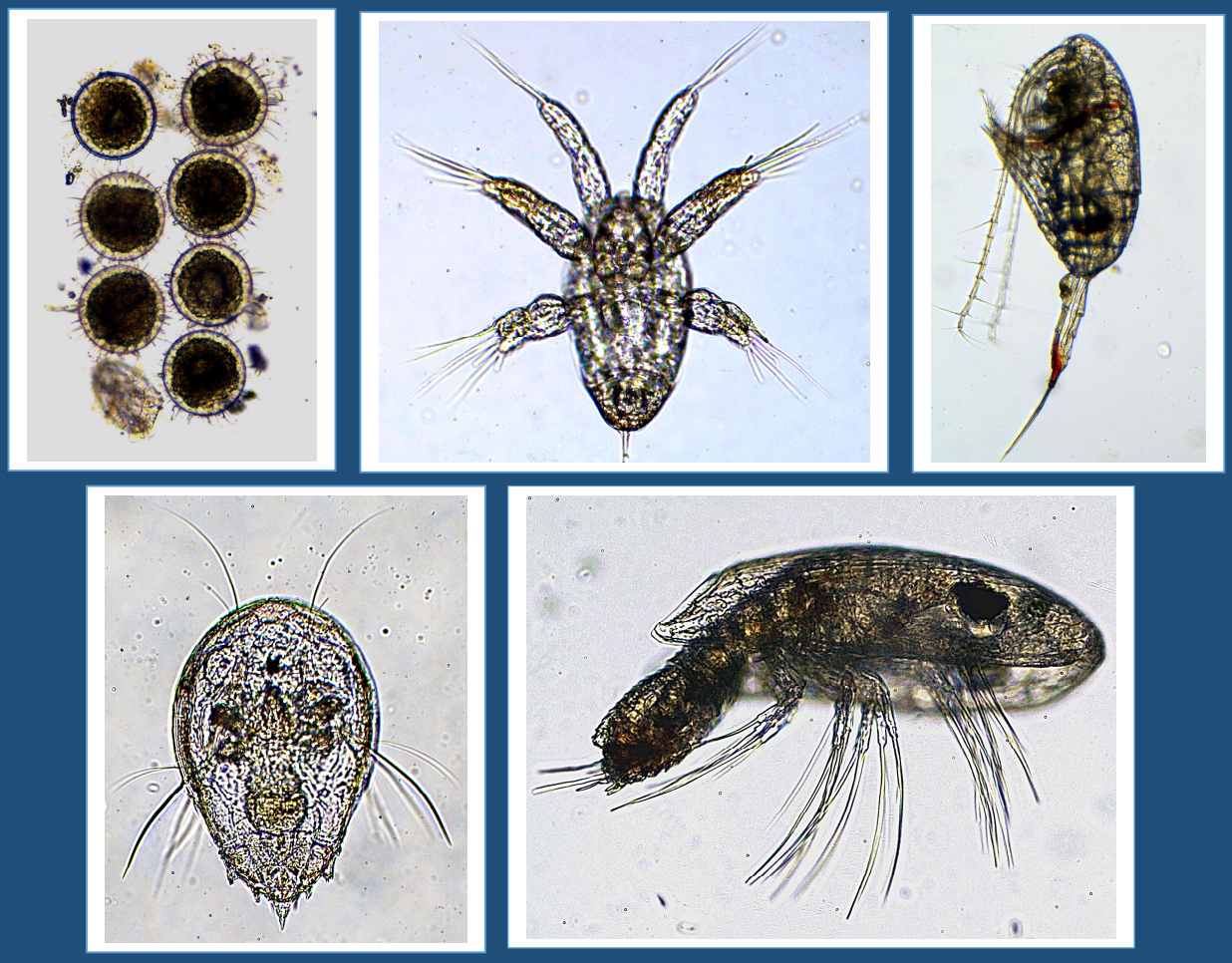
IDENTIFICATION OF COPEPOD EGGS, NAUPLII AND COPEPODITES, AND FACETOTECTAN NAUPLII AND CYPRIDS

David V.P. Conway



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Front cover from top, left to right: *Centropages typicus* eggs; *Calanus helgolandicus* second nauplius stage; *Pseudocalanus elongatus* female; Facetotectan nauplius; Facetotectan cyprid.

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Introduction

Class Copepoda is one of the most ecologically important zooplankton groups and consequently one of the most studied. Identification information for the adults of the species included here is widely available (e.g. Conway, 2012a, Wootton & Castellani, 2017), or can be downloaded from Razouls *et al*. (2005-2024). In contrast, basic information on the identification of copepod developmental stages is diffused through the literature and sparse, particularly the comparative morphological details necessary to distinguish between the nauplii of the main copepod orders. Stage identification information is always useful to know, but crucial in laboratory experimental studies such as determining moulting interval at different temperatures and food concentrations, or field studies on larval fish gut contents compared to food availability in the plankton etc.

While it may seem puzzling to combine copepod and facetotectan developmental stage information here, it is probable that during routine sample analysis, facetotectan nauplii have in the past been sometimes wrongly categorised with copepod nauplii, as some biologists are not very aware of them. Their inclusion here is hopefully also to encourage future researchers to study this intriguing group, towards identifying their currently undetected adult stages.

