ICES

Zooplankton Methodology Manual

Edited by

R.P. Harris, P.H. Wiebe, J. Lenz,
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PREFACE

Zooplankton are the diverse, delicate and often very beautiful, assemblage of animals that drift the waters of the world's oceans. These microscopic organisms play a key role in the pelagic food web by controlling phytoplankton production and shaping pelagic ecosystems. In addition, because of their critical role as a food source for larval and juvenile fish, the dynamics of zooplankton populations, their reproductive cycles, growth, reproduction and survival rates are all important factors influencing recruitment to fish stocks. It is this latter role which has made zooplankton ecology of particular interest to ICES.

The International Council for the Exploration of the Sea, ICES, is the oldest intergovernmental organization in the world concerned with marine and fisheries science. Since its establishment in Copenhagen in 1902, ICES has been a leading scientific forum for the exchange of information and ideas on the sea and its living resources, and for the promotion and coordination of marine research by scientists within its member countries. Each year, ICES holds more than 100 meetings of its various working groups, study groups, workshops and committees.

Membership has increased from the original eight countries in 1902 to the present 19 countries which come from both sides of the Atlantic and include all European Coastal states except the Mediterranean countries eastward of, and including, Italy. ICES established a Study Group on Zooplankton Production in 1992 chaired by Hein Rune Skjoldal, of the Institute of Marine Research, Bergen, Norway. The Study Group were given as terms of reference to:

(a) review existing methods for measuring biomass and production processes;
(b) make proposals for improvement and standardization of methods, and prepare a methodological manual;
(c) consider the need for laboratory and seagoing workshops to intercalibrate experimental methods and evaluate new technology.

The Study Group has met eight times, in March 1992 in Bergen; in March 1993 in Las Palmas; in March 1994 in Plymouth; in June 1995 in Woods Hole; in March 1996 in Bergen; in March 1997 in Kiel, May 1998 in Santander, and May 1999 in Reykjavik. In 1997 Roger Harris of the Plymouth Marine Laboratory, United Kingdom, assumed the chairmanship.

The Study Group decided at the first meeting to produce a Zooplankton Methodology Manual recognizing the need for improvements and standardization in methods for studying this important and challenging group of organisms. To assist in the review of methods and to provide input to the issue of standardization and improvement of methods, three special workshops were convened. The first was a seagoing workshop onboard RV *Johan Hjort* and RV *A.V. Humboldt* on zooplankton sampling methods (June 1993). The two others were laboratory workshops at the University of Bergen, on production methods using the copepods *Acartia tonsa* (October 1993) and *Calanus finmarchicus* (April 1994). A fourth workshop was arranged by US GLOBEC in Hawaii using marine copepods (April 1994). Results from these workshops have been incorporated by the Study Group in producing this Manual.

ICES changed the status of the Study Group to a Working Group on Zooplankton Ecology (WGZE) in 1994. The Working Group has taken over the task of completing work with the Manual.

The Scope of the Zooplankton Methodology Manual is to provide an *updated review* of basic methodology used in studies of zooplankton including recommendations on improvements, harmonization and *standardization* of methods. The chapters aim to maintain a balance between being introductory and comprehensive. They provide an overview of methods that are useful, for example to graduate students who are starting in a new field. They emphasize the sources of error and the strengths and weaknesses of methods for various purposes and tasks. It has not been possible, however, to go into great detail for all methods, and reference to recent reviews and detailed descriptions of methods is used where possible and appropriate.

Each chapter begins with a review of methods which in most cases is accompanied by recommendations regarding choice and conduct of methods. These reviews consider the background and history of the methodology, the basic principles, sources of variability, equipment and procedures, comparative evaluation of alternative methods, general recommendations, and extensive literature references. Where possible detailed descriptions of standard protocols are included. The aim is to give practical instructions on *how* to carry out particular measurements and procedures. Equipment, procedures, data analysis and interpretation are described, where possible. These protocols either define standard methods, or give examples of little-known methods. If many methods are used, or many instruments, guidance is given on the most highly recommended, or the most often used, or likely to be used. In some cases it proves difficult to propose an agreed standard protocol. It is however, possible to provide guidelines that reduce the variability in methods and contribute towards harmonization and standardization.

The various chapters of the Manual have been reviewed by the ICES WGZE, and in addition peer reviewers from outside this group have evaluated each chapter independently. Grateful thanks are due to these reviewers for their valuable contribution to the overall project.

Each chapter is authored by an expert, or group of experts, selected from both members of the WGZE and other international specialists. The writing has been organized and co-ordinated by the main author assisted by co-authors. Chapter 1 provides an introduction to zooplankton. Chapters 2, 3, 4 and 5 consider sampling and experimental design, collecting zooplankton, techniques for assessing biomass and abundance, and the specialized methodology required for protozooplankton enumeration and biomass estimation. Chapters 6 and 7 describe new and emerging optical and acoustic techniques for estimating zooplankton biomass and abundance. In chapters 8, 9 and 10, methods for measuring zooplankton rate processes are described; feeding, growth and reproduction, and metabolism. Chapter 11 gives a modern account of methods for population genetic analysis of zooplankton, and Chapter 12 a comprehensive treatment of modelling zooplankton dynamics.

