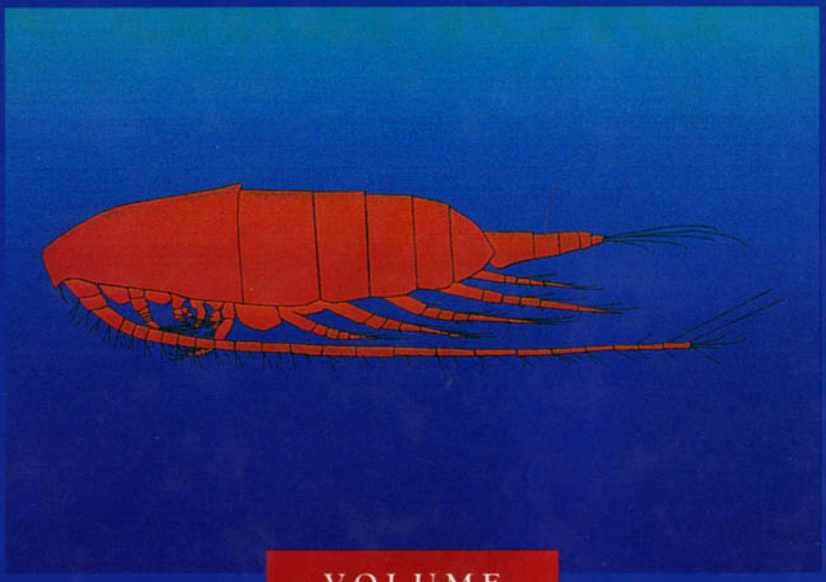
Advances in MARINE BIOLOGY

THE BIOLOGY OF CALANOID COPEPODS



VOLUME 33

J Mauchline

Series Editors
J H S Blaxter, A J Southward and P A Tyler

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The Biology of Calanoid Copepods

by

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Dedicated to my wife Isobel

Preface

Calanoid copepods have been of intense interest to marine biologists for more than a century. Many scientific papers have been published over the years, but this is the first assessment of their biology, as a whole, that has been attempted.

Many colleagues throughout the world have encouraged and helped in the production of this work. My initial interest was stimulated by Dr J. H. Fraser and Dr S. M. Marshall many years ago. I wish to acknowledge, in particular, the helpful correspondence and/or discussions with G. A. Boxshall, J. M. Colebrook, F. D. Ferrari, A. Fosshagen, the late A. Fleminger, H. Grigg, L. R. Haury, C. C. E. Hopkins, K. Hülsemann, S. Kasahara, I. A. McLaren, S. Nishida, M. Omori, G. -A. Paffenhöfer, J. S. Park, T. Park, S. Razouls, H. S. J. Roe, K. Schulz, S. -I. Uye, J. C. Vaupel Klein, P. Ward, K. F. Wishner, and J. Yen. A special debt of gratitude is owed to Miss E. Walton, the Librarian of the Dunstaffnage Marine Laboratory, who has put up with my vagaries for years and obtained outside library loans of some very obscure publications; I especially thank her for her perseverance and patience. Finally, it is a pleasure to acknowledge the helpful comments, and aid in proof-reading of the manuscript, of the Editors Professor J. H. S. Blaxter, Professor A. J. Southward and Professor P. A. Tyler.

John Mauchline

1. Introduction

Copepods are probably the most numerous multicellular organisms on earth. They outnumber the insects although the insects are more diverse, having more species than copepods. They are aquatic animals, primarily marine, although they also occur in vast numbers in fresh water environments. Humes (1994) estimates that there are some 11,500 species, divided between about 200 families and 1650 genera, known at the end of 1993. He attempts to estimate the actual numbers of species on earth and suggests that as few as 15% of existing species are known at present.

The Copepoda form a subclass of the phylum Crustacea. The name copepod originates from the Greek words *kope*, an oar, and *podos*, a foot, and refers to the flat, laminar swimming legs of the animals. As Huys and Boxshall (1991) point out, there is no popular English name for them although the Norwegian *Hoppekrebs*, German *Ruderfusskrebs*, and the Dutch *Roeipootkreeft* reflect the derivation of the name Copepod. There are ten orders of copepods (Table 1) containing different numbers of families, genera and species:

The Platycopioida are marine, benthopelagic species, two living in anchialine caves in Bermuda.
The Calanoida are primarily pelagic, 75% are marine, 25% live in fresh water. Some marine species are benthopelagic or commensal.
The Misophrioida are primarily benthopelagic and inhabitants of anchialine caves – only two species are pelagic – and the Mormonilloida are pelagic marine species.
The Cyclopoida are divided between marine and fresh waters and can be pelagic, commensal or parasitic.
The Gelyelloida occur in karstic systems in France and Switzerland.

Table 1 Classification of copepods. The numbers of marine families (F), genera (G) and species (S) recognized in each order are indicated; these numbers are approximate because of the continuous addition of new taxa and modifications of older ones. After Huys and Boxshall (1991) and Humes (1994).

	F	G	S
Subclass Copepoda Milne-Edwards, 1840			
Infraclass Progymnoplea Lang, 1948			
Order Platycopioida Fosshagen, 1985	1	3	10
Infraclass Neocopepoda Huys & Boxshall, 1991			
Superorder Gymnoplea Giesbrecht, 1882			
Order Calanoida Sars, 1903	41[1]	195[1]	1800[1]
Superorder Podoplea Giesbrecht, 1882			
Order Misophrioida Gurney, 1933	1	11[4]	19[4]
Order Cyclopoida Burmeister, 1834	12	80[2]	450[2]
Order Gelyelloida Huys, 1988	1	1	2
Order Mormonilloida Boxshall, 1979	1	1	2
Order Harpacticoida Sars, 1903	47	300[3]	2500[3]
Order Poecilostomatoida Thorell, 1859	46	>260	1570+
Order Siphonostomatoida Thorell, 1859	37	245	1430+
Order Monstrilloida Sars, 1903	1	4[4]	74[4]

[1]Excluding Diaptomidae and fresh water genera in other families.
[2]Marine and fresh water combined (Bowman and Abele, 1982).
[3]Approximate values derived from Bowman and Abele (1982).
[4]Approximate numbers derived from Razouls (1996).

The Harpacticoida are primarily marine species, 10% living in fresh waters. Most species are benthic, a few pelagic or commensal.
The Poecilostomatoida and Siphonostomatoida are marine, commensal or parasitic species.
The Monstrilloida are marine species that are pelagic as adults but parasitic when young.

The phylogenetic relationships of these orders are examined by Huys and Boxshall (1991) and reviewed by Ho (1990, 1994). There are several proposed cladograms illustrating possible linkages, one of which is given in Figure 1. An excellent summary of the development of current ideas on the evolutionary structure within the Copepoda is provided by Huys and Boxshall (1991). The Platycopioida superficially look like calanoid copepods because the division between the prosome and urosome is between the fifth pedigerous segment and the genital somite. This division is more anterior in all other copepods, being between the fourth and fifth pedigerous segments. The Platycopioida are nearest to the hypothetical ancestral stock of the Copepoda and the Calanoida are next. The gross morphology of the Calanoida is uniform (Figure 2) unlike that within other orders of the Copepoda (Figure 1 and Dudley, 1986; Huys and Boxshall,

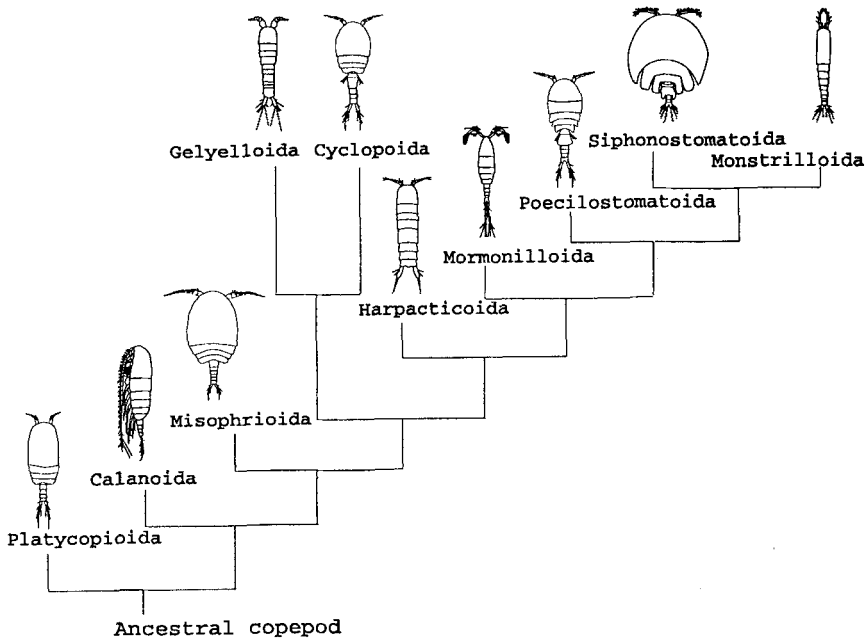


Figure 1 Phylogenetic relationships within the Copepoda. (After Huys and Boxshall, 1991; Ho, 1994.)