Issued in the 140th year since the opening of the Marine Biological Association (MBA) Plymouth Laboratory, this guide is based on northern European species, but the information will also be applicable to those found over a wider area. Traditionally, most zooplankton identification guides use black and white line drawings, in parallel with descriptions. While line drawings can show features very clearly, they often do not give a good visual impression of the organism, so this guide has been prepared almost exclusively using colour images of mainly live, but occasionally preserved specimens from the Plymouth plankton.

Classification system

The classification of organisms is often contentious and continually evolving, the rate of change considerably increased by advances in molecular techniques, giving more accurate information on interrelationships than those based solely on morphological criteria. The continually updated and online World Register of Marine Species (WoRMS) classification scheme has been followed here (http://www.marinespecies.org).

Photographic equipment

Images were taken with simple equipment. The main camera used was a Sony Alpha NEX-5R 16.1MP digital camera, fitted with a x2 adapter to fit a microscope trinocular head or eyepiece tube. Different extension tubes were used, depending on magnification required. The main microscopes used were a Kern OBN-13 trinocular compound microscope, a Zeiss Standard 14 binocular, compound microscope and a Zeiss Stemi 2000-C trinocular stereomicroscope.

Photographic images can give a true impression of an organism, but often lack depth of field. Even image stacking software often cannot adequately capture complex structures and of course cannot be used on live, moving organisms. Images often had to be captured quickly and quality sometimes suffered.

Acknowledgements

My thanks to the MBA staff operating our research vessel “Sepia” for collecting offshore plankton samples for me, from which many of the specimens included in this guide were taken. I am privileged to have access to the superb resources available at the National Marine Biological Library at the MBA and appreciate the support given by library staff. My thanks to David Pond for the loan of photographic equipment and I would also like to thank Elaine Fileman from the Plymouth Marine Laboratory for suggesting alterations to the manuscript.

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Class Copepoda

According to the WoRMS website there are currently nine orders of marine copepods in Class Copepoda. However, only six of these, in two superorders, are regularly sampled in the northern European area (see below). The adults of the remaining three orders (Platycopioida, Misophrioida and Mormonilloida) are not planktonic, or very rare, so are not considered here.

Most holoplanktonic species sampled are in Orders Calanoida, Cyclopoida and Harpacticoida, but planktonic stages from Orders Monstrilloida, Siphonostomatoida and Polyartha (previously Canuelloida) regularly occur, mainly in inshore samples. Copepoda classification has previously included an additional order, Order Poecilostomatoida. This categorization is sometimes still used, but recent molecular evidence indicates that Poecilostomatoida should, at least for the time being, be reassigned as a suborder of Order Cyclopoida (Khodami *et al*., 2019) and renamed Suborder Ergasilida. Of the copepods described here, Ergasilida includes families Corycaeidae and Oncaeidae.

Superorder Gymnoplea

Order Calanoida - the commonest and most studied, mainly planktonic order.

Superorder Podoplea

Order Cyclopoida - many are planktonic, but a large number are parasitic or commensal.

Order Harpacticoida - mainly benthic, relatively few are truly planktonic.

Order Monstrilloida - parasites of benthic polychaetes and molluscs, but have some planktonic stages.

Order Siphonostomatoida - parasites of fish and various invertebrates, but have some planktonic stages.

Order Polyartha - benthic or commensal, but some have planktonic larval stages.

Copepod eggs and reproduction

Copepod eggs are usually the main invertebrate egg found in finer mesh net plankton samples. There are different copepod egg laying strategies. They may be individually spawned directly into the sea or held, usually in bundles with or without an enclosing membranous sac, attached to the female genital somite.

Many Calanoida, such as *Calanus*, *Temora, Acartia* and *Paracalanus* spp. spawn their eggs in high numbers, directly into the sea, emerging from the genital pore like an oil droplet (Fig. 1). In most calanoids that carry their eggs, they are held tightly together ventrally in a single mass that may not have a true egg sac (Huys & Boxshall, 1991). Females of *Paraeuchaeta norvegica* (Fig. 2) are regularly collected bearing an egg mass. This may become detached during sampling and preservation, but remain intact in the sample. In *Pseudocalanus elongatus* (Fig. 3), the eggs are only loosely attached and not very cohesive, so are often found individually in samples. *Pseudodiaptomus marinus* is unusual for a calanoid in having a pair of egg masses, but they are packed together, appearing as one (Fig. 4). Closely related species may follow the same spawning strategy, but within the same family different species may have different strategies (Kosobokova *et al*., 2007).

Fig. 1. *Paracalanus parvus* female egg laying.

Fig. 2. *Paraeuchaeta norvegica* females with egg masses.

Fig. 3. *Pseudocalanus elongatus* female ventral, with loose egg mass.

Fig. 4. *Pseudodiaptomus marinus* female ventral, with paired egg masses.

A few Cyclopoida copepod females carry single egg masses, but most are paired, attached dorsally or laterally. These paired masses are often compressed together, appearing like a single mass, as in *Oncaea* spp. (Fig. 5), the eggs tightly squashed inside. *Oncaea* spp. females are sometimes collected bearing just egg remains (Fig. 6), the larvae having been released. This can occasionally also be observed in other orders. *Ditrichocorycaeus anglicus* have a loose, double egg mass (Fig. 7), while *Oithona* spp. have a pair of widely separated and elongated egg masses attached laterally, usually containing single or double rows of eggs (Fig. 8).