While striving to be a comprehensive treatment of modern methods in zooplankton ecology, it is inevitable that some topics have not been covered. In particular it was the original intention to include chapters on methods for investigating zooplankton behavior, and for studying population dynamics. The former chapter was never commissioned, while the latter although originally written as part of the ICES Manual project, was ultimately published as a separate scientific article; Aksnes *et al.* 1997. Estimation techniques used in studies of copepod population dynamics – a review of underlying assumptions. *Sarsia*, **82**:279–298. This may still be referred to as being complementary to the work. The original concept of the Zooplankton Methodology Manual included a related CD-ROM to include data, graphics and video images, particularly relating to sampling methods, and deriving from the seagoing workshop. This is not included with the Manual, however the WGZE are still considering the preparation and distribution of such a CD-ROM.

The ICES WGZE has been encouraging and co-ordinating zooplankton monitoring activities in the ICES area, and this Manual should contribute to these activities. Similarly, the development of major international initiatives with a particular focus on zooplankton, particularly the IGBP/SCOR/IOC co-sponsored Global Ocean Ecosystem Dynamics (GLOBEC) project, and the Living Marine Resources module of the Global Ocean Observing System (GOOS-LMR) make the publication of this Manual particularly timely. While not formally adopted by either program, the ICES Zooplankton Methodology Manual will contribute significantly to the standardization of methodology that both GLOBEC and GOOS-LMR strongly endorse.

The preparation of the Zooplankton Methodology Manual has by definition been a team effort. The members of the WGZE and the Editors have lead in this, over the years of development. It is a great pleasure to acknowledge the enthusiasm, dedication and patience of all the authors and co-authors during this process. I am particularly grateful to Dr Sarah Stafford, Clare Nehammer and Teresa Netzler of Academic Press who have all worked with me during the editing and production of the Manual.

Plymouth
December 1999

Roger Harris

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1 Introduction

J. Lenz

1.1 INTRODUCTION

Zooplankton occupies a key position in the pelagic food web as it transfers the organic energy produced by unicellular algae through photosynthesis to higher trophic levels such as pelagic fish stocks exploitable by man. The availability of zooplankton of the right size and at the right place and time during the first feeding period of fish larvae constitutes the famous match/mismatch hypothesis (Cushing 1990). Apart from predation, it is regarded as the most important environmental factor controlling the year class strength of a large number of commercial fish stocks known to be subject to strong fluctuations. Zooplankton grazing also largely determines the amount and composition of vertical particle flux. This not only fuels the benthos community but contributes to the removal of surplus anthropogenic CO_2 from the atmosphere through sedimentation and burial of organic and inorganic carbon compounds.

It is thus important to increase our comparatively sparse knowledge of all aspects of zooplankton ecology by a joint effort on the basis of intercomparable methods for understanding and predicting the impact of environmental changes on fish stocks. We also need to know more about the role of zooplankton in modeling the cycling of biogeochemical key elements such as carbon, nitrogen and phosphorus in the sea.

During the last decade, zooplankton research has gained a fresh impetus as mirrored by the very well attended International Symposium on Zooplankton Production, which took place in Plymouth in August 1994 under the auspices of the International Council for the Exploration of the Sea (ICES) (Harris 1995). In the keynote lecture, the 'pivotal role of zooplankton' in controlling phytoplankton production and shaping pelagic ecosystems was stressed by Banse (1995). The great significance of zooplankton research is also recognized in two current large international research programs. Within the Joint Global Ocean Flux Study (JGOFS) zooplankton plays an important role in regulating particle flux to the deep sea. The impact of climatic change on zooplankton population dynamics influencing the recruitment success of pelagic fish stocks forms the main focus of Global Ocean Ecosystem Dynamics (GLOBEC).

1.2 GENERAL DEFINITIONS

The term 'plankton' was coined by the German founder of quantitative plankton and fishery research Victor Hensen (1887). It is derived from the Greek word 'planao' meaning to wander and it has the same etymological root as 'planet'. It embraces all those organisms drifting in the water whose abilities of locomotion are insufficient to

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withstand currents, as opposed to nekton, the community of actively swimming organisms such as large crustaceans, cephalopods, fishes and aquatic birds and mammals. Although the adjective ‘planktonic’ has been established for a long time and is widely used, a plea is made in favor of the more correct term ‘planktic’ in which the syllable ‘on’ is deleted. The same problem is correctly solved in the corresponding term ‘benthic’ which is already in wider use than ‘benthonic’.

Although exposed to the forces of turbulence and currents, almost all zooplankton species have developed some means to move, at least to change their vertical position within the water column. Protozoans use either flagella and cilia or change their specific weight by ion exchange or incorporation of oil droplets, for instance. Movement by cilia is also common in many invertebrate larvae, for example in polychaete trochophores, mollusks and echinoderm larvae. Medusae and salps move by peristaltic contractions, and lobate ctenophores and pteropods move by flapping their lobes and wings respectively. Chaetognaths as ambush predators, which catch their prey in one swift movement, contract their longitudinal muscles and use their fins. Pelagic polychaetes and crustaceans have developed a large variety of special swimming appendages like parapodia and swimming legs. Appendicularia use their tails as oar blades. Small cephalopods employ the same mode of propulsion as the adults and fish larvae already possess rudimentary fins.

Zooplankton may be distinguished from phytoplankton either on the basis of morphology or mode of nutrition, autotrophic or heterotrophic. From the latter viewpoint zooplankton may be defined as the community of all phagotrophic organisms. According to their food preferences they can be classified as herbivorous, detrivorous, omnivorous or carnivorous. Heterotrophic plankton also include the osmotrophic bacteria, termed bacterioplankton. Mixotrophy, the combination of auto- and heterotrophy, is quite commonly found in flagellates and other protozoans like foraminiferans, radiolarians and ciliates, and it occurs in some metazoan phyla, too, for instance in cnidarians and mollusks. A further distinction is made between obligatory and optional mixotrophy.