1991) where benthic, commensal and parasitic life styles have been adopted.

This volume examines the Platycopioida and Calanoida in detail but is primarily restricted to the marine and brackish water environments. There are, however, many fresh water species. They belong primarily to three families within the Calanoida: the Temoridae, Centropagidae and Diaptomidae. The genus *Senecella*, originally ascribed to the Pseudocalanidae but now to the Aetideidae, contains two species, one in north American fresh water lakes, the other in brackish waters of the Kara and Laptev Seas. The fresh water copepods are described in detail by Dussart and Defaye (1995) and reference to that work should be made for further information. Evolution within the Centropagidae is discussed by Maly (1996).

Calanoid copepods are of prime importance in marine ecosystems because many are herbivorous, feeding on the phytoplankton, and forming a direct link between it and fish such as the herring, sardine, and pilchard. Copepods are at the small end of the size spectrum of food of the baleen whales but sei, bowhead, right and fin whales consume large quantities of

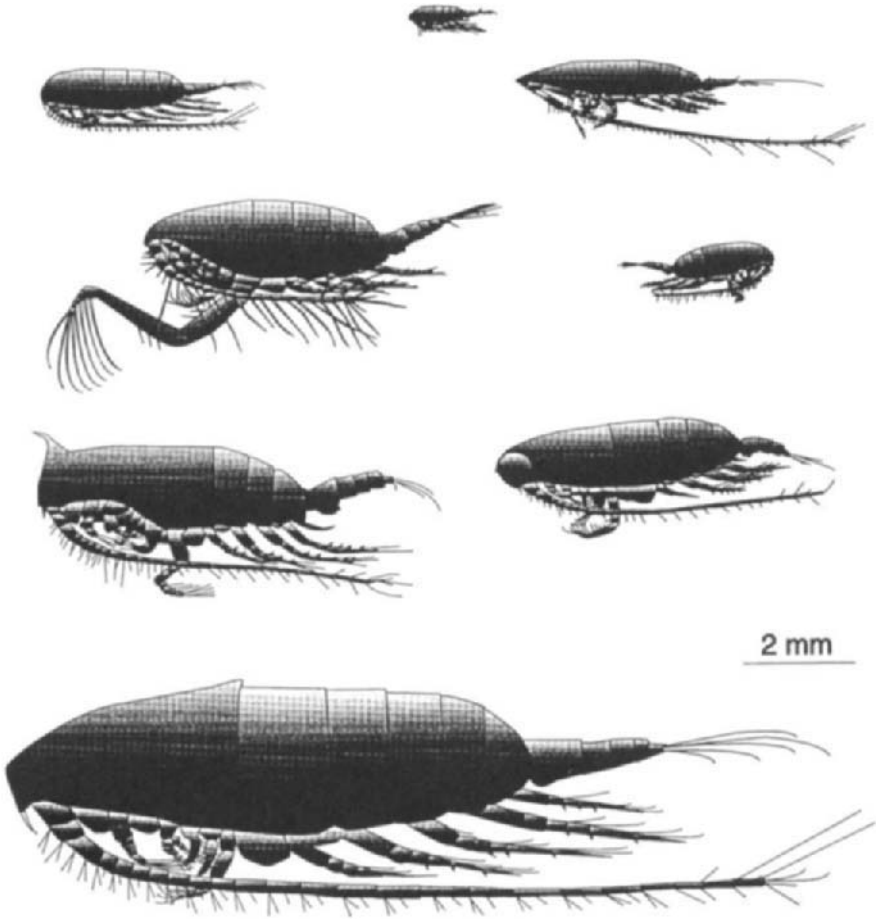


Figure 2 Body form of a variety of species of calanoid copepods. From top, and then left to right: *Acartia* sp., *Calanus finmarchicus*, *Rhincalanus nasutus*, *Pseudeuchaeta brevicauda*, *Aetideopsis multiserrata*, *Gaetanus latifrons*, *Cephalophanes refulgens*, and *Bathycalanus princeps*.

them in the north Atlantic, north Pacific and Antarctic Oceans (Gaskin, 1982). Copepods are also eaten by a vast variety of invertebrate species, both pelagic and epibenthic.

Pelagic copepods dominate the numbers of organisms caught in plankton samples from most sea areas, representing 55 to 95% of the numbers caught (Longhurst, 1985). They are most dominant in the Arctic and Antarctic Oceans and also over continental shelves in middle latitudes. Their numbers

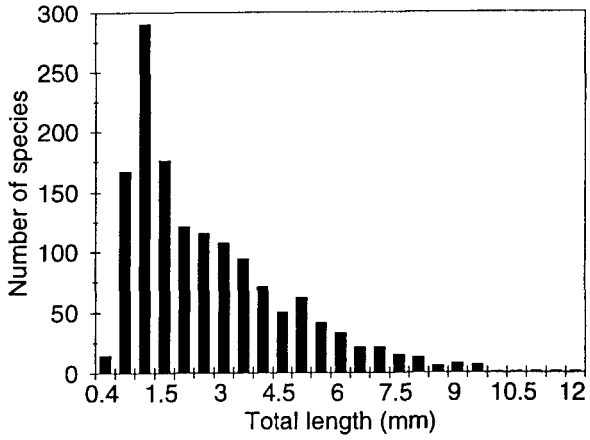


Figure 3 Size frequency distribution of calanoid copepod species.

relative to other organisms vary seasonally in middle and high latitudes. Their body size is small, most species having a body length of 0.5 to 2.0 mm (Figure 3). Consequently, their proportion in terms of biomass of plankton is lower, being in the range 25 to 80% depending on the region, season, and presence or absence of aggregations of other organisms such as siphonophores and euphausiids. The size record for a calanoid copepod is for a female *Bathycalanus sverdrupi* caught at 2000 to 2050 m depth in the Gulf of Guinea by Owre and Foyo (1967); it measured 18.0 mm in total length. The second largest copepod caught is a female *Bradycalanus pseudotypicus enormis* from 2893 m depth that measured 17.5 mm in total length (Björnberg, 1967a). One of the smallest species recorded is the cave-dwelling *Nanocopia minuta*; the female measured 0.27 mm and the male 0.25 mm in total length (Fosshagen and Iliffe, 1988).

1.1. THE SCIENTIFIC LITERATURE

The study of calanoid copepods is a complex and dynamic activity. The literature is huge and increasing all the time. There is no annotated bibliography to provide easy access although Vervoort (1986a,b, 1988) has listed, alphabetically by author, papers referring to any copepod whether calanoid or not. The list is very comprehensive but does not give direct access to literature on individual taxa. *Zoological Record* remains the principal source of such information in the pre-CD ROM eras.