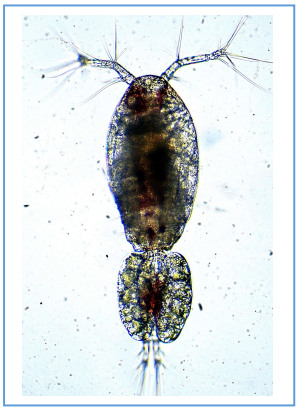

Fig. 5. *Oncaea waldemari* female dorsal, with paired dorsal egg masses.

Fig. 6. *Oncaea waldemari* female dorsal, with hatched egg remains.

Fig. 7. *Ditrichocorycaeus anglicus* female dorsal, with paired dorsal egg masses.

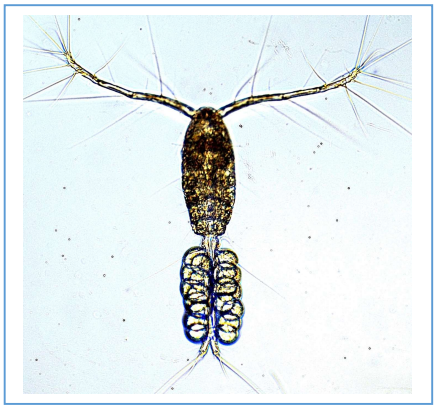

Fig. 8. *Oithona similis* female dorsal, with paired lateral egg masses.

Harpacticoida females, with few exceptions carry a single egg mass ventrally, as in *Goniopsyllus clausi* (Fig. 9). *Euterpina acutifrons* eggs do not have an obvious sac membrane (Fig. 10), but if dislodged from the female, remains as an intact egg mass.

Fig. 9. *Goniopsyllus clausi* female ventral, with single egg mass.

Fig. 10. *Euterpina acutifrons* female lateral, with single egg mass.

In Monstrilloida, there are no egg sacs. The eggs are carried adhering to a pair of slender, trailing, ovigerous spines that extend from the genital somite ventrally (Fig. 11).

In the highly modified Siphonostomatoida, Family Caligidae are fish parasites and the commonest siphonostome group sampled. The eggs are disc-shaped and compressed into a single row in each of the paired, cylindrical egg sacs (Fig. 12). Siphonostomes in other families, which are parasitic on invertebrate hosts, have an appearance more reminiscent of cyclopoid copepods and typically have paired circular egg sacs.

Fig. 11. *Monstrilla longicornis* female lateral, with eggs on ovigerous spines.

Fig. 12. Caligoid copepod female ventral, with lateral egg sacs.

Copepod eggs of all orders are usually spherical with a smooth surface (Figs. 13, 14; Koga, 1968, 1973). *Calanus helgolandicus* and C. *finmarchicus* sometimes have a rough membrane covering the egg (Fig. 15). Most copepod species do not have eggs with a gap called the perivitelline space, between the inner and outer egg membranes, except in a few calanoids, where it is typically very wide, as in *Subeucalanus crassus* (Fig. 16). In a few calanoid species, the eggs are covered in spines, as in *Centropages typicus* (Fig. 17). This species free-spawns their eggs in long strips two eggs wide, the strips often found intact in samples. *Candacia armata* has even stronger surface spines on their eggs, which are reported to develop after the eggs are laid (Bernard, 1965).

Several copepod species, probably in response to deteriorating environmental conditions, can produce diapause eggs with an egg membrane differing from the normal eggs. These are adapted to remain viable in the bottom sediments, for several years even, to seed future generations (Lindley, 1990). This ability has

developed in at least some Calanoida families, such as the Pontellidae, Acartiiidae, Temoridae and Centropagidae. Even non-diapause eggs have been shown to be very resilient. Eggs of several species have been shown to pass through the guts of larval fish undigested, but not remaining viable (Conway *et al*., 1994; Fig. 18). However, eggs of brackish water *Eurytemora* spp. hatched normally even after traversing the guts of larval fish for up to 6.5 hours, an excellent survival strategy.

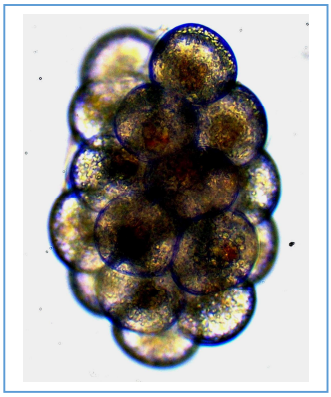

Fig. 13. *Euterpina acutifrons* eggs, 60 µm diameter.

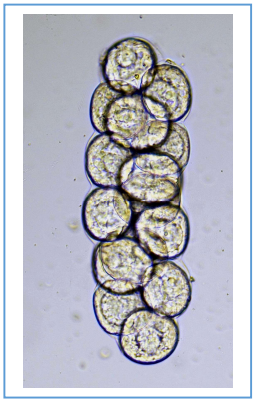

Fig. 14. *Oithona similis* eggs, 60 µm diameter.

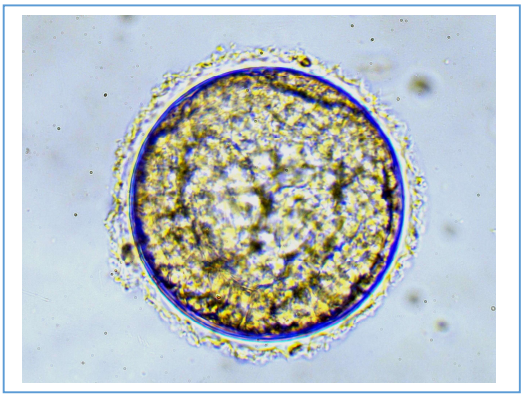

Fig. 15. *Calanus helgolandicus* egg. Total diameter 200 µm, inner egg 175 µm.

