, mouth opening, shape of net, measuring volume sampled, dividing samples, water disturbance during counting, for the LHPR: tightly/loosely closed housing	low	high
human error	error evolving from the people implementing the sampling, sources of error: e.g. mood, boredom through repetitive work, differences between people, overlooking organisms, misidentification	low	high
artefacts	changing what we measure, e.g. gelatinous species lost, distortion of body shape, changes in body volume, fragility of aggregates, etc.	few	many
workload	total effort required for sampling and analysis, involves very different aspects, e.g. 2 years of work for 3 people in the laboratory, work of other people supplying goods and services to the laboratory, educational training, etc.	small	high
automation	% machine labor of workload	depends	
manual labor	% human labor of workload	little	high
costs	money in Euro/Dollar, environmental cost of research chemicals, etc.	low	high
sophistication	level and amount of technical/scientific knowledge required	low	high
reliability vs. chance	well known methods will give results for sure vs. new methods hold possibility to overcome former shortcomings	depends	
comparability	the value of most data depends on whether they can be related to other data	high	low
development, investment needed	the less known a method is the more project resources are used up (relative)	low	High

Table 12: Criteria for comparison of zooplankton identification/sorting methods.

data	level of identification (lid)	
	descriptive value	index value
biomass	bulk measurement	0
numbers with size categories	number	0.5
group	e.g. copepods, amphipods, fish larvae	1
genus	e.g. <i>Calanus</i> , <i>Acartia</i>	2
species	e.g. <i>Calanus finmarchicus</i>	3
stages, sex	for each additional "degree of freedom" e.g. copepod nauplii = 1 (group) + 1 (stage) = 2 e.g. <i>Acartia clausi</i> f./m. = 3 (species) + 1 (sex) = 4	+1

Table 13: definition of level of identification (lid)

Biomass was given an lid-index value of zero because as Henderson and Steele (1995) have stated, it has been apparent for some time that biomass data are inefficient measures of zooplankton.

Zooplankton sampling was reviewed in 41 North Sea field study papers selected by chance. They cover all North Sea ICES boxes (Fig. 20) and many decades of the 20th century (Fig. 21).

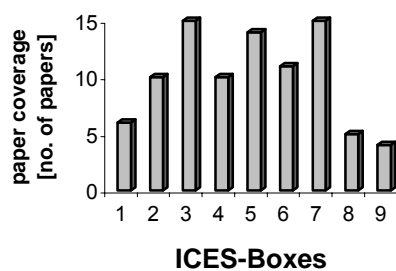


Fig. 20

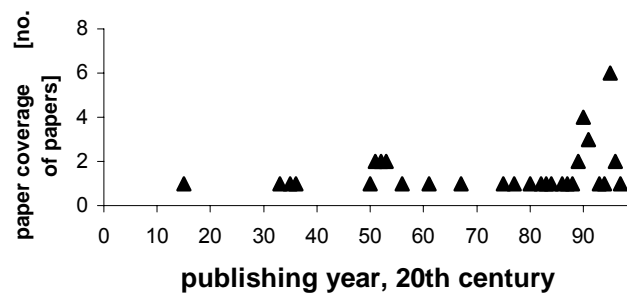


Fig. 21

Five papers took zooplankton samples for experiments only and two reported biomass values. All remaining 34 papers have "levels of identification" (table 13) larger than zero. Figure 22 displays "number of taxonomic categories" versus the "level of identification" index.

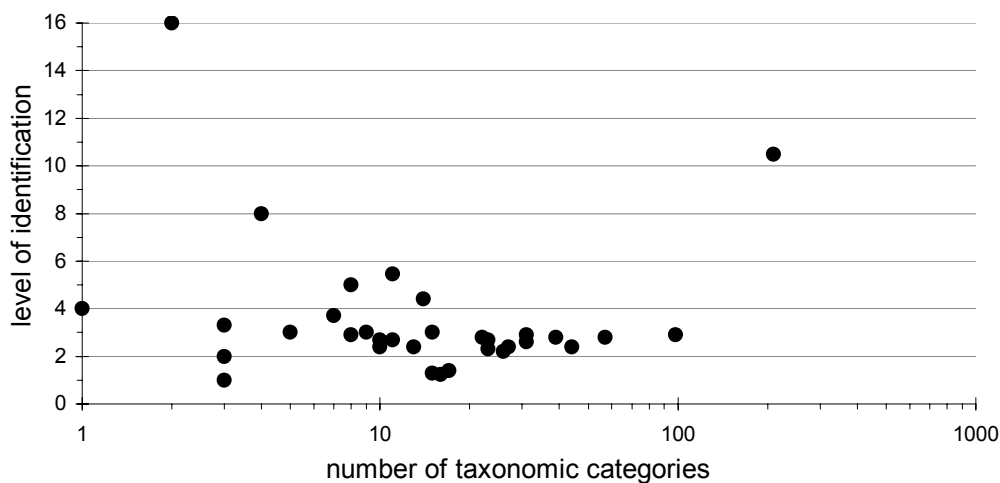


Fig. 22: traditional sampling/counting in 34 North Sea field study papers

As mentioned above none of the 1300 North Sea field study papers contained in the literature database (Krause pers. com.) used any of the new optical, acoustic, or genetic methods for identifying and counting zooplankton. In order to establish the level of identification and

	instrument	lid-index	Reference	application, explanation	categories
Silhouette	Optical Plankton Counter (OPC)	0.5	Herman 1988, 1992 Sprules et al. (1992) Vessey (1996) Beaulieu et al. (1999)	250 µm to app. 20 mm; automatic, real-time analysis	several size groups
	Shadow Image Particle Profile Evaluation Recorder	1 (goal: 2)	Center for Ocean Technology, St. Petersburg, Florida, USA and Department of Marine Science, University of South Florida, USA	double Silhouette recording; automatic image analysis; depends on characteristic outline of body; in development	Calanoid copepod, Cressis sp. Pteropod, Sgitta sp. Chaetognath, larvacea, salp, hydromedusae
3d	holography	1	Hamner et al, (1988) Foster & Watson (1997) Chaldividan et al. (1998)	in development	
genetic	Genetic markers	3	Miller 1976 Bucklin et al. (1989) Olson and Hood (1994)	Screening for specific species; only few markers available	1 category per marker
acoustic	acoustic devices	0.5	Pieper et al. (1990) Smith et al. (1992) Greene et al. (1998)	Influenced by tissue and size	ranges of energy reflected
video	Ichthyoplankton Recorder (towed)	1	Petersen (1996), HYTEC, Montpellier, France	automatic image analysis not satisfying; lid = 2 to 3 by manual image analysis; developed since: 1989	Fish eggs, fish larvae, prey, organisms 0.5 to 20 mm
	Zooplankton Profiler (vertical hauls)	1	Petersen (1996), HYTEC, Montpellier, France	automatic image analysis not satisfying; lid = 2 to 3 by manual image analysis; developed since: 1989	organisms 0.1 to 3 mm
	Video Plankton Recorder (VPR)	1 (semi-automatic image analysis)	Schulze et al. (1992) Davis et al. (1992) Benfield et al. (1998) Davis et al. (1996) Paffenhöfer et al. (1991)	cladocerans, copepods, chaetognaths, euphausiids, fish larvae, insect larvae, pteropods; lid = 2 by manual image analysis	up to 10 groups at 90% accuracy
combinaton	computational intelligence sensor (optic, acoustic)	2	Culverhouse and Williams (2000)	in development other researchers do separate video and acoustic measurements of the same water column; this sensor does video and acoustic measurements at once	

Table 14: non-traditional survey instruments

number of categories of these new methods additional papers from other areas of the world and general methods papers had to be used (Tab. 14).