The calanoid copepods, excluding the fresh water family Diaptomidae and the fresh water genera of the family Centropagidae (Table 9, pages 51–52), currently consist of some 41 families, 195 genera and 1800 species. Most species are extremely rare, some 1170 of them having 1–20 literature citations. A further 430 species have 20–50 citations and about 90 species have between 50 and 100 citations (Mauchline, unpublished). The remaining 72 most commonly cited species are listed in Table 2. The absolute number of citations is approximate because many references to the occurrence of copepods in the diets of other organisms have not been searched for. The list, however, indicates those species and genera that have received much attention. It reflects work in inshore coastal species and in the north Atlantic and north Pacific Oceans. It also shows which species are important in the economics of the oceans although there are one or two omissions; for example, the dominant species over large areas of the Antarctic Ocean, *Ctenocalanus citer*, *Metridia gerlachei* and *Drepanopus forcipatus*, are missing and reflect the relative lack of research there compared with other sea areas. Deep-sea species are also not prominent unless they are eurybathic and occur frequently in shallower depth horizons e.g. *Euchirella* spp., *Heterorhabdus* spp., *Undeuchaeta plumosa* (Table 2). Thus, knowledge about individual species varies considerably.

This volume is not a comprehensive review of all the literature but an attempt is made throughout to quote references that give easy access to secondary compilations on topics, whether they be on individual species or on ecological, physiological or other subjects. The reference lists of cited papers have been examined to evaluate coverage of their topic. Emphasis is placed on recent papers but older, significant contributions are also cited. References to descriptions of species are also treated in the same way in the world list in Chapter 4.

All aspects of the biology of calanoids are reviewed but some in more detail than others. The reactions of calanoids to concentrations of phytoplankton are described but no attempt is made to assess the information on estimates of the varying proportion of the phytoplankton stock grazed by copepods. This is a difficult field because of the dynamics of the phytoplankton and the selective capabilities of the copepods. Sautour *et al.* (1996), for example, found that the herbivorous copepods of the Gironde Estuary, dominated by *Paracalanus parvus* and *Temora longicornis*, grazed 17 to 21% of the total primary production and 9 to 14% of the phytoplankton stock. Some 70% of the phytoplankton stock, however, was less than 5 μm and too small to be available to the copepods. Consequently, they estimated that the copepods removed 35 to 68% daily of the size fraction of the stock available to them. Such estimates can only be approximate and can only be used to infer food excess or limitation for the copepods. The linking of diel vertical migration of the copepods to

Table 2 The most commonly cited species of calanoid copepods in the scientific literature. (Mauchline, unpublished).

100–200 citations	
Acartia bifilosa	*Eurytemora herdmani*
Acartia danae	*Haloptilus longicornis*
Acartia discaudata	*Heterorhabdus papilliger*
Acartia negligens	*Heterorhabdus spinifrons*
Calanoides acutus	*Isias clavipes*
Calanoides carinatus	*Labidocera wollastoni*
Calanus glacialis	*Lucicutia flavicornis*
Calanus pacificus	*Mecynocera clausi*
Calanus propinquus	*Mesocalanus tenuicornis*
Calocalanus pavo	*Neocalanus cristatus*
Calocalanus styliremis	*Neocalanus plumchrus*
Candacia aethiopica	*Paracalanus aculeatus*
Centropages furcatus	*Pleuromamma robusta*
Cosmocalanus darwini	*Pleuromamma xiphias*
Ctenocalanus vanus	*Pontellina plumata*
Eucalanus attenuatus	*Rhincalanus gigas*
Eucalanus bungii	*Rhincalanus nasutus*
Eucalanus crassus	*Scolecithricella minor*
Eucalanus elongatus	*Scolecithrix danae*
Euchaeta acuta	*Tortanus discaudatus*
Euchirella mesinensis	*Tortanus forcipatus*
Euchirella rostrata	*Undeuchaeta plumosa*
Eurytemora affinis	*Undinula vulgaris*
200–300 citations	
Acartia longiremis	*Metridia lucens*
Aetideus armatus	*Neocalanus gracilis*
Anomalocera pattersoni	*Pareuchaeta norvegica*
Calanus hyperboreus	*Pleuromamma abdominalis*
Calanus (Nannocalanus) minor	*Pleuromamma gracilis*
Clausocalanus arcuicornis	*Pseudocalanus minutus*
Euchaeta marina	*Temora turbinata*
Metridia longa	
300–400 citations	
Acartia tonsa	*Centropages typicus*
Centropages hamatus	*Temora stylifera*
400–500 citations	
Calanus helgolandicus	*Pseudocalanus elongatus*
500–600 citations	
Paracalanus parvus	*Temora longicornis*
>600 citations	
Acartia clausi	*Calanus finmarchicus*

phytoplankton production and its consumption is complex because of variations in time and space. Longhurst *et al.* (1984) conclude that such a project in an area like the eastern Canadian archipelago is especially difficult because much of the phytoplankton sediments to the sea floor.

As mentioned above, copepods contribute to the diets of very many invertebrates, fish and whales. No attempt is made to list the species that prey on copepods although a few are mentioned when pertinent to the topic being discussed.

1.2. ENVIRONMENTAL SAMPLING

Beckmann (1984) concludes that a few oblique samples of deep-sea copepods in the Red Sea characterize large areas over extended time whereas many samples in space and time are required for the variable epipelagic, coastal and estuarine populations. Nobody would argue with this generalization. Copepods, like other planktonic organisms, are not randomly distributed in the sea but occur in patches both horizontally and vertically. This is discussed in some detail in the chapter on behaviour where their occurrence in patches, aggregations and swarms is described. This patchy distribution affects the sampling of a population as described by Wiebe (1971) and Wiebe and Holland (1968). The length of tow and the size of the net used are very important and can only be determined through pilot investigations and experience. At a fixed station on the Scotian Shelf, Sameoto (1978) found that the numbers of copepods caught, especially *Calanus* and *Pseudocalanus* species, were related to the tidal cycle. The period of observation was only over 26 h and he concluded that the tides carried a patch of these copepods past the sampling point and possibly returned them on an elliptical path past the sampling point on more than one tidal cycle. The effects, on sampling, of the transport of water by currents through a region are modelled and discussed by Power (1996). Broad considerations, therefore, of the region to be sampled for copepods must be examined along with the objectives of the sampling programme.

a. Are there marked gradients of temperature, salinity, depth, or tidal currents?
b. Will the copepods occur throughout the region to be sampled or are there species that are likely to have restricted distributions?
c. Is the sampling programme exploratory?
d. Are quantitative results in terms of biomass, numbers, or of horizontal or depth distributions of species required?

Answers to these questions will determine the sampling strategies to be

adopted and the gear to be used. Good general introductions to sampling are given by Tranter and Fraser (1968) and Omori and Ikeda (1984). Nets for sampling pelagic, neustonic, and benthic copepods are discussed and illustrated as are the various methods of their deployment. Since then, Wiebe *et al.* (1985) describe new developments of the Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS), an excellent and adaptable system for studying vertical and horizontal distributions of copepods quantitatively. Williams *et al.* (1983) use a double Longhurst/Hardy Plankton Recorder (LHPR) to resolve the vertical distributions of nauplii and copepodids of *Calanus helgolandicus*. The MOCNESS and LHPR are both for sampling offshore. An interesting continuous pump sampler that incorporates a plankton net as a collector and pumps the catch from the codend to the surface is described by Herman *et al.* (1984); profiles of the density of copepods in the surface 100 m of the ocean can thus be determined. Environmental probes can be mounted on the frame to provide simultaneous physical and chemical information. Herman (1992) adds an optical plankton counter to the codend; this counter is capable of sizing, and in some cases, identifying species or stages of copepods. A much simpler and less sophisticated sampler for quantitative investigation of shallow-water coastal copepods is described by Kršinić (1990). It is essentially a trap that can be opened and closed by messenger to sample the plankton in the volume of trapped water. A diver-operated device that can sample pelagic or benthopelagic copepods is described by Potts (1976); this idea could be modified in different ways, even to produce a very simple net that fits on a diver's arm (Kirkwood and Burton, 1987).

High-frequency acoustics, in the range of 100 kHz to 1 MHz, are capable of detecting individual zooplanktonic organisms as well as mapping patchiness in the pelagic realm. They have been used in studies of deep sound-scattering layers but the central problem is the identification of the species of copepod or plankton organism causing the scattering. Wiebe and Greene (1994) review current uses and the future potential of these methods.