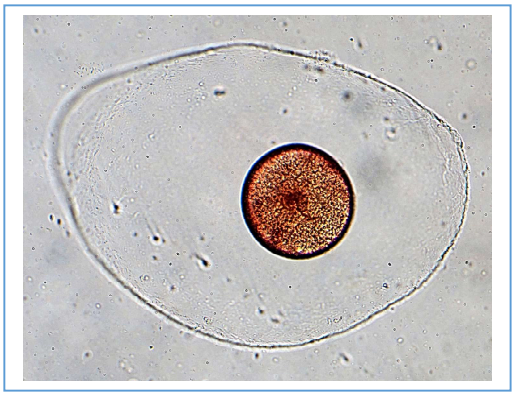

Fig. 16. *Subeucalanus crassus* egg. Total diameter ~750 µm, inner egg 200 µm.

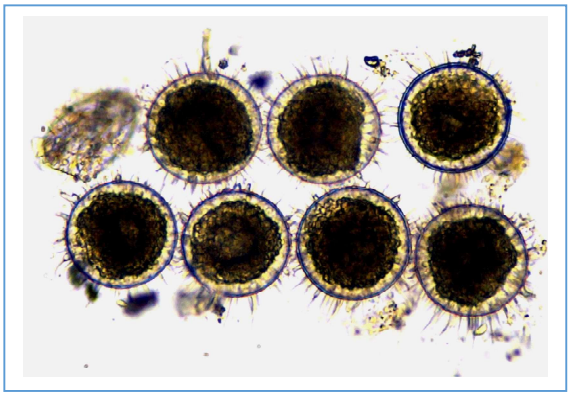

Fig. 17. *Centropages typicus*, part of egg string. Egg diameter 72 µm excluding spines.

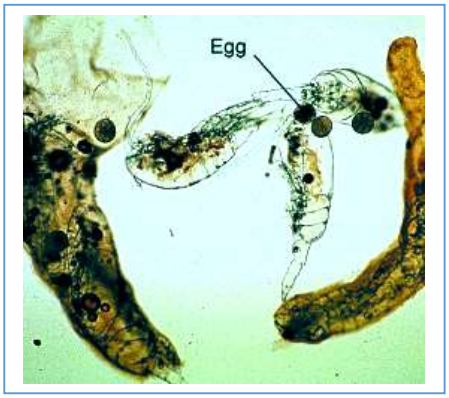

Fig. 18. Larval turbot (*Scophthalmus maximus*) faecal sacs, containing female *Pseudocalanus elongatus* exoskeletons and their undigested eggs.

Egg diameters of some common copepod species found in the northern European area, are given in Table 1. Diameter can vary slightly seasonally and with geographical location. There is overlap in size range between some species, but egg measurement, in conjunction with their appearance and knowledge of the species present in the same samples, can often lead to their positive identification. Eggs of other common invertebrates such as chaetognaths and euphausiids usually have much larger eggs.

Table 1: Examples of egg diameters of some northern European copepod species (from Conway, 2012a).

Species	Egg diameter (μm)
CALANOIDA	
Acartia clausi	72-84
Calanus finmarchicus	135-180 (~200 including any membrane)
Calanus helgolandicus	153-191 (~200 including any membrane)
Candacia armata	170-190
Centropages hamatus	62-80
Centropages typicus	~70
Eurytemora affinis	73-98
Eurytemora americana	~90
Metridia lucens	170-200
Paracalanus parvus	50-70
Pseudocalanus elongatus	100-133
Subeucalanus crassus	~250 (~750 including outer egg membrane)
Temora longicornis	76-86
Temora stylifera	~80
Paraeuchaeta norvegica	410-460
CYCLOPOIDA	
Ditrichocorycaeus anglicus	54-70
Oithona similis	~56
Oithona nana	~50
Oncaea venusta	40-60
Oncaea waldemari	~40
HARPACTICOIDA	
Euterpina acutifrons	54-73
Microsetella norvegica	~40

Copepod spermatophores and fertilization

Female copepods are fertilised by the male attaching a spermatophore, typically sausage-shaped in at least calanoid copepods, to the female's genital somite (Fig. 19), in what can be a complex sequence of actions (Ohtsuka & Huys, 2001). Males are occasionally collected carrying a spermatophore in one of their fifth pair of legs (Figs. 20, 21). The sperm are stored by the female until required in a pair of small chambers called seminal receptacles (Fig. 22) inside the genital somite. However, not all species have seminal receptacles, those without requiring repeat mating. In some species, such as *Paraeuchaeta norvegica,* multiple spermatophores are sometimes found attached; some empty (Fig. 23). Eggs and spermatophores can be present at the same time (Fig. 24).

Fig. 19. *Acartia tonsa* female, genital somite lateral, with attached spermatophore.

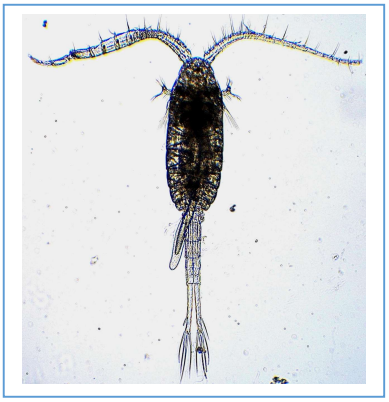

Fig. 20. *Eurytemora affinis* male ventral, carrying a spermatophore.