Results

The new techniques generally only allow for the low level of identification of one or as in the case of genetic markers are restricted in the number of categories. Thus, the new methods can only substitute traditional zooplankton studies that suffice with this coarse information.

For the traditional North Sea field studies the lowest level of identification was one. It occurred in a study (Schaumann et al. 1988) about red tide exclusion of herbivorous species. The number of categories was also low (3 categories). The study mainly used gut pigment analysis, thus circumventing the problem by using phytoplankton in order to get information about zooplankton.

The second lowest level of identification of 1.3 with medium number of 15 categories was found in a study (George 1995) about zooplankton distribution during the tidal cycle. A lid of 1.25 was found in a study (Gran & Ogilvie 1915) about the distribution of zooplankton in space on a large scale for 16 categories. A lid of 1.4 in 17 categories was found in a study (George 1996) about zooplankton distribution during the seasonal cycle. A lid of two in only three categories was found in a study (Glover & Pope 1956) about vertical zooplankton distribution on a diurnal time scale (relative abundance only). A lid of 2.2 in 26 categories was found in a large-scale biogeographic survey (relative abundance only) (RAE 1951).

The highest levels of identification were found in studies (Fransz 1975; Escaravage & Soetaert 1995) dealing with ecological questions of carbon-flux, e.g. of key species or relating primary production to calanoid copepod production. The lowest lid of an ecological study was 2.3 dealing with top-down control of copepods.

Conclusion

As Schmidt et al. (1992) stated the OPC is successfully used to count particle concentrations and measure size equivalents (area of shadow). Taxonomic identification needs to be done separately. In cases of few dominant species that occupy different size categories OPC counts can be related to key species by accompanying net hauls.

Acoustic measurements are still struggling to convert signals into biomass or concentrations. The advantage is a large sampling volume, but the better the resolution the smaller the volume sampled.

Genetic methods are well suited for screening purposes but not for surveys. In surveys, unexpected species might be encountered. These would not show up by the use of genetic markers, since no marker specific to them would have been used in sample treatment.

The first generation of new optic-devices with automated counting/identification have lid's of one, because mainly they rely on analysis of organism outlines (Schulze et al., 1992). This low taxonomic information level allows only for general distribution measurements. In contrast, current ecological questions linking zooplankton species to primary production and carnivorous predators need high levels of identification (Henderson and Steele, 1995). When measuring and modeling fluxes of carbon, nitrogen, etc. through the environment, rough taxonomic information can lead to erroneous data since predator prey interactions are often species specific.

The second generation of new devices (Shadow Image Particle Profile Evaluation Recorder, Computational Intelligence Sensor, Holomar) improve the amount of information per organism either by combining optic with acoustic measurements or by getting more optic information per organism, i.e. two pictures from different angles or holography. These methods are still being developed. Thus, it is not clear, yet whether they will succeed in improving the level of identification to 2 as planned and do so for many categories at once.

But even if these methods succeed it will not be until the third generation of automatic counting and identification devices with a lid of three (species level) until such new methods can be used to answer the detailed ecological questions we currently have. There are ideas such as imaging internal structures or adding physiological indices detectable from absorbance or fluorescence (Schulze et al., 1992) but such methods are not known to be planned yet.

The difficulty of automatically counting and identifying zooplankton can be compared to the task of counting all people of one country, distinguish them by sex, and tell their age by satellite video. It is not known that anybody has even attempted such a thing.

Figure 23 illustrates how lowering the amount of “time needed” to real-time has had a tremendous tradeoff in information content. In conclusion it can be said that we need to do a lot of development work and that it is still some time off until we will find an adequate automated replacement of manual taxonomic identification, but we need to keep in mind as Davis et al. (1996) stated “when the theoretical potential will be eventually put into practise we can expect major new scientific insights in Biological Oceanography”.

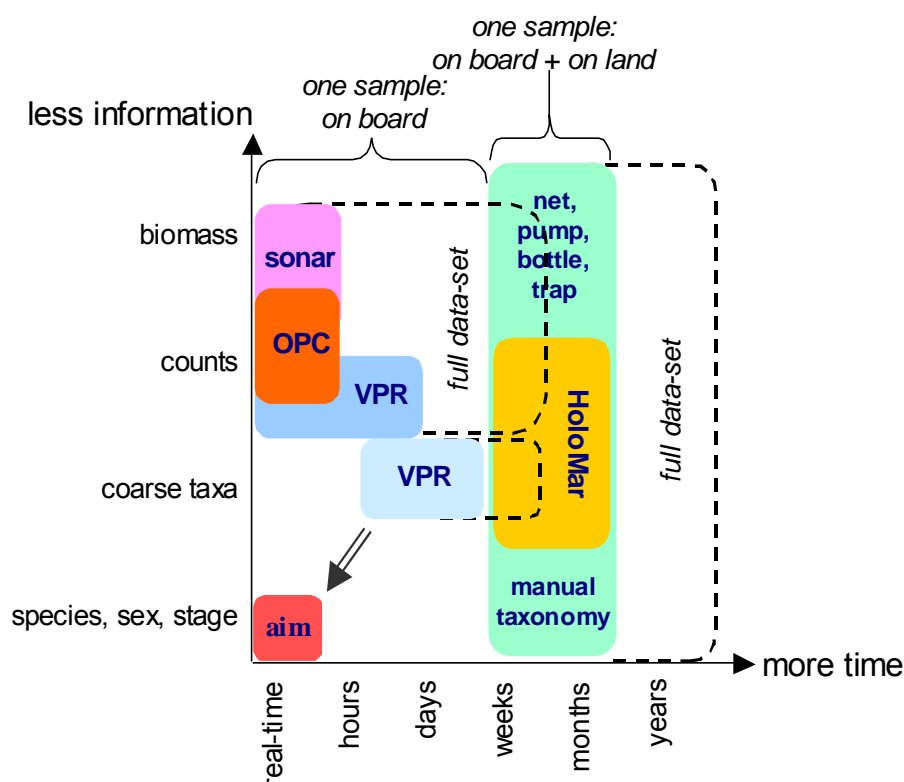


Fig. 23: information vs. time

6. Deficiencies

Trophodynamics, ontogeny, physiology and ethology represent the degrees of freedom according to which the specificity of the ecological requirements of each zooplankton species is composed. Many examples of functional relationships regarding each of these dependencies have been described separately. They represent pieces of a mosaic pattern which is still not identifiable as a pictorial concept, though the comparative treatment of selected functional relationships reveals lucidity at least in some components. The development of unifying concepts in zooplankton ecology is still in its infancy. This is so with respect to the integrative and simultaneous treatment of the trophodynamic, ontogenetic, physiological and ethological interdependencies of the zooplankton populations. As also the year class sizes of fish and benthic populations with planktonic larvae depends primarily on the success of this develop-

mental stage, the separation of the disciplines zooplankton research, benthic research and ichthyology is impeding the possible common research success. As this is so the development of prognostic procedures has not reached the level it should have with respect to the social demand for a resilient utilisation of the marine biodiversity under a regime of global change.