Some copepods live in areas of the environment that are difficult to sample. Those associated with the surface film of the sea, neustonic species, are sampled by nets on floats at the surface (Omori and Ikeda, 1984). A sampler, not referred to by them, is the multiple net device of Schram *et al.* (1981) that samples contiguous subsurface layers. Under-ice samplers are described by Kirkwood and Burton (1987) and Nishiyama *et al.* (1987). A net-pump is used by Møhlenberg (1987) to sample copepods in the water column. Here, the water is pumped into the net which is deployed in the surface 25 m of the water column. This net could be used in a variety of shallow water environments and adapted for a diver.

The nature of the investigation, the characteristics of the sea area to be

sampled, and the specifications of the boat or ship available will strongly affect the sampling methods and gear selected. Pilot investigations are strongly recommended. The same net will not collect adult and copepodid stages of copepods with the same efficiency, and one that samples adults will usually catch very few nauplii. Anderson and Warren (1991), for example, tested the catch rates of small and large Bongo nets for copepodids of *Calanus finmarchicus*. They discuss mesh sizes and mouth sizes of nets and their effects on catch rates and recommend that individual copepodid stages be targeted in sampling programmes. A mesh size of 75% of the body or prosome width of the nauplius or copepodid catches about 95% of those of that size in the water (Nichols and Thompson, 1991).

1.3. PRESERVATION OF SAMPLES

Steedman (1976) and Omori and Ikeda (1984) describe fixation and preservation procedures for plankton samples in detail. The best general fixative is formalin buffered with borax (sodium tetraborate); 30 g of borax to one litre of analytical reagent grade formalin, colloquially known as 40% formalin since that is the concentration of formalin in it. Plankton samples should be decanted from the bucket of the net into sample bottles of known volume. The settled volume of the plankton or copepods should not exceed 20% to 25% of the volume of the bottle. The sample plus associated sea water should fill less than 90% of the volume of the bottle. Buffered formalin is then added to fill the remaining 10% of the volume of the bottle, so resulting in a 4–5% solution of formalin in sea water. A clearly written label for the sample should be inserted, the bottle capped and then inverted gently several times to mix the formalin with the sample. The sample should remain in the formalin for at least 10 d. The formalin can then be drained off and the sample transferred to a preservative fluid. Formalin is detrimental to health and working with formalin-preserved samples is to be avoided.

The best preservative is a version of Steedman's fluid (Omori and Ikeda, 1984). The one used by the author for 20 years differs in that it has proportionately less formalin. This is because it is never used as a fixative but only as a preservative for copepods already fixed in 5% formalin. The formula for one litre of the fluid is:

40% buffered formalin	25 ml
Propylene phenoxetol	10 ml
Propylene glycol	100 ml
Filtered sea water	865 ml

The sample, which has been fixed in formalin, is transferred to the preservative fluid as follows. The fixed sample is gently decanted into a sieve and the formalin drained off. The sieve used depends on the size spectrum of the plankton sample. A simple method is to line a baker's sieve for flour with a sheet of the plankton gauze identical to that used in the original sampling net. The sample in the sieve should then be gently washed by passing filtered sea water through it several times. The sheet of plankton gauze plus its contained sample is then gently lifted from the sieve and the sample decanted into a container half-filled with the fixative. Once the entire sample has been transferred, the container is topped-up with fixative, the label (see next section), with the details of collection of the sample, inserted, and the container sealed.

The low formalin content of the preservative fluid makes the samples comfortable to work with. The copepods do not become brittle and so legs do not suffer damage. Internal tissues such as gonads preserve well and are in good condition even after 20 years in the fluid. Samples that have inadvertently been allowed to "dry out" are easily reconstituted by addition of further fluid. Stored samples, however, should be properly curated and the levels of preservative present in the containers inspected at intervals. The length of interval will depend on the environmental temperature that the samples are subjected to. The colours of the copepods and other organisms will survive preservation longer if the samples are stored in darkness.

1.4. METHODS OF STUDY

The stored samples must have labels in them. The amount of information on the labels will vary depending on the investigations being made and suggested formats of labels are given by Omori and Ikeda (1984). The labels are of good-quality paper; the best type of paper easily available is often the letter-headed notepaper of the institute or laboratory. It is good practice to insert two or more labels in the sample, one having as much detail as wished, the others simply having a sample identity number. This is done because some paper labels disintegrate during prolonged storage. Indelible inks or computer-printed labels should be used. The full details of each sample should be stored in a secure file.

There is a considerable advantage in separating the copepods from the other organisms in the samples if they are the ones of principal interest. The copepods can then be stored in vials that are placed in larger, reservoir containers. This allows easy curation during extended investigation of the taxonomy and distribution of species. This is when there is an advantage in

having small labels with a sample number as opposed to large labels with full sampling details.

Working on quantitative samples often requires an additional label within the sample. This will give details of the number of specimens removed for further study. Identification to the species level sometimes requires detailed studies of sub-samples before the individuals in the original sample can be identified and counted. Quantitative investigations often require that representative sub-samples be used for analysis because it is not practicable to use the entire sample. Removal of such a sub-sample should be indicated on a label within the original sample.

Steedman (1976) and Omori and Ikeda (1984) describe in detail recommended procedures for examining copepods alive and in preserved samples. An appendix to Huys and Boxshall (1991) reviews a wide variety of such techniques. The use of stains is described in the above works. They can have quite specialized functions such as, for example, that of Nile Red used for detecting lipid storage within the bodies of copepods (Carman *et al.*, 1991).

A major requirement, especially in taxonomic studies of copepods, is the preparation of semi-permanent mounts of whole animals or dissected parts such as the appendages. There are a variety of media used and Koomen and Vaupel Klein (1995) and Stock and Vaupel Klein (1996) review their uses. Stock and Vaupel Klein (1996) recommend Reyne's fluid but it has a limited shelf-life and contains chloral hydrate which is poisonous. The author uses polyvinyl lactophenol, obtained commercially and with a longer shelf-life; it is tinted, before use, with the stain lignin pink and material to be mounted can be transferred directly to it from water. Its viscocity allows arrangement of appendages that is maintained when the cover slip is added. Such preparations are kept flat for several weeks and then stored on their sides in conventional slide cabinets. The edge of the cover slip may require flooding, on annual inspection, with additional mountant to counter evaporation. Conversely, a sealant can be applied around the edge of the cover slip at the time of preparation or when the slide enters storage.

The Scanning Electron Microscope is increasingly used to study such aspects as morphology of appendages, sensilla and even stomach contents of copepods. Felgenhauer (1987) describes the techniques involved in preparing copepods for examination by SEM while Toda *et al.* (1989) have developed a dry-fracturing technique for making observations on the internal anatomy and stomach contents.

Attempts have been made to automate counting and measuring of copepods, and even the identification of species. Image analysers have been investigated in this context with some success (Rolke and Lenz, 1984; Estep *et al.*, 1986; Noji *et al.*, 1991). Automation may help considerably in the future with processing of coastal samples with a low diversity of species, one

or two of which are dominant. It is less promising for analysing oceanic samples of high diversity. Image analysers also allow biometrical studies, such as that of Jansá and Vives (1992) on the area presented by the dorsal aspect of species.