Species spending their whole life in the pelagic realm are termed holoplanktic as opposed to meroplankton, which drift in the sea only for part of their life cycle. Among the protozoans, the majority of flagellates and ciliates as well as all pelagic foraminiferans and radiolarians belong to the first group. Also classed in the same group are from among the metazoans the siphonophores, ctenophores, pelagic polychaetes, heteropods, pteropods, ostracods, copepods with few exceptions, hyperiids, euphausiids, chaetognaths, appendicularians and salps.

Concerning the meroplankton, we distinguish between species which switch over from plankton to nekton during their juvenile stage, for example cephalopods and fish, and those which change from a planktic to benthic life and vice versa. Here we find a large variety of life strategies. A special case is the life cycle of most hydrozoans and scyphozoa, which exhibit two alternating generations. A summer generation of pelagic medusae with sexual reproduction is followed by a winter generation of benthic polyps with vegetative propagation.

Two contrasting modes of behavior are found among the other meroplankton groups, depending on their main habitat. We have plankton organisms with benthic resting stages and benthos organisms with planktic larvae. Cysts are produced by protozoans, flagellates and ciliates, and resting eggs by rotifers, cladocerans and some copepod families (Madhupratap *et al*. 1996) for surviving unfavorable environmental conditions. Propagation through planktic larvae is found in many benthos groups, for example polychaetes, mollusks, echinoderms, bryozoans, and barnacles and decapods among the crustaceans. Depending on the time period spent as drifting plankton and the availability of food, the larvae are either lecithotroph, living off their yolk reserves, or planktotroph, feeding on phyto- and zooplankton.

1.3 SIZE CLASSIFICATION

Marine zooplankton comprises a large variety of different organisms with some ten thousands of species if meroplankton is included. Their sizes range from tiny flagellates, a few μm large, up to giant jellyfish of 2 m diameter, and thus span six orders of magnitude. To cope with this enormous size range – volume and weight span eighteen orders of magnitude – a first attempt at size classification was already undertaken as early as 100 years ago in the first days of quantitative plankton research (Schütt 1892). He distinguished between micro-, meso- and macrozooplankton. This first classification has since been extended and modified several times. The latest revision (Sieburth *et al.* 1978) is now widely accepted (Figure 1.1).

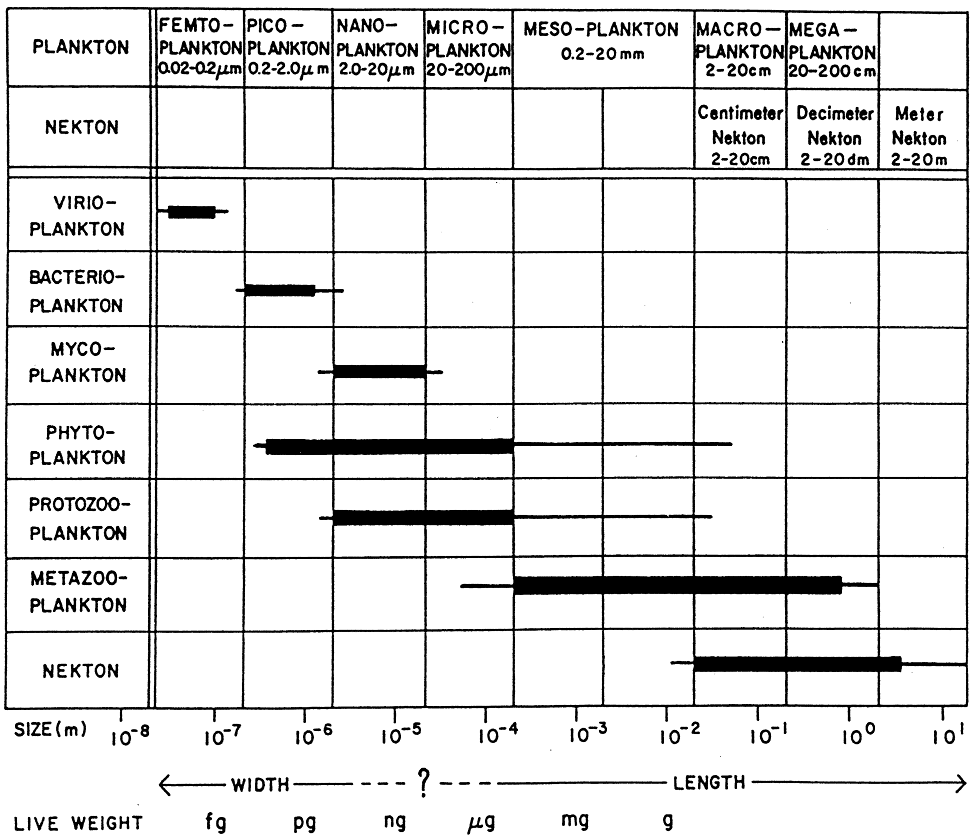

Fig. 1.1 Size spectrum of different taxonomic-trophic compartments of plankton including the size range of nekton modified after Sieburth *et al.* (1978) used with permission.

Zooplankton ranges over five size classes from nanoplankton to megaplankton. Since the finest mesh size of plankton gauze was, for a long time, 20 μm, this value defined the lower boundary of the so-called 'net plankton' which could be sampled by plankton nets, neglecting the smaller nano- and picoplankton. For this reason, the size class division (in Figure 1.1) is based on a factor of 2 instead of 1. Each size class covers one order of magnitude except mesozooplankton, which covers two orders. This exception is justified by the fact that the doubled size range corresponds to the size spectrum of traditional zooplankton samples taken by a mesh size of 200–330 μm. Such samples usually contain the bulk of crustacean plankton and, if present, of meroplanktic larvae as well. Moreover, the limits of this size class (0.2–20 mm) almost exactly match the size range of copepodites and adult copepods that generally constitute the dominant zooplankton group.