Stock investigations: It is necessary to establish comprehensive high-resolution spatio-temporal data sets about zooplankton species of all size-classes as it is already given e.g. for temperature or salinity.

Up to now it has hardly been possible to rely on sufficiently exact data sets which can give information about long-term trends in zooplankton stocks in the entire North Sea. This is to some degree also the case for the CPR data, the potential and limits of which need to be clearly defined so that the demands placed upon them are not set too high. There is a need for gear which undulates over the entire water column and is capable of obtaining quasi-synoptic, large scale stock assessments. That means that there is a pressing need for development of modern, standardised and automated methods for large scale three-dimensional stock assessments of zooplankton in order to achieve data sets with a spatial and temporal resolution similar to that already available for physical parameters for years now. This will permit a simultaneous cooperative evaluation of the data in future interdisciplinary projects.

A large number of publications exist which are concerned with the development of new techniques and which mainly employ acoustical, optical or genetic methods. However, up to now no new instruments and methods could be applied successfully to deliver stock assessment data in the same quality as guaranteed by competent microscopy. The great disadvantage of this classical method is that it is extremely time-consuming.

Investigations of processes: Individual observations and measurements of zooplankton processes such as feeding, respiration, excretion, egg production and growth rates are of great importance, since they are used as dynamic factors in mathematical modelling of processes and mass turnovers. Reliable data are urgently needed here. Of course, a first step for obtaining such data would be the analysis and testing of existing data from the literature. Nevertheless, standardised methods should be developed for the measurement of the different parameters. Further, it should be attempted to find more possibilities and methods for gaining such measurements in the field in order to guarantee the authenticity of the results for natural ecosystems.

7. Recommendations

Based on the analysis of the status of research on zooplankton ecology following recommendations are made:

Data concept:

- Analysis of the available stock data on zooplankton, i.e. collection in data banks and testing for comparability.
- To achieve full access to long-term zooplankton time series for German scientists. This includes the CPR-series as well as the unrestricted publication of the Helgoland Roads data.
- Analysis of the abundantly available process data for zooplankton, i.e. collection in data banks and testing for comparability.

- Standardisation of all methods for determining exact process data such as feeding, respiration, excretion, growth and reproduction rates.
- To establish comprehensive seasonal high-resolution spatio-temporal data sets within the framework of international programmes. The only present and published and accessible data set that meets these conditions is the FLEX data set for the Fladenground.

Ecodynamic concept:

- To develop concepts for the understanding of a predation driven, unstructured ecosystem compartment such as the zooplankton.
- To better understand the role of different diets for plankton fecundity.
- To better understand the role of turbulence in the performance of the shallow water systems over the Doggerbank and the southern North Sea.

Research technology:

- To apply new technologies in connection with traditional approaches for instance for species identification (i.e. population genetics), abundance estimation (i.e. optical and acoustical counting).
- Further development of acoustical and optical (video) stock assessment gear for the various sized groups of the zooplankton for three-dimensional, large scale in situ operation with user friendly software including simultaneous determination of physical and chemical environmental parameters by means of sensors.

Status concept:

Still research is necessary to establish a view of a pristine zooplankton and thus to define the state of the pelagic ecosystem. The development of such indices should necessarily include the analysis of the historic data. Sophisticated concepts such as Lenz's paper on the role of the microbial food in an evolutionary context should be taken into account (Lenz 1992)

As the term zooplankton is a human artefact which aggregates many size classes expanding over six orders of magnitude and diverse functional and taxonomic entities no uniform recommendations can be given. Ecosystem theory has to be part of any question specific investigation being aware of the heterogeneous functional relationships controlling permanently and temporarily the zooplankton species, their dependency from and their influence on the other components on the marine ecosystems.

Within this framework special attention should be given to:

- The formation of year class sizes in fully pelagic - and meroplanktonic benthic - or nektonic species - an annual repetitive decisive process with strong economic and social consequences,
- the influence on such processes of climatic, anthropogenic and system inherent controls,
- the rules governing the direction, timing and amount of throughput of biomass from primary producers to the end-consumers,
- the development of weighted prognostic tools for the well directed management and sustainability of the marine biodiversity,

- the full utilisation of research products for an international inventory on the abundance and distribution of zooplankton species and their functional biodiversity parameters, which is accessible for the above investigations by computer programs enabling advanced knowledge engineering,
- the North Sea wide elaboration and continuation of regional and long-term measurements as a data basis to be utilised for prognosis and/or for the calibration of the prognostic skill,
- within these investigations the now available tools of biochemical, optical and acoustical measurements with a high degree of automation should be developed further and standardised internationally,
- pilot investigations on focal problems within this framework, especially in areas which are promising with respect to available highly significant statistical correlation.
- theoretical ecology on selected topics such as the key- and keystone species concept, the „bottom up“ and „top down“ paradigms, flow analysis, and artificial intelligence,
- the development of tested simulation modules for any investigation as a contribution to the data and functional model inventory.

8. Some „challenges“ with respect to zooplankton in the North Sea from the viewpoint of the Hamburg projects

During the past thirty years a series of large interdisciplinary North Sea projects were planned and carried out in Hamburg including the Fladen Ground Experiment as well as the ZISCH, PRISMA and KUSTOS projects. In the course of these projects a tremendous amount of experience, data and knowledge has been accumulated. It is therefore logical to draw upon this capital when considering the future course of North Sea research. However, it is first of all necessary to take an inventory of the data gained and the knowledge derived to define the present status and to decide where the next interdisciplinary bridges can be built in order to further the understanding of the complex North Sea ecosystem. Although this work has not yet been concluded, a few observations and considerations from the viewpoint of zooplanktology will be discussed in the following which arose, in part, during the course of the above-mentioned projects.

The North Sea can be roughly divided diagonally from the mouth of the Humber (England) to the tip of Skagen (Denmark) into two parts. The northern part is an oceanically influenced shelf region while the southern part is strongly influenced by the land. The Dogger Bank represents a topographic border between the two. With respect to zooplankton, the two regions have some characteristic differences in species compositions and life history types. These differences in life cycles and in the interplay of ecosystem compartments in the various marine areas are in our opinion not well enough understood.