Fig. 21. *Paraeuchaeta norvegica* male dorsal, carrying a spermatophore.

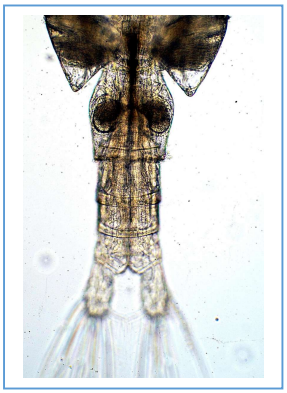

Fig. 22. *Calanus finmarchicus* female, genital somite and seminal receptacles.

Fig. 23. *Paraeuchaeta norvegica* female, genital somite with several spermatophores attached.

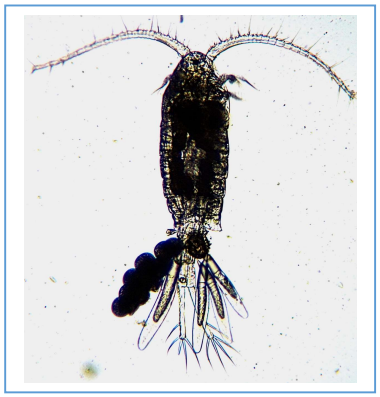

Fig. 24. *Eurytemora affinis* female, with eggs and spermatophores attached.

Copepod naupliar stages

When a copepod egg hatches a nauplius stage emerges, the typical crustacean larva (Fig. 25). The commonest nauplii sampled inshore are often those of barnacles, but barnacle nauplii can be easily distinguished as they have an obvious pair of horns on the frontolateral edge of the cephalic shield, the curved plate covering the anterior body. Copepod nauplii moult through a set number of stages, usually six (N1-N6; Figs. 25-30, 31) before they moult and transform into the first of the copepodite stages (C1) that are more reminiscent of the adult form. Almost all the Calanoida, Harpacticoida and free-living Cyclopoida have six naupliar stages, exceptions being mainly parasitic species (Izawa, 1987). It is thought that at least the first naupliar stage of many copepods may not feed, obtaining enough nutriment from the egg to carry them through their first moult. As an example of naupliar development, figures 25-30 illustrate the six stages of the calanoid *Calanus helgolandicus.* The morphology of a typical N6 calanoid nauplius and *C. finmarchicus* naupliar stages, in diagrammatic form, are given in Figure 31a and 31b respectively.

C. helgolandicus is a large, well-studied species, with clearly defined naupliar stages. It has eight paired appendages when it reaches N6, the maximum possible. All free-living copepods have basically similar naupliar development to *Calanus*, but there can be slight to considerable differences from the described pattern in other calanoids and copepod orders (Ogilvie, 1953; Lovegrove, 1956; Björnberg, 1972; Koga, 1984).

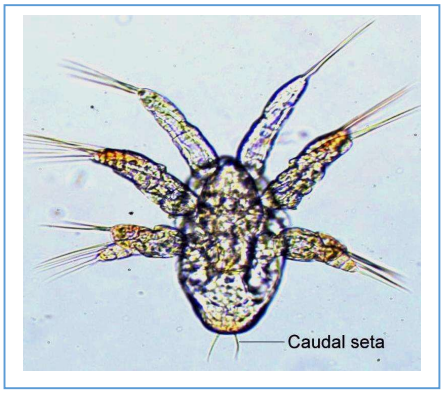

Fig. 25. *C. helgolandicus* N1 ventral, 0.23 mm (images not to same scale).

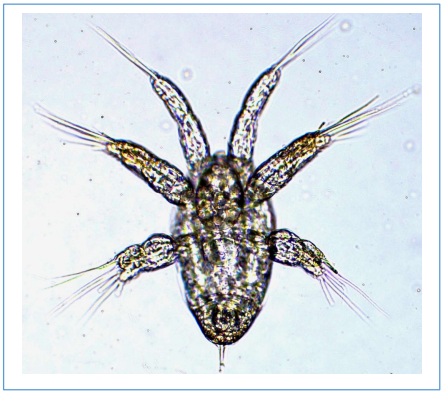

Fig. 26. *C. helgolandicus* N2 ventral, 0.27 mm.

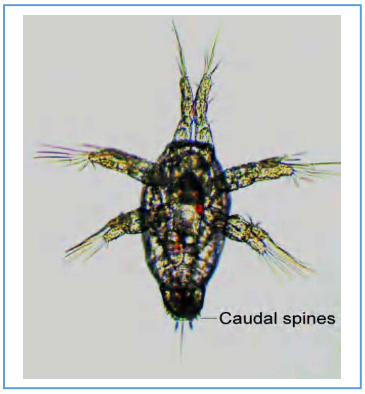

Fig. 27. *C. helgolandicus* N3 ventral, 0.38 mm.

Fig. 28. *C. helgolandicus* N4 ventral, 0.45 mm.

Fig. 29. *C. helgolandicus* N5 ventral, 0.50 mm.

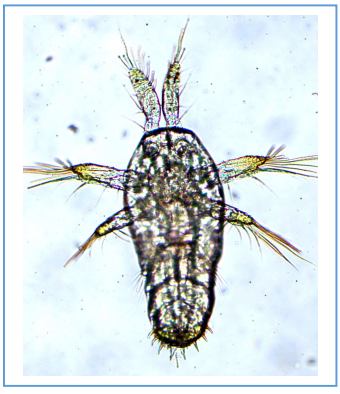

Fig. 30. *C. helgolandicus* N6 ventral, 0.58 mm.