The main constituents of nanozooplankton (2–20 μm) are heterotrophic nanoflagellates feeding on bacteria. Most other protozoans, especially the ciliates, belong to the next size class, the microzooplankton (20–200 μm). This size class also covers the eggs and early development stages of crustacean plankton and meroplanktic larvae. Small hydromedusae, ctenophores, chaetognaths, appendicularians, doliolids, fish eggs and larvae together with the older stages of crustacean plankton and meroplanktic larvae comprise the mesozooplankton (0.2–20 mm) already mentioned.

In the next two size categories, species numbers diminish. Macrozooplankton (2–20 cm) are the larger specimens of hydromedusae, siphonophores, scyphomedusae, ctenophores, mysids, amphipods, euphausiids, salps and eel larvae, for instance. Only a few organisms reach the size of megazooplankton (20–200 cm). These are mainly large

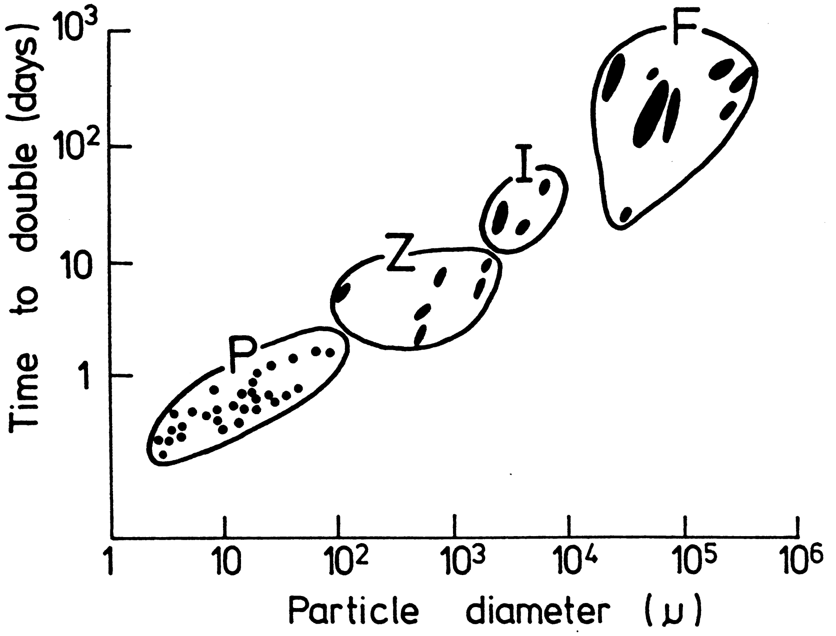

Fig. 1.2 The relationship between organism (particle) size expressed as equivalent spherical diameter and doubling time from data for phytoplankton (P), herbivores (Z), invertebrate carnivores or omnivores (I) and fish (F) from Sheldon *et al.* (1972) modified by Steele (1977) used with permission.

jellyfish, siphonophores and scyphozoa, and pelagic tunicates, pyrosomes and chain-forming salps.

Body size is a decisive factor in governing growth rate and doubling time of plankton organisms. Since within the pelagic food web most predators swallow their prey organisms undivided, body size also determines food-chain relationships. An example for its significance is the famous diagram by Sheldon *et al.* (1972) and modified by Steele (1977) as shown in Figure 1.2.

The methods described and discussed in this manual deal with net plankton, mainly with micro-, meso- and macrozooplankton which embrace most of the dominant species in meso- and eutrophic ecosystems.

1.4 MAIN SYSTEMATIC GROUPS

Another way of classifying planktic organisms is to consider their systematic position and biochemical composition. The first step is to distinguish between proto- and metazooplankton. Among the protozoans the ciliates, especially naked ciliates, form the ecologically most important group. Their division rate is so rapid as to enable them to almost keep pace with phytoplankton. Thus they react immediately to algal growth and take advantage of the food supply offered. In neritic ecosystems they are often the first grazers of the phytoplankton spring bloom (Smetacek 1981).

Characteristic of metazooplankton is a comparatively long life-span, ranging from several days in rotifers and few weeks in small crustaceans to several years in large euphausiids in polar regions. A long life-span generally goes hand in hand with a long development period. This is most pronounced in crustaceans where in some groups organisms have to pass through many larval stages before reaching sexual maturity.

Since crustaceans are represented in zooplankton mainly by eight orders, cladocerans, ostracods, copepods, cirripeds, mysids, amphipods, euphausiids and decapods, these organisms generally dominate the samples. They are collectively termed crustacean plankton as opposed to the so-called gelatinous plankton. In the latter group the organisms are characterized by a gelatinous body, the most prominent representatives being the common jellyfish (Scyphomedusae). Gelatinous zooplankton comprises various systematic groups, indicating that this particular mode of adaptation to planktic life in the sea was arrived at through independent evolutionary processes. We refer to cnidarians with hydromedusae, siphonophores and scyphomedusae, the ctenophores and the pelagic tunicates with pyrsomes, doliolids, salps and appendicularians. The latter are included not because of their body constitution but because they have gelatinous houses which are regularly abandoned and rebuilt. Occasionally, a single species in other groups has acquired a gelatinous body too, for example in heteropods and ostracods. The high water and also salt content of these organisms causes a substantial shift in the ratio between organic matter content and wet weight, dry weight and inorganic matter content as compared with crustacean plankton, for instance. It further enables gelatinous species to grow very fast manifested by the huge swarms frequently encountered.