The mesozooplankton in the northern North Sea and at the continental slope

One of the most important representatives of the mesozooplankton in the northern North Sea is the large copepod *Calanus finmarchicus*. In late spring and in summer it comprises up to 80% of the zooplankton biomass. It is considered to be an important source of food for fish. The energy transfer occurs via a relatively short food chain (diatoms-copepods-fish). At the continental slope of the southern Norwegian Sea it is present in large stocks throughout the year and it becomes concentrated in summer (July, August) partly in very thin water layers characterised by large temperature (and density) gradients, i.e. in the warm summer mixed surface layer (0-80m) but also in the transitional zone between Atlantic Water and Arctic Bottom Water (400-800m). In the mixed surface layer the stocks are reproductive, consisting of

all developmental stages. By contrast, the stocks in the transitional zone between Atlantic Water and Arctic Bottom Water consisting of the older copepodite stages V(VI) and some full-grown but not yet fertile females are already diapausing. In autumn and winter finally the bulk of the stocks of *Calanus finmarchicus* is withdrawing to the deep water layers.

In the northern North Sea (e.g. Fladen Ground, approximately 150m deep) *Calanus finmarchicus* doesn't dominate until late spring and summer. In winter it is hardly present, but during the spring diatom bloom it develops large stocks. It becomes concentrated in the mixed layer warmed by solar radiation in spring, the zone in which the exponential growth phase of the algae bloom occurs. Only about a week after the breakdown of the phytoplankton spring bloom does it begin with intensive diurnal vertical migrations, whereby the magnitude of the migrations increases with each developmental stage reached. The older stages then achieve two vertical shifts per day of more than 80 m. In July the stocks of *Calanus finmarchicus* in the Fladen Ground consist mostly of the older copepodite stages V and IV. Although they still carry diurnal vertical migrations, these only reach the level of the summer thermocline at night and during the day they appear to remain near the bottom. This phenomenon of summer sinking of the *Calanus* stocks in the northern North Sea has been described in several publications. These observations lead to the following questions:

- Where do the spring reproduction stocks of *Calanus finmarchicus* in the northern North Sea originate? Why do the older stocks sink to deeper water layers in summer? Have they to reach their winter refuge at depth now but are unable to do so because of the shallowness of the shelf sea? Are they therefore subject to intense predation by benthic organisms and thus unable to constitute reproductive stocks in the following spring? Must the northern North Sea be „innoculated“ each year with fresh stocks from the Atlantic?
- Which mechanisms cause the diurnal and the seasonal vertical migrations of *Calanus finmarchicus*? Are they of an active or a passive nature? Since we observed in the Fladen Ground that the populations didn't initiate diurnal migrations until food became scarce – namely after the breakdown of the algae bloom – an active, energy consuming vertical migration of the 2.5 mm organisms of more than 160 m daily seems doubtful. It also seems unlikely that the seasonal vertical migrations of up to 1000 m in one direction are carried out actively. Particularly after half a year of „diapause“ at depth the organisms need the reserves acquired during the feeding phase for moulting, mating and egg production in the mixed layer. Apparently, not all of the grown individuals of the spring generation disappear from the mixed layer, but rather a part of the population remains there and produces one or two summer generations in the North Sea.

For all of these migrational phenomena endogenous mechanisms are conceivable which support the organisms in their diurnal locomotion as well as their seasonal emigration. Research into this should pay particular attention to the chemistry of the animals. For example, is there a temporal phase shift between the synthesis of proteins with a high specific weight and light reserve substances such as wax esters and other lipids? This might account for periodic density changes in the organisms which lead to corresponding vertical shifts in the populations. Certain physical properties of the wax esters such as the fact that they are much more compressible than water should also be of interest. Through this property an initiated ascent or descent could become amplified. Under good nutritional conditions, particularly the older developmental stages have a well-filled oil sac which almost runs through their whole body. Are animals in this condition „condemned“ to sink to depth until they are caught up in a pycnocline (e.g. the transition zone between Atlantic Water and Arctic Bottom Water)? After a longer „diapause“ in this zone a new density change in spring, perhaps caused by gonadal development, might initiate the upwards movement.

Our ZISCH results show for the spring of 1987 a wedge of high zooplankton biomass stretching from the shelf edge to the Dogger Bank. No comparably high mesozooplankton bio-

mass was found in the southern North Sea. The dominant organism was *Calanus finmarchicus*. This type of plankton population flowing into the northern North Sea between the Norwegian Trench and the Shetland Islands has been described repeatedly in older publications. Plant nutrients also enter the North Sea from the shelf edge by this route, as can be seen from the data of the ZISCH winter cruise. ZISCH and PRISMA investigations also show that the heavy metal concentrations in *Calanus sp.* increase significantly from the German Bight to the shelf edge, where the highest values were to be found. Furthermore, the ZISCH investigations also showed the highest concentrations of cadmium and mercury in the benthic hermit crab to be in the northern North Sea influenced by the Atlantic from the shelf edge. It can thus be assumed that nutrients as well as heavy metals and zooplankton flow into the northern North Sea between the Norwegian Trench and the Shetland Islands. These observations prompt the following questions:

- What are the sources for the plant nutrients and the heavy metals? Is it possible that the Continental Slope Jet, which flows up to 500-600 m depth parallel to the shelf edge (Northeast Atlantic Current) to the north, plays an important role here?

For, as described above, the transitional zone between this ocean current and the Arctic Bottom Water which flows below it to the south represents the winter location of the resting *Calanus finmarchicus* populations, since the organisms are apparently caught by these water layers. This zone might be also a sink for organic (and heavy metal contaminated) matter which has been transported from the coastal regions and subsequently has sunk to depth at the shelf edge until being caught up in pycnoclines. If the Continental Slope Jet – as described in work carried out in Hamburg – periodically rotates clockwise along its axis (upwelling), then the contaminated material would come back up to the water surface and then be transported by surface currents back to the shallow shelf of the northern North Sea.

After its ascent to the mixed layer, *Calanus finmarchicus* enters the North Sea by the same surface currents and could thus take up the heavy metals with its food. After sinking to greater depth in summer it, in turn, would pass these on to benthic organisms such as the hermit crab as they predate upon it. The exuvia from twelve moultings, which are suspended in the water and slowly sink to the bottom, could also be an input source for the sediment. It is well-known that heavy metals adsorb to chitin. During the Fladen Ground Experiment in spring of 1976 we found up to 200 000 exuvia m⁻² in the 100 m water column.

Climate fluctuations, as seen in the NAO-index, and the resulting changes in wind conditions lead to different convective and advective processes at the shelf edge of the North Sea. In years with pronounced westerly winds (high NAO index) the *Calanus finmarchicus* stocks seem to be lower but the herring recruitment was higher than in years with less frequent westerlies. This presents questions which have been investigated partially but which have not yet been satisfactorily clarified:

- Which consequences do the fluctuations in upwelling and advection caused by differing wind stress have on the inoculation of the northern North Sea with nutrients, contaminants as well as populations of important zooplankton organisms?
- Pronounced west wind conditions in winter lead to higher temperatures, stronger turbulence and probably also to a later stratification of the water column in spring in the North Sea. Does this lead to a later and shorter spring phytoplankton bloom? What consequences would this have for the summer populations of *Calanus finmarchicus*? What role does the Match-Mismatch theory of Cushing play here?