2. External Morphology, Internal Anatomy

The overall body form of platycopioid and calanoid copepods is closely similar but different from those of other orders of copepods (Dudley, 1986). The former conform to the gymnoplean tagmosis in which a distinct division between the prosome and urosome is situated between the fifth pedigerous segment and the genital somite (Figure 4). All other copepods conform to the podoplean tagmosis in which an often less distinct separation of the

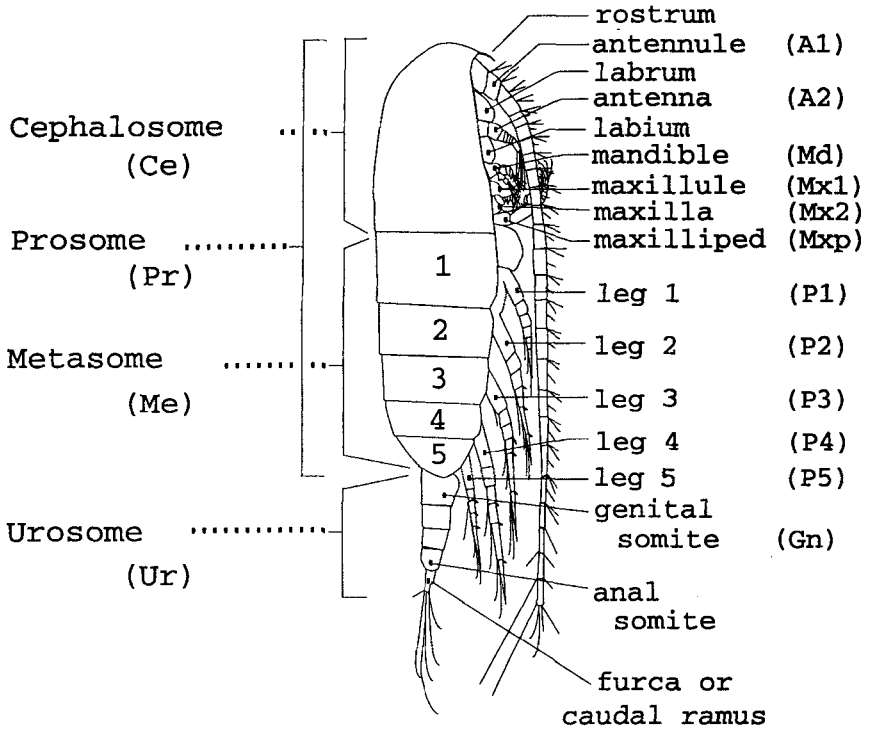


Figure 4 Diagrammatic illustration of the external morphology and appendages of a female calanoid copepod. The metasome has five clearly defined segments, numbered 1–5; this species has five pairs of swimming legs and so these five metasome segments are synonymous with pedigerous segments 1–5. Legs 1–5 are the swimming legs.

prosome and urosome is present, between the fourth and fifth pedigerous segments (Figure 1). Huys and Boxshall (1991) present a detailed comparative study of the morphology of all copepods and reference should be made to them for further information.

The lack of variety in the gross body form of platycopioid and calanoid copepods has required the full illustration of the animal and its appendages to be given within type descriptions of species. Thus, browsing of such taxonomic papers as Giesbrecht (1892) or Sars (1903, 1925) illustrates the amount of variety that does exist. Detailed descriptions of differences in external morphology are not reviewed here unless within a functional or broader context.

2.1. EXTERNAL MORPHOLOGY OF ADULTS

The body is divided into several regions, the cephalosome, metasome and urosome (Figure 4). Frequently, the first segment of the metasome is fused with the cephalosome, and/or the fourth and fifth segments of the metasome are fused. Thus, the metasome in some species may seem to have as few as three segments. The urosome consists of the genital somite and several segments posterior to it. The genital somite consists of fused segments that are separated in the corresponding males, and results in males apparently having an extra segment in the urosome (Figures 4, 5A). The cephalosome and metasome together are known as the prosome. This is a clearly defined part of the body and its length, from the anterior end of the cephalosome to the posterior lateral edge of metasome segment 5, is used as a direct measure of body length or size. This measurement is preferred to that of total body length because the urosome is often flexed, even damaged at times, causing larger errors when examining length/frequency distributions in statistical analyses of populations.

Copepods, like other crustaceans, have paired appendages that function in swimming, detection and obtaining food, and in mating. They are complex in form, and reference to Huys and Boxshall (1991) is required for the terminology applied to the constituent parts. Females and males are

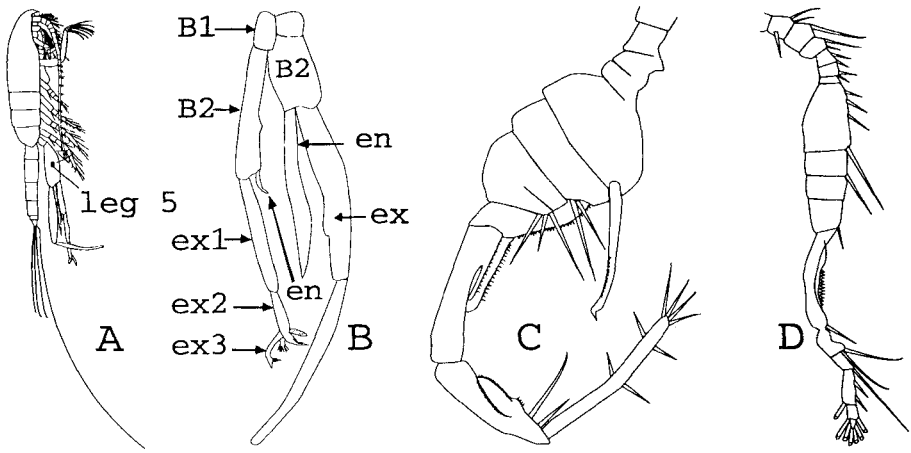


Figure 5 Diagrammatic illustration of the external morphology and some appendages of a male calanoid copepod. A, general lateral aspect of a male *Pareuchaeta norvegica*. B, pair of fifth legs of *P. norvegica* (key to components is in Figure 6, page 18). C, geniculate right antennule of a *Pontella* species. D, geniculate right antennule of a *Candacia* species.

distinguished by sexually dimorphic characters that usually develop during the later copepodid stages. Males are usually smaller in body size than females, have additional apparent segments in the urosome, often greatly modified fifth legs, and many have modified antennules (Gilbert and Williamson, 1983).

2.1.1. Antennule (antenna 1)

The antennule of females in the family Epacteriscidae can have as many as 27 segments, and in the Ridgewayiidae 26 segments, but in the typical female calanoid there are only 25 segments (Figure 6). Fusion of segments is present in many species (Huys and Boxshall, 1991), so that, for example, antennules of *Pontellopsis* species show as few as 16 segments. The antennules of the female and many males are bilaterally symmetrical. Males of families originally classed in the section Heterarthrandria, as opposed to Amphascandria or Isokerandria, by Giesbrecht (1892) and Sars (1903) have their antennules bilaterally asymmetrical. These classes within the Calanoida have now been abandoned (Huys and Boxshall, 1991). This asymmetry results from the right antennule being geniculate, that is knee-like with an articulation separating proximal and distal regions (Figure 5C and D); the left antennule is similar to those of the corresponding female. Males in families in the superfamily Arietelloidea, however, usually have the left antennule geniculate, the right being similar to those of the female. There are genera, within this superfamily, that have their left or right antennule geniculate and even species, *Pleuromamma* species for example, in which there is variation between individuals.

The antennule of the nauplius VI, like that of previous naupliar stages, has three segments but these are transformed to the 9 or 10 segments, depending on whether the distal two are fused, of the copepodid I (Hülsemann, 1991c). The proximal 6 segments of the antennule of the copepodid I generate all further segments of the adult antennule, the distal 6 or 7 remaining unaltered throughout the development of the sequential copepodids.

The boundaries between the antennular segments 2 to 25 have ring-like arthrodial membranes that allow limited flexure (Boxshall, 1985). The junction between segments 8 and 9 in many species, however, is modified, the distal part of the antennule breaking off easily (Bowman, 1978a). The relative lengths of the antennular segments vary little within a species. Sewell (1929, 1932) expresses the lengths of the various segments as parts per thousand of the whole length of the antennule, thus producing an antennular formula. This formula has been used by, for example, Vervoort (1963, 1965) and Boucher and Bovée (1970) but in more recent times by only