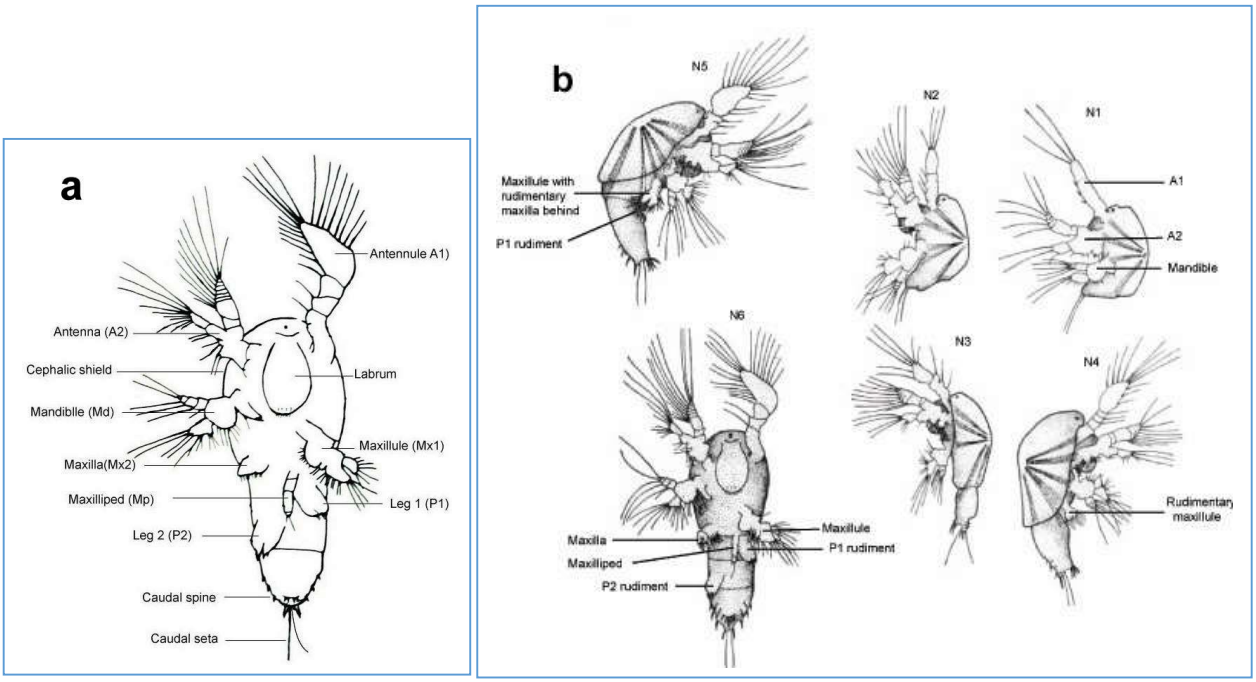

Fig. 31. Calanoid nauplii, typical morphology and development. a) Morphology of an N6 calanoid nauplius, ventral (after Koga, 1984); b) Naupliar developmental sequence of *Calanus finmarchicus* (after Marshall & Orr, 1955). For clarity, in both figures only alternate appendages are drawn.

In N1 and N2 (Figs. 25, 26) the nauplius body is largely covered by a cephalic shield (Fig. 31). Typical of most calanoid nauplii, after subsequent moults the posterior body extends to an increasing distance beyond the shield (Figs. 27-30, 31b), as it gradually lengthens.

Caudal setae and spines are present or gradually develop on the hind body. Setae are defined as generally fine and parallel-sided, while spines are more robust, tapering and may be movable, but this definition is not always rigidly adhered to. In N1 and N2, there are only two fine caudal setae, arranged roughly parallel to one another (Figs. 25-26). From N3, increasing numbers of robust, short spines appear after each moult and form the caudal armature (Figs. 27-30, 31b, 32-35). Each of these spines is paired with an identical spine on the opposite side, so at least in *C. helgolandicus* the spines on each side of the hind body are a mirror image of the other. In some calanoid nauplii, the spines are similarly paired, but pairs may differ in length (Figs. 42, 46). From N3-N6, a pair of fine caudal setae are still present, but these now point in different directions, which appears to be a particularly obvious characteristic of calanoid nauplii, so a useful feature to separate them from nauplii of other orders. They are sometimes referred to as sensory setae or feelers. They can be difficult to see in the same field of view, unless the caudal region is viewed laterally and are most clearly visible in figures 34 and 44.

In common with all copepod species, N1-N3 have only three pairs of well-developed appendages (Figs. 25-27, 31b). The anterior pair are the antennules (A1), each of which are uniramous (Fig. 31a, b). The second and third pairs are the antennae (A2) and mandibles (Md), each of which are biramous. In all stages, a single median naupliar eye is usually present. The mouth is situated ventrally, covered by a flap-like labrum.

From N4 the remaining paired appendages progressively start to appear (Fig. 31b), initially quite rudimentary. In N4 rudimentary maxillules (Mx1) appear (Fig. 33), then in N5, maxillae (Mx2) and the first pair of legs (P1; Fig. 34). In N6 (Fig. 35) the maxillipeds (Mxp) and second pair of legs (P2) appear. Appendages acquire further setae and or segments at each moult, and by N6 the hind body has at least some rudimentary somites visible.