The Mesozooplankton in the southern North Sea

One of the main reasons for the limitation of *Calanus finmarchicus* in its geographical distribution to the North Atlantic and northern North Sea is probably its pronounced herbivorous way of life. This is probably also responsible for the development of the periodic „diapause“ in the life cycle of this large copepod. In connection with the breakdown of the diatom bloom in late spring, it „makes sense“ for this organism to bridge over poor food conditions at depth with a reduced metabolism. This is only possible in regions with deep water.

In the shallow southern North Sea the predominant copepods are the smaller species such as *Acartia clausi*, *Pseudocalanus elongatus*, *Paracalanus parvus*, *Temora longicornis* and *Centropages hamatus*. To be sure, these species can occur overall in the North Sea mesozooplankton. However, these species are characteristic inhabitants of shallow and even partially enclosed marine regions with extreme environmental conditions such as strong temperature fluctuations as well as pronounced salinity gradients and eutrophic conditions through freshwater and nutrient inputs from estuaries and river systems. Such conditions are typical, for example, for the German Bight, the area off the coast of The Netherlands as well as in the western Baltic. It appears that the small copepod species have developed special strategies for surviving in such shallow regions. For example, *Acartia clausi* and *Centropages hamatus* form resting eggs which can withstand seasons with poor growing conditions in the sediment. It is known that *Pseudocalanus elongatus*, *Paracalanus parvus* and *Temora longicornis* also have reproductive phases in winter. The small copepods also have a stronger tendency to switch the basic food supply and even, as is the case with *Pseudocalanus elongatus*, to take detritus as a main food source. It is known from *Acartia clausi* that it can also feed carnivorously on ciliates, which live on ultraphytoplankton (e.g. flagellates). It is generally assumed that the small copepods can consume ciliates as well as heterotrophic flagellates and are therefore omnivorous. Our own observations in the German Bight showed that *Acartia clausi* could even maintain populations during a strong *Phaeocystis* bloom.

Particularly in summer there is a dominance of ultraphytoplankton (flagellates) in the German Bight, whereby the input of phosphorus and nitrogen by rivers and the atmosphere supports this phenomenon. In this case a large proportion of the primary energy flows through bacteria (microbial loop) and reaches the copepods via flagellates and ciliates. In this way, bacteria production is tapped for the higher trophic levels, but in comparison to the shorter food chain in the central and northern North Sea much less energy reaches the higher levels. Each additional trophic step generally costs around 90% of the available energy.

In addition, the species composition and the stock sizes of the phytoplankton during the past decades have changed, in part through anthropogenic phosphate and nitrogen inputs in many parts of the North Sea, particularly near the coasts. In Dutch and German coastal areas there has been an increase in productivity and larger phytoplankton biomasses since the 1970's. Furthermore, the small flagellates have increased in relation to the diatoms. Above all, *Phaeocystis* sp. must be mentioned in this connection. But also the alga *Chrysochromulina polylepis*, which was responsible for a mass bloom in the Skagerrak and Kattegat in the summer of 1988 is an example for this. It is of interest to know whether such developments represent an advantage for the small copepods and what consequences this could have for the whole ecosystem. In this connection it would be advisable to take up an interesting hypothesis described briefly in the following and subject it to further investigation:

Large phytoplankton (diatoms, dinoflagellates) are preferably eaten by large copepods as a result of their coarser filtering apparatus. Copepods such as *Calanus finmarchicus*, however, are preferred by fish larvae and pelagic fish (e.g. herring) as food. Small zooplankton, on the other hand, consumes smaller algae (e.g. flagellates) and is preferred by gelatinous zooplankton (medusae) as food. Medusae can develop better if smaller copepods predominate, since larger copepods suffer losses through damage to their feeding apparatus and consumption of their juvenile stages. If eutrophication, i.e. increased nitrate and phosphate but

constant silicate concentrations, should lead to mass development of smaller primary producers, this would be an advantage for the smaller zooplankton, which could finally result in a „tipping“ of the trophic net from one producing primarily fish to one producing primarily jellyfish.

The above-mentioned scenario still largely has hypothesis character, i.e. there is still much to be investigated, especially with respect to the detailed questions. In the following, some of these are formulated:

- What sources of food can be used by the smaller copepods during the various seasons and how efficient is their utilisation? To what degree do primary producers form the nutritional basis? To what degree are they (seasonally) dependent on the utilisation of secondary producers (e.g. heteroflagellates, ciliates) or even on detritus? What role is played by the microbial loop? Finally, what form of nutrition is most significant for reproduction?
- Which life strategies and reproductive cycles are developed by small copepods under the extreme environmental conditions in the German Bight? This includes the determination of the duration of life cycles and the timing of reproductive phases and diapauses.
- What nutritional role do small copepods play for fish larvae and pelagic fish? Are they the main food source or are they seasonally replaced by other zooplankton (e.g. meroplankton)?
- If it is true that the copepods mainly utilise the production from the microbial loop, what consequences does this have for the food net on the whole? For example, does the implicit lengthening of the food chain mean less nutritional efficiency for the final member (fish)?
- What role is played by the gelatinous zooplankton, e.g. the medusae? How much influence do they have as competitors for fish larvae and fish? Unpublished KUSTOS results show that the hydromedusae in the German Bight can reach great abundances during the summer.

9. Appendix (Tables)

Table 1: Excretion of CO₂ by zooplankton.

Process	State variable	Controlling factor	Methods	Fluxrates yes/no	Time scale e/y/d	Area	Reference	Comments
Community respiration								
Respiration and excretion	Zooplankton biomass	Temperature	Incubation	yes	d/y	Black Sea	Petipa 1981; Volovik et al. 1994	app. 10-15 % biomass d ⁻¹ can be expected to be released, this is close to the figure for <i>Oithona</i> (see below)
Respiration and metabolic activity	Zooplankton biomass	Chl a, temperature	ETS, incubation	yes & no	e - temperature dependent e - bloom related d/y - areal variation due to chl a and T, for size-dependent model see (Blanco et al. 1998; Yurista 1999)	Biscay, Canary Islands	Hernandez-Leon & Gomez 1996; Martinez 1997	The ratio reflects metabolic state on a ocean-wide scale - on a short-term scale these measurements both reflect the animals activity level (Hernandez-Leon & Gomez 1996) steno- and eurythermy in species has to be considered (Yurista 1999)
Species specific respiration								
	<i>Oithona similis</i> (Copepoda)			yes	e		Nakamura & Turner 1997	daily ration app. 41 % of body carbon, of which app. 90 % are needed for respiration
	<i>Calanus</i> sp. Metridia sp.	onset of spring	incubation	yes	e	Swedish Fjord	Bamstedt & Tande 1988	respiration depends on developmental stage, diapausing species have almost zero values
	general copepods		ETS measurement	yes	e/y	Swedish Fjord	Bamstedt et al. 1990	Procedure to deal with ETS measurements, budget: respiration accounts for app.50 % to 100 % of daily assimilated food. Assimilation efficiency = 0 %
	<i>Temora</i>						Berner 1962	
	<i>Acartia tonsa</i>	incubation		yes	d	Mediterranean Sea	Cervetto et al. 1993	diel variation - respiration higher during daytime in deeper water
	gelatinous zoopl.	incubation		yes	d/e/y	Black Sea, English Channel	Biggs 1977; Volovik et al. 1999)	According to (Welch et al. 1997) the respiration ration for gelatinous zooplankton is 64 % of rate of total zooplankton respiration, probably due to higher assimilation efficiency which can reach 70 % . According to (Lucas et al. 1997) 61% of ingested food is respired and 39 % is assimilated (<i>Aurelia</i>), ratio decreases to 80- to-20 % for smaller specimen