Other ecologically important groups, not belonging to crustacean or gelatinous plankton, are rotifers in brackish waters, pteropods, chaetognaths, and especially fish larvae.

1.5 SPECIES DIVERSITY

Table 1.1 gives an overview of the main marine zooplankton groups with their approximate species numbers. The figures in brackets are very rough estimates since relevant data are lacking. This is especially true of the meroplanktic larvae, where estimates rely on the number of the parental benthos and nekton species. The figures quoted may therefore give only an idea of the vast species diversity in these groups. Summing up the figures listed in Table 1.1, one arrives at a total of around 36 000 species. Holoplankton with about 6000 protozoan (16%) and about 4000 metazoan species (11%) makes up roughly a quarter (27%). The bulk (73%) consists of the lesser known meroplankton with uncertain estimates, and the total should therefore be taken as only a tentative measure of the order of magnitude.

In most aspects of zooplankton research, accurate species identification is a necessary but often not easily achievable prerequisite. The help of experts in systematics might be needed. Even if only the biomass distribution is investigated during a survey by applying bulk methods like volume or weight measurements, at least a rough inspection of the main species composition would provide valuable information.

A first impression of the vast diversity of zooplankton organisms may be obtained from the excellent drawings by the Scottish planktologist James Fraser (1962), reproduced in Figures 1.4–1.16 at the end of this chapter. The following contains a short but in no way exhaustive list of introductory guides, plankton books, identification sheets and recent monographs on various zooplankton taxa.

There exist several introductory guides which are well written and contain a large number of informative drawings. Newell and Newell (1973) present boreal plankton, Wickstead (1965) tropical plankton and Tregouboff and Rose (1957) subtropical plankton in the Mediterranean Sea. Todd and Laverack (1991) provide a special introduction to neritic boreal zooplankton, this differs from other guide books in presenting photographs of preserved specimens as encountered by the normal investigator. Two very readable and well illustrated books which give a general account of the life of North Atlantic plankton are Fraser's (1962) *Nature adrift* and Hardy's (1970) *World of plankton*, whereas Raymont's (1983) *Zooplankton* is recognized as a comprehensive textbook.

The identification sheets, edited by ICES since 1947, are a collection of leaflets dealing with all zooplankton taxa from Foraminifera to fish larvae occurring in the northeast Atlantic and its adjacent seas. Most of them contain an identification key and table of geographical distribution. A table of contents of the sheets is found in Todd and Laverack (1991).

The monographs listed below also include accounts of the biology of various zooplankton groups. Dinoflagellates (Taylor 1987) play an important role in the systematically diverse group of heterotrophic flagellates. Ciliates are described by Corliss (1979), Foraminifera by Hemleben *et al.* (1989) and Radiolaria by Anderson (1983). The Hydro- and Scyphomedusae are presented by Russell (1953, 1970) in two volumes. Siphonophores are dealt with by Alvariño (1971) and Mackie *et al.* (1987) and ctenophores by Reeve and Walter (1978). An account of boreal meroplanktic larvae, especially of polychaetes and mollusks, is given by Thorson (1946). Heteropoda are described by Tesch (1949) and Pteropoda by Pruvot-Fol (1942) and Tesch (1946, 1948, 1950). Juvenile cephalopods are treated by Sweeney *et al.* (1992).

Details on the crustacean plankton are found in the following monographs: Cladocera (Egloff *et al.* 1997), Ostracoda (Angel 1993), Copepoda (Rose 1933; Marshall and Orr

Table 1.1 Systematic overview of the main zooplankton taxa with approximate species numbers (figures in brackets are very rough estimates), plankton status (holo- or meroplankton) and size class distribution (cf. Figure 1.1). Crosses indicate the distribution: rare +, common ++, dominant +++.

Systematic groups	Holo–Mero Plankton		Nano 2–20 μm	Micro 20–200 μm	Meso 0.2–20 mm	Macro 2–20 cm	Mega 20–200 cm
Protozooplankton							
Heterotrophic Flagellates (600)	+++		+++	+++	+		
Ciliata (1000)	+++		+	+++	+		
Foraminifera (Globigerina) 30	+++			++	++		
Radiolaria 4500	+++			+	+++	+	
Metazooplankton							
Cnidaria							
Hydromedusae (500)	+	+++			++	++	+
Siphonophora 150	+++				+	++	+
Scyphomedusae 250	+	+++			+	++	++
Ctenophora 80	+++				+	++	+
Rotatoria (100)		+++		++	++		
Polychaeta (100)	+++				++	++	+
Polychaeta Larvae (3000)		+++		+	++		
Mollusca							
Heteropoda 30	+++				++	++	
Pteropoda 100	+++				+++	+	
Cephalopoda 500	+	+++			++		
Veliger Larvae (10 000)		+++		+	+++		
Crustacea							
Cladocera 30	+	+++			+++		
Ostracoda 350	+++				+++	+	
Copepoda							
Calanoida 1200	+++	+		+	+++		
Cyclopoida 100	+++			+	+++		
Harpacticoida 100	+++			+	+++		
Cirripedia Larvae (800)		+++		+	+++		
Mysidacea 600	+++				++	++	+
Amphipoda (Hyperiidea) 300	+++				+++	+	
Euphausiacea 90	+++				++	++	
Decapoda 200	+++				+	+++	
Decapoda Larvae (6000)		+++			+++	+	
Echinodermata Larvae (2000)		+++			+++		
Chaetognatha 50	+++				++	++	
Tunicata							
Copelata 60	+++				+++	+	+
Thaliacea 45	+++				++	++	+
Fish Larvae (3000)		+++			+++	+	

1955; Mauchline 1998), Cirripedia (Southward 1987; Anderson 1994), Mysidacea (Mauchline 1980), Hyperiidea (Bowman and Gruner 1973; Vinogradov *et al.* 1996), Euphausiacea (Mauchline and Fisher 1969; Mauchline 1980), Decapoda (Omori 1974; Dall *et al.* 1990) and decapod larvae (Gurney 1939). Chaetognaths are described by Alvariño (1965) and Pierrots-Bults and Chidgey (1988). Pelagic tunicates are treated by Fraser (1981) and Bone (1997) and fish larvae by Fahey (1983) and Moser *et al.* (1984).