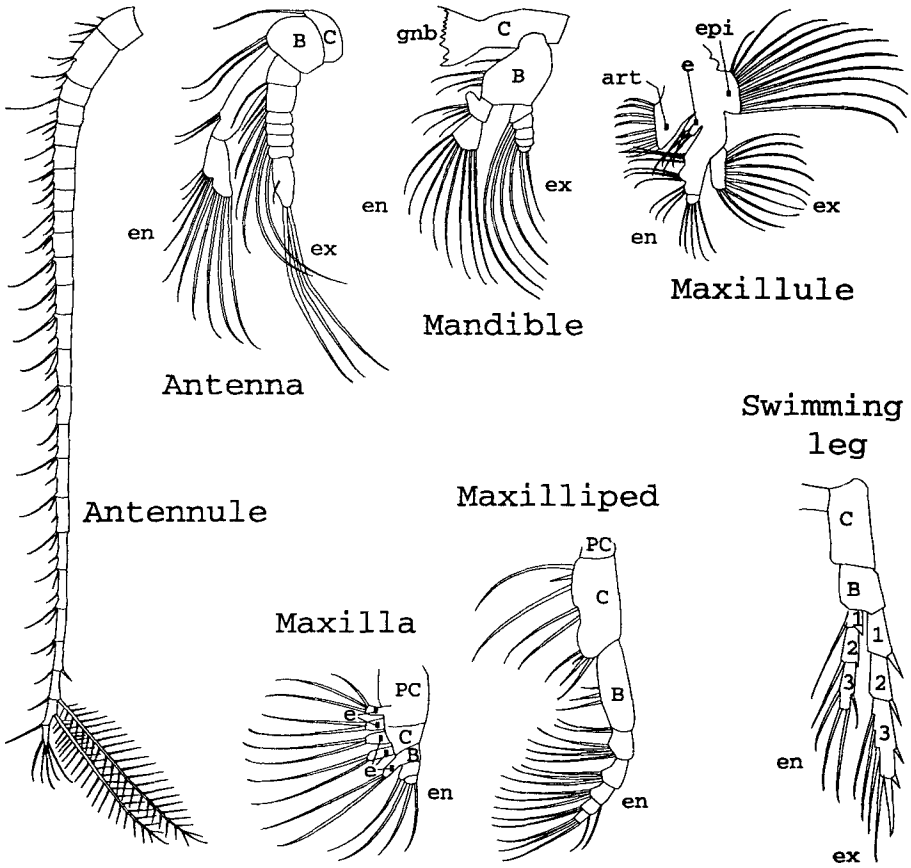


Figure 6 Diagrammatic representations of the appendages of a calanoid copepod. The swimming legs usually have developed endopods and exopods with up to three segments, numbered 1–3 here. Terminology after Huys and Boxshall (1991).
art, arthrite; B, basis; C, coxa; e, endite; en, endopod; epi, epipodite; ex, exopod; gnb, gnathobase; PC, praecoxa.

Soler *et al.* (1988). It is a cumbersome measurement to make but may still be useful.

The antennules are furnished with setae and sensilla or aesthetascs. The copepod often hangs vertically in the water column with the antennules held out laterally to slow down its sinking rate. The aesthetascs function to detect food, water disturbance and predators (Gill and Crisp, 1985a; Légier-Visser *et al.*, 1986; Jonsson and Tiselius, 1990; Kurbjeweit and Buchholz, 1991; Yen

et al., 1992; Bundy and Paffenhöfer, 1993; Lenz and Yen, 1993). The male antennules are used to grip the female during mating.

2.1.2. Antenna (antenna 2)

The antenna, unlike the antennule, is biramous, with an endopod and exopod (Figure 6). The endopod is usually of 3 segments, the second and third being partially fused. The exopod contains 8 or 9 segments and patterns of their fusion vary (Huys and Boxshall, 1991). The antennae, in conjunction with the other mouthparts, form an integral part of the food-gathering and handling mechanism of the copepod (Gill, 1987).

2.1.3. Labrum and Labium

The labrum and labium are not normally considered with the paired appendages but they form the margins of the mouth (Boxshall, 1985). The labrum is a muscular lobe, forming the anterior margin of the mouth, often ornamented with spines, and containing the eight labral glands, four on each side (Arnaud *et al.*, 1988a,b), opening on its posterior surface. These glands produce secretions that may bind the food together and initiate digestion in the buccal cavity. Nishida and Ohtsuka (1996) suggest that labral glands in species of the heterorhabdid genus *Heterorabdus* produce an anaesthetic or poison that is injected into prey through a hollow tooth (spine) in the mandible (see next section).

The paired lobes of the labium form the posterior and part of the lateral margins of the mouth. The paired lobes are derived by fusion of the paragnaths (Huys and Boxshall, 1991). The labium is also ornamented with rows of spines.

2.1.4. Mandible

The mandible is biramous (Figure 6), having an endopod of 2 segments and an exopod of 5 segments. The basal segment forms the gnathobase with its spined, distal edge for macerating the food. The development of these spines during the moult cycle has been investigated by Miller *et al.* (1990). The numbers and form of the spines (teeth), which have abrasive tips of silica (Sullivan *et al.*, 1975; Miller *et al.*, 1980), and the setulation of the endopod and exopod relate to the diet of individual species (Anraku and Omori, 1963; Ohtsuka *et al.*, 1996a) and Itoh (1970) has developed an "edge index" to quantify the differences. Schnack (1989) combines determination of the

edge index of the gnathobase with the minimum intersetule distances on the maxillules and maxillae to draw conclusions about dietary potentials of species. The overall form of the gnathobase and the disposition of the spines is often such that it can be used to identify the species. The gnathobase resists digestion in the stomachs of predators and Karlson and Båmstedt (1994) have investigated their usefulness in estimating predation rates on populations of copepods.

The mandibles of the Heterorhabdidae have the ventral spine enlarged (Figure 25, key figs. 59, 60). Nishida and Ohtsuka (1996) state that this isolated spine is hollow with a subterminal pore and a basal opening. The basal opening is aligned with the cuticular pore of a large labral gland that is situated under the posterior face of the labrum. An anaesthetic or poison, secreted by the gland, is thought to be transferred, through its cuticular pore, into the basal opening of the mandibular spine. It then travels up the internal canal of the spine to be injected through the subterminal pore into the prey. Such a feeding technique has not previously been described in a copepod.

2.1.5. Maxillule (maxilla 1)

The maxillule (Figure 6) is a complex laminar appendage whose constituent parts are defined by Huys and Boxshall (1991). It is biramous with a 3-segmented endopod, some segments often fused, and a single segmented exopod. The setulation and overall form relate to the diet of the species (Anraku and Omori, 1963; Schnack, 1989; Ohtsuka *et al.*, 1996a).

2.1.6. Maxilla (maxilla 2)

The maxilla (Figure 6) is also a laminar appendage whose constituent parts are defined by Huys and Boxshall (1991). It is uniramous and 7-segmented. Its form also relates with the diet of the species, strong spines replacing setae in a few species (Landry and Fagerness, 1988; Ohtsuka *et al.*, 1996a).

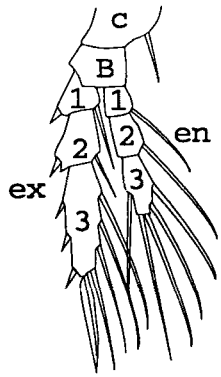
2.1.7. Maxilliped

The maxilliped (Figure 6) is uniramous and 9-segmented according to Huys and Boxshall (1991), although most species have only 6 free segments in the endopod. It can be greatly developed as in *Pseudeuchaeta* species (Figure 2), and armed with setae or spines dependent upon the feeding strategy of the species.

2.1.8. Swimming Legs

The first four metasome segments of females and males always have paired, biramous swimming legs that are similar in both sexes. In some families, such as the Calanidae, a fifth pair of legs, similar to the first four pairs, is present. In other families, such as the Aetideidae and Euchaetidae, the fifth pair is usually absent in females but present, although considerably modified (Figure 5B), in males. The fifth pair of legs present in females can be considerably reduced in size and structure while that in males is normally enlarged as it functions to grasp the female during mating. The exopods and endopods of the five pairs of legs have a maximum of 3 segments each but their numbers may be reduced in one or more pairs of legs. The distribution of setae and spines on the legs also varies so that the morphology of the legs is very important in the identification of families, genera and species (see next chapter).

Sewell (1949) suggested a spine and setal formula to summarize the setation of appendages. It discriminates between spines, denoted by Roman numerals, and setae, given by Arabic numerals. Legs are examined in the order anterior to posterior, proximal before distal segments. Spines or setae on the outside of the segment are defined before those on the inside, those on the same segment being linked by a hyphen (Figure 7). Exopod and endopod segment 3 have a terminal armature that is interposed between the lateral ones so that the order is outer, terminal and inner armatures. This formula can be adapted for other appendages and may be useful in future, computerized, identification keys for species.