Table 2: Effects of turbulence on different parts of the pelagic ecosystem in different types of studies

(+) increased turbulence with positive effect, (-) increased turbulence with adverse effect, (+ and -) equivocal or dome-shaped response, (0) no response

Compartment	Variable	Relationship and source
Experimental studies		
Phytoplankton	Settling rate	(-)[1-7]
	Cell size	(+) [2, 3, 8, 9]
	Cell abundance	(+)[10-13]; (0) [12]
	Chlorophyll a	(+) [12-15]
	Cell growth	(+)[16-18]; (-)[16, 17, 19, 20]
	Diatom/Flagellate-ratio	(+)[2, 3, 9, 14, 15, 21, 22]
	Species composition	change but no clear effect
	Nutrient uptake	(+)[18, 23]; (-)[18]
	Timing of bloom	no clear effect
Microzooplankton	Predation/grazing rate	(+) [24, 25]; (-/0) [25]; (-) Noctiluca [26]
	Growth rate	(+) [24]
	Cell size	(-) [24]
Mesozooplankton (copepods)	Abundance/Biomass	(-) [10-14]; (+) [13]
	Metabolic rate	(+)[10, 27-30]
	Excretion rate	(+) [10, 31]
	Predation rate/grazing rate	(+) [29, 30, 32]; (-) [8, 10, 29, 32]
	Growth rate	(+)[33]
	Age structure/sex ratio	no clear effect
	Egg production	(+) [34]
Mesozooplankton (non-cops)	Abundance (gelatinous ZP)	(-)[35]
	Migration (vertical distribution, brachyuran crabs)	(-) [36](+) [37]
Ecosystem	Community productivity	(+)[13, 38-40]; (-/0) [39-41]
	Ecosystem productivity/Respiration	(+) [14]
Theoretical studies / models		
High Re-animals	Contact rates	(+) [42]; (+ and -) dome shaped response [43]
Copepods	Perception	- [44, 45]
Fish larvae	recruitment	trough-shaped due to patch dissipation and subsequent increase encounter rates [46] similar : [47]
	Feeding	(+) tidally mixed [48] especially in nursery regions ; [49]
Field data / observations		
Mesozooplankton	Abundance (copepods)	(-) time-series at Helgoland Roads [50, 51]; (+and -) dome shaped reaction to tidal stirring [52], tidal estuary [53]
	Abundance (gelatinous ZP)	(-) [54, 55]
	egg production	(+) aspects of timing : after storm [56], see also [47]

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Table 3: Excretion of DIM, DOM and POM by zooplankton. For P excretion rates Redfield-ratio corrected similar to N

Process	State variable	Controlling factor	Methods	Fluxrates yes/no	Time scale e/y/d	Area	Reference	Comments
Excretion	Ammonia	temperature, zooplankton abundance	field measurements, experimental	Yes	d	general, Swedish fjord	Banse 1995; Miller & Glibert 1998	up to 2 ng-N h ⁻¹ cop ⁻¹ not constant over time : increases due to plankton bloom by increased metabolic activity for Metridia (Bamstedt & Tande 1988)
Excretion	Urea, primary dissolved amino acids		experimental	Yes	d		Miller & Glibert 1998	up to 2 ng-N h ⁻¹ cop ⁻¹
Fecal pellet production, sloppy feeding	DOC, DON	temperature, zooplankton abundance		Yes	d	general		25 % (without fecal pellets contribution) to 40 % (incl. fecal pellets) of removed C without release
Fecal pellet production	POC	zooplankton abundance, phytoplankton	pellet measurements	Yes			Mauchline 1996	Copepods: ca 50 % of daily ration excreted (range 10 to 80 %)

Table 4: Selection of zooplankton models.

Special reference to North Sea zooplankton indicated by bold model number

#	Name/Type	Zooplankton term	ref. and comments
1	Mechanistic 3D-model Species specific	only herbivore grazing, minimum of two values chosen $\frac{\delta H_k}{\delta t} = \text{mixing} + \min \left[\mu^{\max}, A \sum_{j=1}^n \Phi P Y \right] H_k$ <p>A = Avogadro constant, Φ=encounter rate coefficient, Y = Yield of predator (=H) per prey (=phytoplankton), H_k = herbivore of species k, P = phytoplankton, μ = max. growth rate under unlimited prey density</p>	(Baird & Emsley 1999); K simplified to a varying mixed layer model and a fixed exchange rate D, H represents sm all protozoans (results: success in one case, one failure)
2	1D-model, based on FLEX-data species and size specific	i) Mixing → part of phytoplankton ii) 12 age classes for herbivorous copepods iii) Grazing and Predation rate assumed constant over water column, predation is quadratic (!: ≈BIOM ²) $\frac{dBiom}{dt} = (Eff * Ass * Graz - Pr ed) * Biom$ $Graz = \frac{C * P}{(B + P)}, \quad Pr ed = \frac{Gx * Biom}{(1 + P / 2)}$ <p>P=Phytoplankton, Gx=Predation rate, B=half saturation grazing, C=maximum grazing rate</p>	(Henderson & Steele 1995), temperature distribution to calculate exchange rates between 5m-layers, vertical diffusivity K at surface $K=3*W^3$ (max. 400 cm ² s ⁻¹ , W=wind speed), at Bottom $K=2*U^2$ (app. 10 cm ² s ⁻¹ , U=current speed), at thermocline $K=0.1$ cm ² s ⁻¹ , linear interpolation to bottom (results: good representation of age class and biomass temporal distribution, better than with linear predation term (see Steele & Henderson 1995)
3	'Blue water'-nitrogen cycle model trophic level	The zooplankton equation is simple, the closing term is linear : $\frac{dZ}{dt} = \sum \beta G - \sum \mu Z - h(t) \frac{Z}{M},$ <p>βG's are the grazing terms for phytoplankton, detritus and bacteria, whereas μZ are the loss terms due to excretion and mortality. i) Mixing : → h(t) refers to mixed layer depth dynamics and thus a changed entity of zooplankton in the mixed layer itself. Special attention was paid to grazing proportions. ii) Grazing is not constant : A sort of switching was allowed for based on different availabilities for the food items. It is assumed that preferences change with food quantity : The weighted preference p' for the first food item with quantity P1 would be : $p' = p_1 P_1 / (p_1 P_1 + p_2 P_2 + p_3 P_3)$ where $p_{1,3}$ are the preferences when all food items are equally available.</p>	relatively complete (Fasham et al. 1990; Fasham 1993), good: differentiated handling of grazing. The application of the weighted preference concept yielded in more stable models, allowing zooplankton to successfully overwinter. However, the authors feel that the parameterization of zooplankton feeding preferences requires further theoretical development.
4	Riley Biomass Model (1947) 1D-model trophic level	herbivor biomass model $\frac{dH}{dt} = (aP - r_f(T) - cS - D) * H$ <p>H=herbivor biomass (from displacement volume); a = assimilation coefficient; P=phytoplankton; $r_f(T)$=respiration as a function of respiration at 0°C and f(T); predation proportional to Sagitta abundance S; D=natural mortality</p>	(Davis 1987) [calculations for groups of stations, advection therefore omitted]
5	Davis' Species Model 1D-model species specific		(Davis 1984b; Davis 1984a) Assumptions are that development rate and fecundity are functions of temperature but independent of food; mortality is a function of predator abundance and its consumption rate [calculations for groups of stations, advection therefore omitted] best of 4-5-6
6	Huntley-Boyd Model (1984) 1D-model size dependent	based on phytoplankton concentration and filter-feeding zooplankton $\frac{dW}{dt} = aCbW^n - kW^m$ <p>a = assimilation efficiency; b, n, m, k = parameters for weight</p>	(Davis 1987) <u>food limitation</u> is determined by calculating the critical food concentration under maximum growth rate. [calculations for groups of stations, advection therefore omitted]