Fig. 32. *C. helgolandicus* N3 lateral, 0.38 mm.

Fig. 33. *C. helgolandicus* N4 lateral, 0.41 mm.

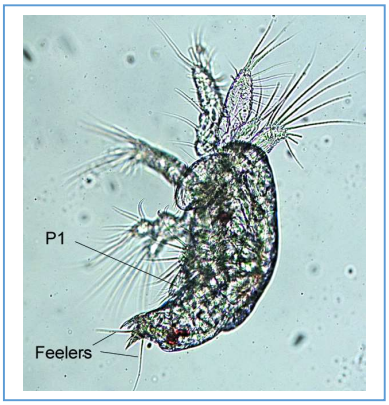

Fig. 34. *C. helgolandicus* N5 lateral, 0.50 mm.

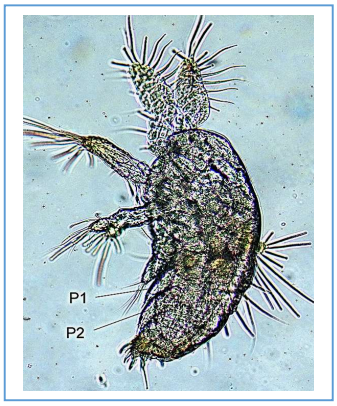

Fig. 35. C. *helgolandicus* N6 lateral, 0.58 mm.

One of the main features used to separate the naupliar stages is the setation of the distal segment of the A1 (Table 2). N1 has three setae (Fig. 36) and they tend to be long, although often damaged in preserved specimens, while N2 has four (Fig. 37). N3 is one of the easiest of the stages to identify, as there are seven setae (Fig. 38), obviously sparse, widely spaced and easily counted compared to later stages. In N3-N6 care must be taken to only count setae on the distal segment, as there is usually a seta at the very end of the previous segment (Fig. 38). N4 can be distinguished by typically having eleven setae, N5 fourteen and N6 sixteen (Figs. 39-41; Table 2). However, abnormalities sometimes arise, probably caused by environmental conditions (Björnberg, 1986) and in figure 35, seventeen rather than sixteen setae were present.

Table 2: *Calanus helgolandicus* nauplii. Number of anterior appendages and legs, length range and number of setae on the A1 distal segment. Measurements from formaldehyde preserved, cultured nauplii (from Conway, 2012a).

Naupliar stage	Number of anterior appendages/legs	Total length range (mm)	Number of setae on the A1 distal segment
N1	3/0	0.21-0.24	3
N2	3/0	0.26-0.28	4
N3	3/0	0.37-0.42	7
N4	4/0	0.40-0.48	11
N5	5/1	0.50-0.55	14
N6	6/2	0.57-0.61	16

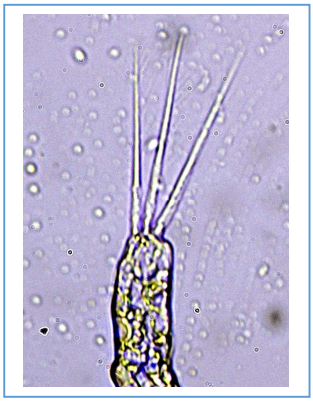

Fig. 36. *C. helgolandicus* N1, A1.

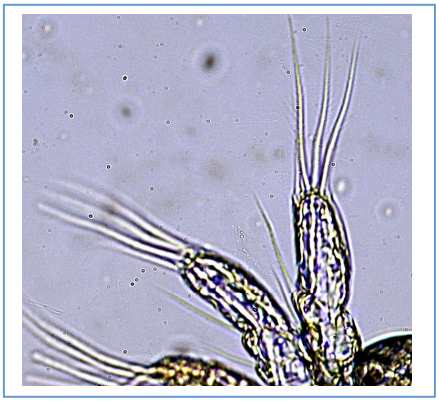

Fig. 37. *C. helgolandicus* N2, both A1.

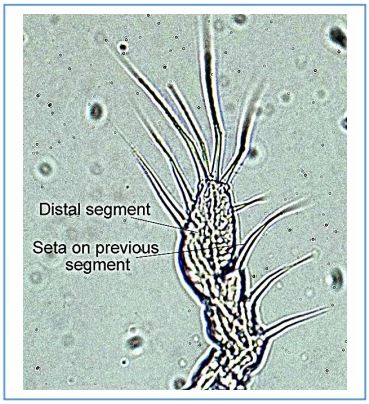

Fig. 38. *C. helgolandicus* N3, A1.

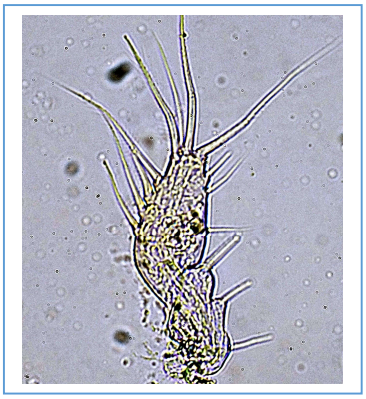

Fig. 39. *C. helgolandicus* N4, A1.

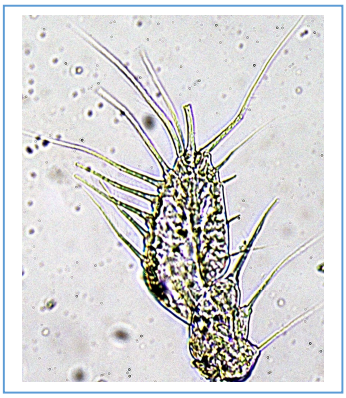

Fig. 40. *C. helgolandicus* N5, A1.