1.6 ECOLOGICAL POSITION

The ecological role of an organism is largely determined by its position and significance in the food web. Decisive characteristics are body size, food spectrum and feeding type. Filter-feeders like copepods, euphausiids and pelagic tunicates, feeding on different size spectra of phytoplankton, organic detritus as well as on nano- and microzooplankton, are primarily herbivores and omnivores. As secondary producers they thus occupy the second and to some extent third level in the food web. Various filter techniques are employed. Copepods and euphausiids use their highly structured mouthparts and feeding appendages, appendicularians a fine-meshed funnel net inside their house and thaliaceans a ciliary mucous net inside their barrel-shaped body. Ciliates, rotifers and many meroplankton larvae feed by means of ciliary currents. Thecosome pteropods employ large mucous nets for trapping their prey.

Raptional feeders are typically predators. Cnidarians and ctenophores catch their prey with stinging or sticky tentacles. Pelagic polychaetes, heteropods, gymnosome pteropods and cephalopods among the mollusks, hyperiids (amphipods) and fish larvae may be regarded as active hunters, whereas chaetognaths are described as ambush predators.

Cladocerans, ostracods and mysids occupy an intermediate position between the typical filter-feeding and the raptional zooplankton. It should, however, be stressed that the above classification has no strict demarcations, since there exist many exceptions in various groups. Ciliates, for instance, have carnivorous members feeding on their own relatives. Some scyphomedusae (Hansson 1997) and ctenophores (Greve 1981) prefer to prey on related species. Similarly in pteropods, gymnosomes feed on thecosomes. There are quite a number of carnivorous species among copepods and euphausiids too, and even a very typical filter-feeder like *Calanus finmarchicus* is able to switch to raptorial feeding, at least under laboratory conditions.

Because of their worldwide distribution, abundance and dominance, the following three groups may be regarded as the most significant secondary producers, the naked ciliates among the protozoa, and the copepods and euphausiids among the metazoa, both the latter specially in boreal and polar regions. Appendicularians and salps are also of importance in some areas, but their occurrence is of a more seasonal character and they are not as ubiquitous as the former groups. Ctenophores can have a high ecological impact as predators, as has been demonstrated in the Black Sea by the recently introduced species *Mnemiopsis leidyi* (Harbison 1994). Scyphomedusae like *Aurelia aurita* can function as top predators in inshore seas and structure the food web by top-down control (Behrends and Schneider 1995).

The functioning of food webs depends on the balance between bottom-up and top-down control. Bottom-up is the resource-driven control. In the pelagic realm, it is primarily exercised by the supply of nutrients determining the amount of primary production. Recently, the pivotal role of zooplankton grazing in controlling phyto-plankton growth has been stressed (Banse 1995) in explaining the apparent paradox of the so-called 'high' nutrient 'low' chlorophyl regions. A high grazing pressure by herbivores prevents phytoplankton blooms.

The top-down control is particularly marked in the microbial food web, where ciliates are the top predators. They themselves are controlled by filter-feeding metazooplankton, thus connecting the microbial with the classical food web (Figure 1.3). Both food web types coexist in all areas of the ocean, but their relative significance changes with region and season. The classical food chain dominates in eutrophic cold-water and upwelling ecosystems. The microbial food web, however, is most significant in oligotrophic warm-