		dependent filtration and respiration and are <u>temperature dependent</u>	therefore omitted] second best of 4-5-6 (Broekhuizen & McKenzie 1995) the model has been adopted to available data, i.e. CPR data per region and month → coarse resolution
7	ERSEM 1995 1D-model per box, 15 boxes advektion-model across box-margins	<p>bulk biomass model : three zooplankton components: micro-, omniv. meso- and carniv. mesozooplankton, handling time and search volume incorporated (see Huntley and Boyd 1984) based on Holling type II functional response, and related to elemental concentrations, example for carbon (other elements are uptaken proportional to their elemental ratio):</p> $I_{X,c} = X_c * \frac{f(T) * V * F_{X,c}}{1 + V * \tau * F_{X,c}}$ <p>with I=rate of uptake of c for Compartment X, f(T)= temprature function, F=local concentration of c relevant to X, V=search volume, τ = handling time</p>	<p>in ERSEM larval fish stages are not modelled (Heath et al. 1997a), although they are very important and can have an impact relatively higher than for age-0 fish (Mehner 1996)</p> <p>only rather faint concordance with data</p>
8	Mules 1D-model modified trophic (<u>focus on salmon!!</u>)	<p>9 compartments ranging from bacteria to salmon including ctenophores for herbivorous zooplankton :</p> $\frac{d\bar{H}}{dt} = \gamma H - \beta H + (H_{bottom} - H)(\bar{E} - W)$ <p>with E = entrainment velocity from bottom to top layer, W sinking velocity)</p>	<p>(Parsons & Kessler 1987) working with a two layer model and depth integrated concentrations and source and sink terms</p> <p>the effects on the ctenophore population (especially temperature) are most important for the model and the outcome of salmon (Bryant et al. 1998)</p>
9	North Sea- Calanus finmarchicus- model 3D model monospecific	<p>ERSEM biomass model adopted (#6), weight specific model, population divided into n weight classes, only adult class reproduces amount R :</p> $R(t) = \beta * N_{adults} = \frac{Assimilation}{weight} * N_{adults}$ <p>assimilation is a Michaelis-Menten-function of uptake with Q10-temperature adjustment. For the non-reproducing classes the relationship is</p> $\frac{dN_i}{dt} = entering - outgrowing = \frac{\gamma_{i-1}N_{i-1}}{w_{i-1}} - (\frac{\gamma_i N_i}{w_i} - mortality_i)$	<p>The analysis was based on FLEX- and CPR-counts of <i>C. finmarchicus</i>.</p> <p>The initial entering of the <i>C. finmarchicus</i> population is sufficiently resembled by the model, whereas it is less sufficient to generate populations in the central and western North Sea.</p>
10	Georges Bank- Calanus finmarchicus- model 3D-model monospecific	<p>16-stage (3 after C5) conveyor belt model, where stages of eggs, N1 and N2 do not feed :</p> $R_i = \frac{dN_i}{dt} = \frac{C_{i-1}}{D_{i-1}} - \frac{C_i}{D_i} - \mu_i C_i ; \text{ with } C = \text{number at stage } i,$ <p>D = duration at stage i, μ mortality at i. Duration calculated according to Belehradek (1935):</p> $D_i(T) = a_i (T - \beta)^\alpha \text{ mit } \alpha = \pm 2.05 \text{ and } \beta = \pm 9.11 ;$ <p>$\nabla \bullet (nv)$ adopted to $\nabla \bullet ((V_L + V_b)n - f(n))$; where $V_b n$ represents - critical - vertical migration : however - they reduced the situation to two swimming cases for which V_b not has to be considered, so that the plankton is treated 2D-ly : (a) equal vertical mixing and (b) concentration in the upper 25 m layer.</p>	<p>(Lynch et al. 1998) based on (Davis 1984a) variable grid net (finite element mesh, MARMAP1, see also G2S net) low mortality and abundant food assumed 2-monthly climatology egg production, stage duration affected by food concentration and by this indirectly affect mortality vertical swimming simplified model requires adjustment to food limitation in order to fit to data then good adjustments to fish spawning grounds and regional distribution of plankton are gained (advected females from the Gulf of Maine) (Volovik et al. 1994)</p>
11	Mnemiopsis-model 1D-model multispecies	<p>for predation of ctenophore on zooplankton a clearance model is applied</p> $G = aW^b \text{ and ingestion } I = G * F * DW$ <p>with G = clearance rate (mg wet weight⁻¹), a = temprature dependent coefficient, W = body weight and b = weight specific decrease coefficient, F= food concentration, DW=ctenophare dry weight</p>	<p>good representation of annual dynamics both for total zooplankton and ctenophores; all calculations species specific and size dependent water dynamics and salinity submodels used to drive ctenophore dispersion salinity data as external forcing used for zooplankton submodel</p>