Coxa		0 - 1
Basis		0 - 0
exopod	1	I - 1
	2	I - 1
	3	III - I - 4
endopod	1	0 - 1
	2	0 - 1
	3	1 - 2 - 2

Figure 7 The spinal and setal formula of Sewell (1949). Spines are given by Roman, setae by Arabic numerals. See text for further explanation.

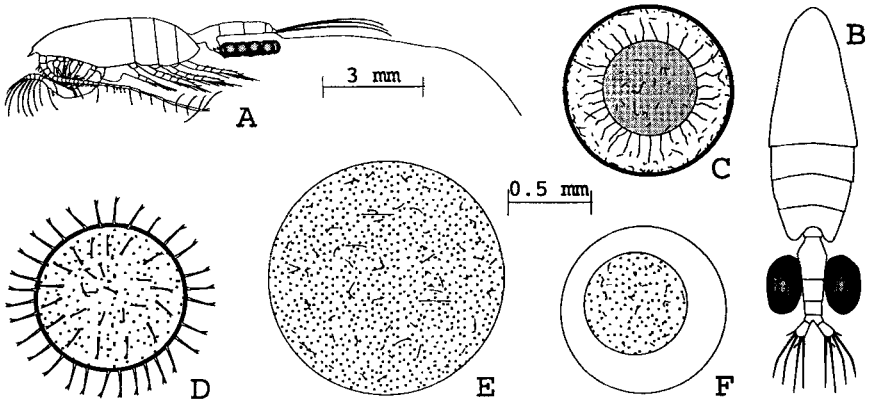


Figure 8 Eggs of calanoid copepods. A. *Pareuchaeta norvegica* with egg mass; B, *Valdiviella insignis* with eggs; C, egg of *Tortanus forcipatus* from sediment; D, egg of *Centropages abdominalis* from sediment; E, pelagic egg of *Calanus finmarchicus*; F, egg of *Acartia spinicauda*. A and B, 3 mm scale; C to F, 0.5 mm scale. (C and D, after Kasahara *et al.*, 1974; F, after Li Shaojing *et al.*, 1989.)

2.2. EXTERNAL MORPHOLOGY OF YOUNG

2.2.1. Egg

Eggs of copepods are either carried by the female attached in a mass to the genital opening or laid freely in the water column. The eggs carried by species such as *Euchaeta* and *Pareuchaeta* are enclosed in cuticular material that glues them together (Figure 8A). The egg mass is often referred to as an egg sac but there is little evidence that the eggs are carried in a bag. The most spectacular eggs are the two large ones carried by *Valdiviella insignis* (Figure 8B), a relatively common deep-sea species. Those eggs that are laid freely in the sea by many small coastal species can be of two types, subitaneous (non-resting) and resting eggs. The subitaneous eggs (Figure 8E, F) are usually relatively thin-walled and unadorned with any "spines". Resting eggs are thicker-walled and often sculptured or have surface "spines" (Figure 8C, D). They sediment to the sea bed where they remain for periods before hatching. Koga (1968) describes the eggs of 18 species, dividing them into those with floating devices (Figure 8D) and those without (Figure 8C, E, F). Further figures of eggs are given by Li Shaojing *et al.* (1989).

Hirose *et al.* (1992) describe the development of a multi-layered fertilization envelope in *Calanus sinicus*; it forms within the perivitelline

space. Some eggs have a perivitelline space (Figure 8C, F) while others do not (Figure 8D, E). The number of membranes bounding the egg is not clear; Toda and Hirose (1991) figure sections in which they discern seven to eight layers. This seems excessive and three layers, a perivitelline, chitinous and cuticular, is a more reasonable interpretation, although there may be a degree of lamination in the outer two.

Identification of copepod eggs in the plankton to the species level is often relatively easy in coastal areas where dominance and size are often the key features. Resting eggs in sediments often have species-specific sculpturing of the membranes (Belmonte and Puce, 1994) and identification to species is again often possible. It is much more difficult to identify the eggs in offshore plankton samples.

A method of determining whether eggs are fertilized or not is given by Ianora *et al.* (1989) who use a fluorescent dye specific for cell nuclei. The unfertilized eggs have only the female nucleus whereas the recently fertilized egg has both female and male pronuclei.

2.2.2. Nauplius

Calanoid copepods have six naupliar stages, abbreviated to NI to NVI, except in some species of *Labidocera* and *Pseudodiaptomus* when the first is omitted and an NII emerges directly from the egg. The first 3 naupliar stages are true nauplii with 3 pairs of appendages, the antennules, antennae and mandibles. The later stages, however, are similar to the metanauplii of other Crustacea because they often have signs of "abdominal" segmentation and rudiments of more posterior appendages (e.g. Figure 9B). The successive naupliar stages within a species are identified by the progressive setation of the distal segment of the 3-segmented antennule (4-segmented when a basal segment is present), and by the progressive development of the armature of the posterior end of the body. The NI of all species has 3 setae on the distal segment of the antennule and 2 spines on the posterior end of the body (Figure 9A). By NVI, there are 9 to 17 setae and 10 or more spines respectively. A setal formula describes the setation of the distal segment of the antennule (Ogilvie, 1953) but it is often difficult to apply. It depends on the presence of a distal aesthetasc (Figure 9E) which is not always present or discernible. The dorsal and ventral setae are counted and the aesthetasc interposed; thus, the formula for the antennule in Figure 9E is 5a7. Difficulties arise when the aesthetasc is absent and/or when minute spines, as distinct from setae with setules, are present. Some authors count everything, others only the setae. These counts identify the naupliar stages within species and the formula has been used in an attempt to distinguish different species. It is most useful when the development of the other

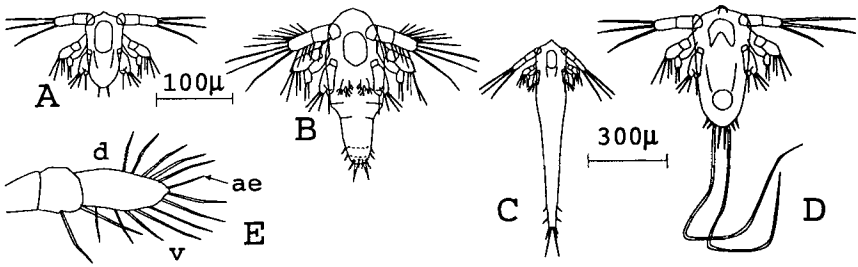


Figure 9 Nauplii of calanoid copepods. A, *Clausocalanus furcatus*, stage I (NI); B, *Paracalanus aculeatus*, NV; C, *Rhincalanus cornutus*, NIV; D, *Euchaeta marina*, NVI; E, antennule showing dorsal (d) and ventral (v) setae and terminal aesthetasc (ae). (After Björnberg, 1972, 1986b.)

appendages is included as well as the armature of the posterior part of the body (Faber, 1966; Björnberg, 1972; Sazhina, 1982). Body size alone often separates species in coastal regions with low diversity. Similarly, general body form can be used because some genera such as *Rhincalanus* (Figure 9C) have an elongated nauplius while that of *Euchaeta marina* has two conspicuous, long, thin setae posteriorly (Figure 9D).

The nauplii of some 83 species have been described (Table 3), and are those of only some 5% of known calanoids. Forty of these species, however, are also listed in the 72 most quoted species in Table 2 so that the development of many of the common species is known. Björnberg (1972, 1986a,b) argues that the form of the nauplius must be taken into account in formulating any taxonomic classification of the Calanoida. This is difficult at present because the nauplii of many families are completely unknown.

2.2.3. Copepodid

The NVI moults to the first of six copepodid stages, abbreviated CI to CVI, that resemble miniature adults. The CVI is the adult. The sequential stages are distinguished by the progressive development of the adult segmentation of the body, the increasing differentiation of the appendages, and successive increases in body size. Descriptions of the copepodids of species listed in Table 3 are given in many of the papers quoted there and by Ferrari (1988).