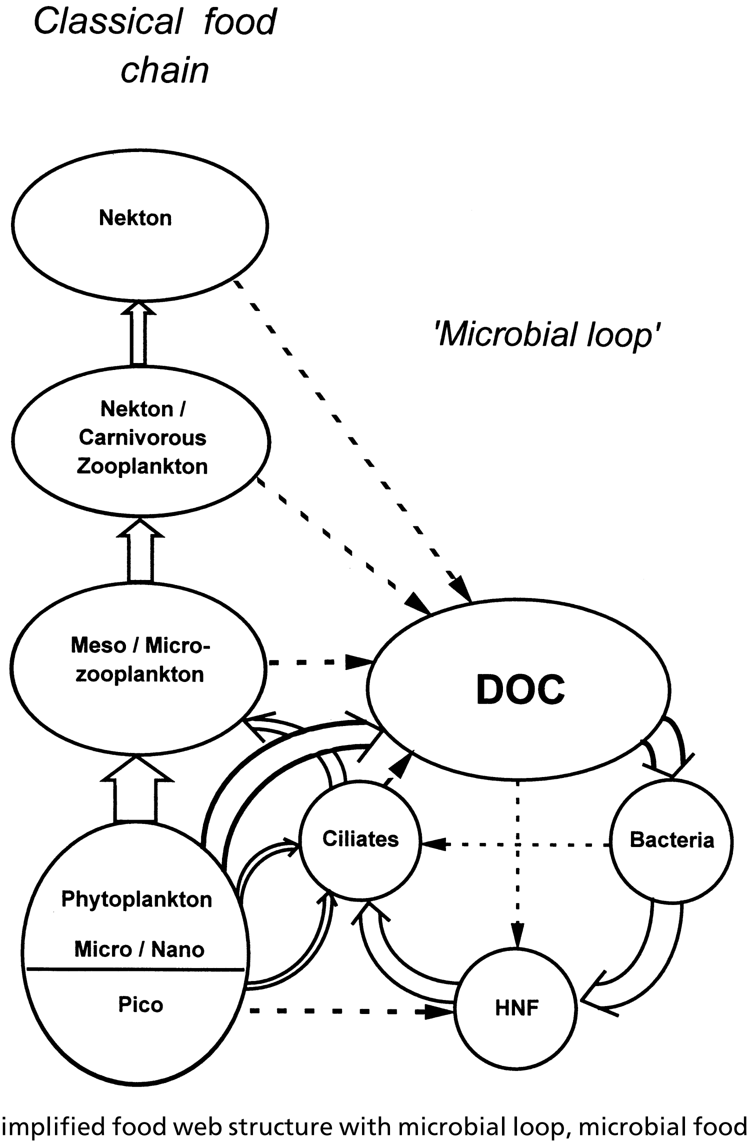

Fig. 1.3 Simplified food web structure with microbial loop, microbial food web and classical food chain. Microbial food web includes microbial loop and autotrophic picoplankton and nanoplankton $< 5\,\mu$m. (DOC = dissolved organic carbon and HNF = heterotrophic nanoflagellates.) Modified after Lenz (1992) used with permission.

water systems and during summer stratification in nutrient-depleted surface waters in higher latitudes (Lenz 1992).

1.7 DISTRIBUTION PATTERN

Zooplankton distribution is governed by water depth, trophic status of the area and temperature regime, to mention the most important factors. Water depth separates neritic from oceanic plankton. Neritic plankton inhabits inshore waters up to about 200 m at the shelf edge. Characteristic of neritic plankton is a high proportion of meroplankton larvae and species with benthic resting eggs. The proximity to the sea bottom favors an exchange between plankton and benthos communities.

Oceanic zooplankton on the other hand is characterized by a general absence of meroplankton and the presence of distinct vertical migrators. Among them are, for instance, larger copepod species and euphausiids. The daily migration, rising at dusk and descending at dawn, often extends over several hundred metres. Seasonal vertical migration as exhibited by many members of the copepod genus *Calanus* in higher latitudes even reaches down to depths of 500–1000 m. The epipelagic (0–200 m) and mesopelagic zones (200–1000 m) are the main domain of zooplankton. Below 1000 m depth in the bathypelagical, their concentration generally decreases logarithmically with depth (Vinogradov 1997).

Species diversity is generally governed by temperature regime and evolutionary age of ocean areas. The highest diversity is thus found in tropical and subtropical regions and the lowest in extreme environments such as polar zones and brackish water areas. Due to the steady water exchange through ocean currents many species enjoy a wide and often even worldwide distribution within their climatic boundaries. This is especially true for the warm-water sphere comprising all three oceans. Sporadic occurrences of neritic species observed since the turn of the century in increasing numbers are now generally explained by the high amount of ballast water transported and discharged all over the world by international ship traffic (Carlton and Geller 1993).

In studying the distribution and seasonal cycle of marine zooplankton, one is always faced with the problem that the sea is a highly dynamic environment with a steady motion and mixing of water masses. Whereas a limnologist, working in a small or medium-sized lake, can be almost certain of dealing with the same population during an investigation period, this is more the exception than the rule for a marine planktologist working in the sea. Because of prevailing currents and advection of new water masses, it is often virtually impossible to follow the same population of organisms (Huntley and Niiler 1995). Observations at a fixed station therefore generally represent a mixture of 'sequences' of different plankton populations passing by and 'seasonal changes' of the same populations. Every plankton sampling program should be accompanied by a detailed oceanographic documentation, especially salinity measurements and increasingly use of hydrodynamic and particle-tracking models, for identifying the impact of water mass changes (Chapter 2).

1.8 GROWTH AND METABOLISM

Growth and metabolism of zooplankton organisms are governed by the interaction of a number of forces which may be either internal or external. Internal factors are body size and physiological properties, such as range of temperature tolerance, developmental stage and physiological state. Feeding activity, for instance, depends on the molting cycle in crustaceans. External factors are food supply and nutritional properties of food, as well as various environmental factors such as temperature, salinity and oxygen saturation. One must distinguish between potential growth rate under optimal conditions and actual growth rate which is often reduced by one or more of the factors mentioned above. An additional factor affecting population growth is top-down control through predation.

Metabolism as well as growth rate is an allometric function of body size. Small organisms have a comparatively higher metabolic rate and grow faster than large ones. This allometric relationship is described by the general equation

$$\boldsymbol{R = aW^b} \tag{1.1}$$

R stands for respiration or any other metabolic rate including growth. W is body size, usually measured as dry weight, and a and b are constants. Whereas a depends on physiological properties of the organisms and environmental conditions, b is a uniform constant attaining the approximate value of 0.75 (Peters 1983). An increase in body size, expressed as volume or weight, by a factor of 1000, which corresponds to a ten-fold increase in body length, results in a reduction of metabolic rate by a factor of 5.6. This value gives an idea of the difference in growth rate between members of two neighboring size classes, for example microzooplankton and mesozooplankton.

Among the external factors governing growth, food supply and temperature are most important. The availability of food varies with season in higher latitudes. Thus the majority of organisms have adapted their life cycle in such a way that they encounter optimal conditions during their reproduction period.