Table 5: Habitat specific dissipation rates and Kolmogorov scales

Site	Dissipation rate ϵ (cm ² s ⁻³)	Kolmogorov scale (cm)	Shear (s ⁻¹)
Open ocean	10^{-6} - 10^{-2}	1 - 0.1	0.01 - 1
Shelf	10^{-3} - 10^{-2}	0.18 - 0.1	0.32 - 1
Coastal zone	10^{-3} - 1	0.18 - 0.03	1 - 10
Tidal front	10^{-1}	0.06	3.16

Table 6: Relationship between wind speed and Kolmogorov scale

Wind speed (m/s)	Kolmogorov scale (mm)
5	16
10	9
15	7
20	6

Table 7: Methods, zooplankton

Accuracy = %-value of real value, i.e. values < 100 % indicate underestimation

Precision = 100 % (of mean) - error

Instruments (all instruments *in-situ*)

PARAMETER		INSTRUMENT	ACCURACY	PRECISION	APPLICATION	SOURCES OF ERROR	COMMENTS	REFERENCES
Zoo-plankton	Abundance	Plankton-Net	app. 75 %	n.d.	vertical or oblique hauls	depending on the type of organism and its motility	the inverse of the 'Filtrations- oder Netzkoeffizient' was taken as a measure of accuracy, which is on average 1.30 to 1.36, which is certainly an optimistic estimate, since Künne showed that efficiency and by this acc. depends on opening width	(Steuer 1910) on accuracy of net sampling : (Künne 1933) and selective avoidance (Fleminger & Clutter 1965; McGowan & Fraundorf 1966; Wiebe et al. 1982)
	Abundance	Plankton-Trawl, i.e. Rectangular-Midwater-trawl RMT8	relatively high due to 8 m ² opening, app. 100 %	n.d.		depending on mesh size	available with multiple-opening device	(Roe & Shale 1979)
	Abundance	Plankton-Pump						
	Abundance	Longhurst-Hardy-Plankton recorder	with 38 cm nose cone opening app. < 75 %	n.d.	sampling in layers, additionally with down-wire-net-monitor*	depending on the type of organism and its motility	ideal instrument for getting control samples for acoustical methods, but not for quantitative sampling; the winding of the silk causes damages to fragile species	(Longhurst & Williams 1976; Brierley et al. 1998) *(Woodroffe 1997)
	Abundance	CPR-recorder	due to small opening rel. small; according to Broekhuizen & McKenzie (1995) 25 % of omnivorous and 60 % carnivorous biomass is obtained	n.d.	sampling in a fixed depth, towed behind ships of opportunity	depending on the type of organism and its motility	relatively small opening, construction allows to be towed at high speed, silk gauze of unusual mesh size, app. 180 µm; the winding of the silk causes damages to fragile species	for copepods see (Robertson 1968)
	Abundance and distribution	Acoustical instruments : echo-sounders 18 kHz - 2 MHz**	depending on target strength response curves, slightly different to FISH	est. 95 %, after calibration with multiple standard targets 0.06 to 0.17 dB	two-dimensional tracking		target strength response curves depend on orientation of the object to the transducer (see Demer and Martin 1995; Jaffe et al. 1998; McGehee et al. 1998)	** (Skjoldal et al. 1993)
	Abundance and distribution	FishTV 8x8 grid of transducers	1 cm resolution at 420 KHz at 10 m		three-dimensional		restricted to a small volume of water, in combination with OASIS (see OASIS)	(Jaffe et al. 1995)
	Abundance and distribution	In situ Video systems	10 to 25 % better than nets; ca. 90 %	n.d.	two-dimensional	relatively narrow field of detection		(Tiselius 1998)
	Abundance and distribution	Optical particle counters	resolution > 80µm					pers. comm. by Doug Sameoto

Combined devices

PARAMETER	NAME	COMPONENTS	COMMENTS	REFERENCES
Zooplankton abundance and distribution	OASIS	FishTV high resolution CCD stroboscope current meters CTD	rel. small volume of water sampled, allows 3D-tracking	(Jaffe et al. 1998)

Table 8: Methods

PARAMETER		METHOD	ACCURACY	PRECISION	SOURCES OF ERROR	COMMENTS	REFERENCES
Zooplankton	Abundance	Sampling with Plankton-Nets	75 %	80 - 90 %		precision of the estimate depending on number of replicates	Downing et al. (1987)
	Abundance	Acoustic data processing		app. 75 %	based on three frequencies and two δ dB values, which have linear r^2 of 25-95 %	based on discriminant classification results based on proportion of misclassifications of six species, identification of species due to linear frequency-frequency relationships	Brierley et al. (1998)
	Biomass	Analysis of displacement volume				applicable only in absence of gelatinous plankton taxa	Wiebe et al. (1975)
	Biomass	Allometric conversion	est. 70-90 %	est. 90 %	ontogenetic stages disregarded	for copepods (see sources of error)	
	Copepod production	Egg Production				valid only for mature females, yielding lowest estimates (four methods tested) according to Kiorboe <i>et al.</i> (1985)	
	Copepod production	Instantaneous growth rate method, productivity following P/B	high	(in general app. 90 % of variance explained by temperature)		requires time consuming laboratory cultures ^{###} , allows temperature dependent extensions to field populations Huntley & Lopez (1992), discussion on the role of maxima instead of mean growth rate values see (Huntley 1996; Kleppel et al. 1996)	Roff et al. (1988) Escaravage & Soetaert (1993)
	Feeding rates/ Grazing	Gut Fluorescence	(slight) overesti-mation	individually highly variable	depends on an estimate of digestion time +; feeding rates are inferred from egg production measurements+	sample freezing and treatment influences value, method requires high number of replicates, unselective according to type of food fed; yielding highest estimates (four methods tested) according to Kiorboe <i>et al.</i> (1985) - recognizing that all methods represent underestimates gut fluorescence is the recommended method	Baars & Helling (1985); Barquero et al. (1998) + Fransz et al. (1991a)
	Feeding rates/ Grazing	¹⁴ C-incubation technique	n.d.		problems with fixation and incubation time (Moens et al. 1999)	not an in-situ method, requires experimental short-term treatment, but applicable to several trophic levels so that measurements with the same method can be achieved for several taxa	Daro (1978)
	Feeding rates/ Grazing	Dilution method			valid for algae < 5 μ m	grazing rates are inferred from maximum algae growth minus algae concentration	after Landry & Hassett (1982); also Kuipers & Witte (1999)
	Metabolic rate	ETS electron transport system	n.d.	individually very variable		method requires high number of replicates, often synonymously used with respiration (Martinez 1997), related to chl _a (Martinez 1997)	Bamstedt (1988); Martinez (1997)
	Copepods as gut contents of predators	biochemical identification	high	vague	no quantitative assessment	requires amplification of DNA, probably time consuming	Bucklin et al. (1995); Lindeque et al. (1999)
	Metabolic state, lipid content in cops	weighting after extraction				highly depending on life history stage (gelatinous tissues even in cops), technical : the use of commercial wax ester standards leads to underestimation by 18-32% (Ohman 1997), extraction methods also extract non-lipids, which in turn leads to overestimation.	Ohman (1997)

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