The terms cephalosome (head), prosome, metasome (thorax) and urosome (abdomen) used in Figure 4 do not correspond to the homologous segmentation of other crustacean orders. The cephalosome of copepods consists of the head fused with the first thoracic somite. Thus in the CI

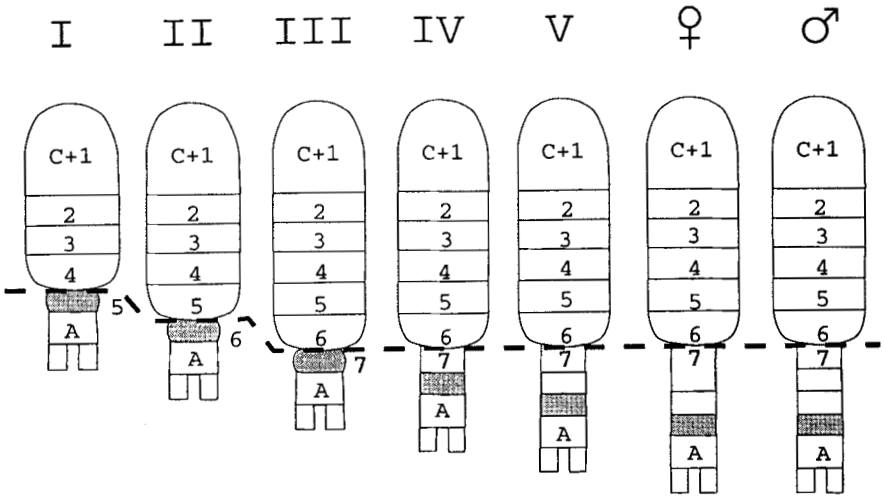


Figure 10 The sequential development of the apparent segmentation throughout the copepodid stages, CI to CV, the female and male. Various combinations of segments can be fused in different genera and species so that the apparent segmentation becomes reduced. The broken line indicates the division between the metasome and urosome. The shaded segment shows the new segment acquired at the previous moult. C + 1, cephalosome plus first thoracic segment; 2–7, thoracic segments; A, anal segment. (After Boxshall, 1985; Hülsemann, 1991a.)

(Figure 10), the body consists of the cephalosome plus four free segments and an anal segment (Figure 10A). Some species, e.g. *Pseudocalanus*, have only three free segments plus the anal segment (Table 4, and Corkett and McLaren, 1978). The numbering of the segments in Figure 10 acknowledges the incorporation of the first segment within the cephalosome (C + 1) (Boxshall, 1985; Hülsemann, 1991a). A new segment is added, immediately anterior to the anal segment, at each successive moult (Figure 10). The new segment in the CI and CII becomes incorporated in the metasome at the next moult (Figure 10) and the division between the metasome and urosome moves one segment posteriorly each time. The new segment in CIII is the 7th thoracic segment that remains in the urosome, the division between the metasome and urosome in calanoids being between the 6th and 7th thoracic segment. This is synonymous with the statement that this division is between the 5th pedigerous segment and the genital somite. Subsequent copepodid stages, CIV to CVI, add segments to the urosome (Figure 10). The numbers of apparent adult segments in both the metasome and the urosome (Table 4) can vary because various combinations of segments become fused. The female genital somite consists of at least two

Table 3 Sources of descriptions of nauplii of marine calanoid copepods.

Acartia bifilosa (Oberg, 1906); *A. californiensis* (Trujillo-Ortiz, 1986); *A. clausi* (Ogilvie, 1953; Klein-Breteler, 1982); *A. danae* (Björnberg, 1972); *A. grani* (Vilela, 1972); *A. lilljeborgi* (Björnberg, 1972); *A. longiremis* (Oberg, 1906); *A. negligens* (Björnberg, 1972); *A. tonsa* (Björnberg, 1972; Sazhina, 1982); *Aetideus armatus* (Matthews, 1964); *Calanoides carinatus* (Björnberg, 1972; Hirche, 1980); *Calanopia thompsoni* (Li Shaojing and Fang Jinchuan, 1984); *Calanus finmarchicus* (Björnberg, 1972); *C. helgolandicus* (Björnberg, 1972); *C. hyperboreus* (Sömme, 1934); *C. minor* (Björnberg, 1972); *Calocalanus pavo* (Björnberg, 1972); *C. styliremis* (Björnberg, 1972); *Candacia aethiopica* (Sazhina, 1982); *Candacia armata* (Bernard, 1964); *Centropages abdominalis* (Koga, 1960b); *C. chierchiae* (Sazhina, 1982); *C. furcatus* (Björnberg, 1972); *C. hamatus* (Oberg, 1906; Klein-Breteler, 1982); *C. kröyeri* (Sazhina, 1960); *C. typicus* (Lawson and Grice, 1970); *C. yamadai* (Koga, 1970); *Clausocalanus furcatus* (Björnberg, 1972; Sazhina, 1982); *Ctenocalanus vanus* (Björnberg, 1972); *Epilabidocera amphitrites* (Johnson, 1934b); *Eucalanus attenuatus* (Björnberg, 1972); *E. bungii* (Johnson, 1937); *E. crassus* (Björnberg, 1972); *E. elongatus* (Björnberg, 1972); *E. pileatus* (Björnberg, 1972); *Euchaeta marina* (Bernard, 1964); *Eurytemora affinis* (Katona, 1971); *E. americana* (Grice, 1971); *E. herdmani* (Grice, 1971a); *E. hirundo* (Björnberg, 1972); *E. hirundoides* (Björnberg, 1972); *E. pacifica* (Chiba, 1956); *E. velox* (Gurney, 1931); *Gladioferens pectinatus* (McKinnon and Arnott, 1985); *Labidocera acutifrons* (Sazhina, 1982); *L. aestiva* (Björnberg, 1972; Gibson and Grice, 1977); *L. bengalensis* (Ummerkutty, 1964); *L. brunescens* (Björnberg, 1972); *L. euchaeta* (Li Shaojing and Fang Jinchuan, 1983); *L. fluviatilis* (Björnberg, 1972); *L. jollae* (Johnson, 1935); *L. minuta* (Goswami, 1978b); *L. pavo* (Goswami, 1978b); *L. rotunda* (Onbé *et al.*, 1988); *L. trispinosa* (Johnson, 1935); *Limnocalanus grimaldi* (Lindquist, 1959); *Metridia lucens* (Ogilvie, 1953); *Microcalanus pusillus* (Ogilvie, 1953); *Neocalanus gracilis* (Sazhina, 1982); *N. tonsus* (Björnberg, 1972); *Paracalanus aculeatus* (Björnberg, 1972); *P. parvus* (Björnberg, 1972); *Pareuchaeta elongata* (Campbell, 1934; Lewis and Ramnarine, 1969); *P. norvegica* (Nicholls, 1934); *P. russelli* (Koga, 1960a); *Parvocalanus crassirostris* (Lawson and Grice, 1973); *Pleuromamma abdominalis* (Sazhina, 1982); *Pontella atlantica* (Sazhina, 1982); *P. meadi* (Gibson and Grice, 1976); *P. mediterranea* (Crisafi, 1965); *Pontellopsis brevis* (Björnberg, 1972); *P. occidentalis* (Johnson, 1965); *Pseudocalanus minutus* (Corkett and McLaren, 1978); *Pseudodiaptomus acutus* (Björnberg, 1972); *P. ardjuna* (Alvarez and Kewalramani, 1970); *P. aurivilli* (Ummerkutty, 1964); *P. binghami* (Goswami, 1978a); *P. coronatus* (Grice, 1969); *P. euryhalinus* (Johnson, 1948); *P. marinus* (Uye and Onbé, 1975); *Rhincalanus cornutus* (Björnberg, 1972); *R. gigas* (Björnberg, 1972); *R. nasutus* (Björnberg, 1972); *Ridgewayia klausruetzleri* (Ferrari, 1995); *Temora longicornis* (Corkett, 1967; Klein-Breteler, 1982); *T. stylifera* (Gaudy, 1961); *T. turbinata* (Koga, 1984); *Tortanus discaudatus* (Johnson, 1934a); *T. gracilis* (Björnberg, 1972); *Undinula vulgaris* (Björnberg, 1966, 1972); *Xanthocalanus fallax* (Matthews, 1964).