There is also a relationship between food supply and energy conversion. The sparser the food the better the digestion. During phytoplankton blooms 'superfluous feeding' has been observed in herbivorous copepods. Their feces contained many undigested phytoplankton cells. In considering energy conversion it is advisable to distinguish between physiological efficiency in individual organisms and ecological efficiency expressing food chain efficiency. The first may be more than twice as high as the latter, where generally only a section of secondary producers, for example herbivorous copepods, are related to total primary production.

Water temperature in the open sea ranges from about $-2\,^\circ$C to approximately $32\,^\circ$C. Zooplankton organisms inhabit all regions of the sea according to their physiological temperature adaption and tolerance limits. These may be narrow, stenotherm, as in polar and deep-sea plankton, or eurotherm, as in temperate and neritic waters of higher latitudes. Within the given tolerance limits of individual species, and within the whole range of sea temperature for the total plankton community, the intensity of all vital processes depends on the prevailing temperature conditions. This temperature dependency is based on the reaction speed of physicochemical processes in living organisms and is described by the van't Hoff law or the so-called Q_{10} rule. For a temperature rise of $10\,^\circ$C, an increase in metabolic rate of two to three times is generally observed (Schmidt-Nielsen 1979). Special adaptations to extreme temperatures in polar seas, for instance, are possible to some degree, but the general validity of this rule for all poikilotherm organisms is not suspended.

Knowing body size, developmental stage and physiological state of a plankton organism and the temperature conditions, it is thus possible to calculate the potential growth rate. In marine copepods, where dominant species often vary comparatively little in body size, temperature has been demonstrated as the main factor governing their growth rate (Huntley and Lopez 1992).

Physical stress factors such as reduction in salinity and oxygen content limit species distribution and diminish growth and body size in those species which are able to tolerate these adverse environmental conditions. Thus brackish water organisms are usually smaller than their marine relatives because of the extra energy spent in physiological adaption.

Assimilated energy is converted both into somatic growth and egg production. Female copepods on reaching the adult stage after the last molting spend all their surplus energy on egg production. Thus egg production replaces somatic growth. Special methods have been developed to measure egg production in order to include it in estimates of zooplankton production.

1.9 REPRODUCTION AND DEVELOPMENT

Vegetative propagation through binary fission predominates in protozooplankton, whereas sexual reproduction is the common mode of propagation in metazooplankton. There are, however, quite a number of exceptions from this rule. The pelagic foraminifera, the Globigerina, multiply, for instance, by multiple fission, producing either vegetative cells or flagellated gametes. Vegetative propagation through budding occurs in hydromedusae and is a regular part of the life cycle of thaliaceans.

Parthenogenesis, the asexual propagation through unfertilized eggs, is a special achievement in rotifers and cladocerans. After a period of propagation through parthenogenesis a sexual generation appears in which the females produce fertilized eggs. These are protected by a thick shell and hibernate on the sea bottom until parthenogenic females hatch in spring.

Vegetative propagation and parthenogenesis have the great ecological advantage that a large population can be built up in a short period. These organisms are thus able to optimally utilize favorable feeding conditions.

Equally advantageous is a direct development from egg or first larval stage to adult, as we have with the ephyra in scyphomedusae. Such a development, which is found in ctenophores, ostracods and chaetognaths, for instance, is usually much faster than passing through a number of different larval stages, as is typical for copepods and euphausiids. Copepods have to pass six naupliar and five copepodite stages before molting into adults.

1.10 STANDING STOCK AND PRODUCTION

The relationship between standing stock and production of a population depends on food supply and climatic conditions and varies largely with season in most areas. The stronger the seasonal impact, generally the greater the variation. A very decisive factor is the temperature governing the growth rate. In cold-water ecosystems dominant species need to maintain a relatively high biomass to assert their predominance, since production rate is slow. In warm-water ecosystems it is possible to build up a large population from a low standing stock because of the high growth rate. The ratio between production and biomass of a species is an important index of its population dynamics and indicates the turnover rate of organic matter. Under optimal food conditions, the highest turnover rate is thus observed in small organisms in the tropics and the lowest in large organisms in polar regions.

Many zooplankton species, especially those in cold-water and upwelling ecosystems, have developed various life strategies to adjust their growth and reproduction period to optimal environmental conditions. One mode of adaption to cope with unfavorable seasonal conditions is to produce resting eggs, as already mentioned. It is common in cladocerans and also occurs in a number of neritic copepod species (Madhupratap *et al.* 1996; Williams-Howze 1997). Another strategy is the evolution of a diapause stage as observed in members of the genus *Calanus* and its relatives, where copepodite stages IV and V, after having accumulated a large lipid reserve, migrate down to great depths and drift there motionless until the beginning of the next growth season.

1.11 CONCLUSION

When measuring zooplankton biomass and estimating its production, one usually tends to deal with the whole community. By employing different mesh sizes in nets and sieves it is possible to separate the main components from each other, for instance microzooplankton from mesozooplankton or small herbivores from larger carnivores by means of size fractionation. This approach may occasionally prove quite successful, depending on the size spectra and diversity of the species. Bulk parameters obtained in this way may provide useful data for modelers. It is, however, always necessary to realize that such data are no more than a methodological compromise, for reality is far more complex. The trophic role and ecological significance of zooplankton communities depends on the diversity, behavior and interaction of their species. These communities are often dominated by so-called key taxa, which play the main role in channeling energy up the food web and exercising top-down control through grazing or predation. Future research should put more emphasis on special environmental adaptations of these predominant species and their ecological significance in forming the food web (Verity and Smetacek 1996).