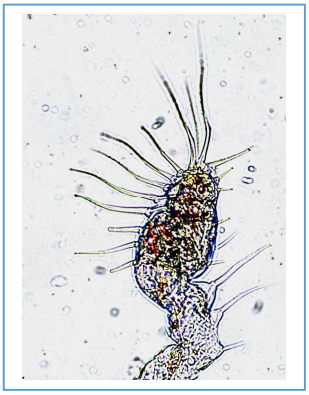

Fig. 41. *C. helgolandicus* N6, A1 with 17 rather than 16 setae.

While the number of setae on the A1 can separate the naupliar stages, they can sometimes be difficult to observe or are damaged, so a combination of features can be used. For example, *C. helgolandicus* N3 has limited caudal armature (Fig. 27) and sparse, widely spaced setae on the A1 (Fig. 38). N4-N6 have quite large numbers of setae on the A1 (Figs. 39-41) and are more difficult to count, so caudal armature (Faber, 1966) and presence and number of rudimentary limbs can be used in staging (Figs. 28-30, 33-35). N4 (Fig. 28) has sparser caudal armature than N5 and N6. N5 and N6 have similar caudal armature (Figs. 29, 30), but the second pair of legs (P2) are very obvious in N6 (Fig. 35).

Apart from changing morphology, separation of naupliar stages is aided by the rapid growth that occurs following moulting, often resulting in no length overlap between successive stages (Table 2; Fig. 50), so under a microscope it is usually possible to do an initial, rough separation of stages of the same species on size alone. While sizes can vary in the same sample and also seasonally, the range is usually quite limited.

Identifying copepod nauplii to their order

There will be an indication from the species of adult copepods present in a plankton sample, which nauplii are likely to be present. However, it is easy to culture females to obtain nauplii of known origin. With gradual experience, most nauplii can usually be identified, at least to the order level, by some reasonably obvious features. Most difficult to identify, are usually the rudimentary N1 and N2 stages.

The main nauplii sampled are usually from orders Calanoida, Cyclopoida and certain Harpacticoida. Most Harpacticoida and also Polyartha are benthic or commensal, so their nauplii tend to be more abundant in shallower water. Monstrilloida and Siphonostomatoida are parasitic and their nauplii are most often found in low numbers inshore, where their hosts are concentrated.

Most free-living copepods have the full six naupliar stages, while parasitic species usually have fewer. Effectively only the first three pairs of appendages are present in all species from N1-N3. The fourth pair of appendages, the maxillules, may be present in some species, usually from N2 or N3, but in very rudimentary form, such as just a setae or spine. The maxillules and remaining four appendage pairs show different patterns of appearance from N4 in different copepod orders and species, if they develop at all.
The nauplii of many copepods have been described in detail, Mauchline (1998) listing some eighty-three species of calanoid nauplii. Oberg (1906), Ogilvie (1953), Lovegrove (1956), Björnberg (1972), Koga (1984) and Li & Fang (1990) give illustrations of a range of nauplii from different orders. Individual nauplii have also been described in many publications, but there are only a few publications giving any information on how to differentiate between the nauplii of the main orders (e.g. Czaika, 1982; Izawa, 1987; Fornshell, 1994, 2005; Dahms *et al*. 2006).

Calanoida nauplii
Calanoid nauplii are usually quite characteristic in appearance and easy to separate to at least their order.

Appearance: The body is typically deep dorsoventrally (Figs. 32-35) and in dorsal and ventral view usually elongated, from at least N2 (Figs. 26-30). With each moult, the posterior body increasingly extends from below the cephalic shield that covers the anterior body, until the nauplii become comma-shape (Figs. 32-35). The posterior body is particularly elongated in some species such as *Anomalocera patersonii* (Fig. 42). However, Family Acartiidae is an exception, the posterior body remaining quite short even in N6 (Figs. 43-44). However, the body is still obviously deep dorsoventrally and a pair of caudal setae can be seen to diverge (Fig. 44; see below). *Acartia* spp. also tend to have a particularly prominent, dark naupliar eye and the anterior cephalic shield edge is not curved, but noticeably straight.

Fig. 42. *Anomalocera patersonii* nauplius, 0.53 mm ventral.

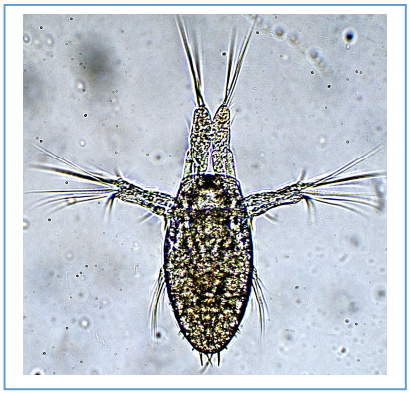

Fig. 43. *Acartia tonsa* N6 dorsal 0.25 mm.

Fig. 44. *Acartia clausi* N5 lateral, 0.21 mm.

Caudal region: In N1 and N2, the caudal armature usually consists of only a pair of fine setae (Figs. 25-26). These are on the posterior body, close to or outside the edge of the cephalic shield in most calanoids. They are arranged approximately parallel to one another and usually visible in the same plane in dorsal view. From N3-N6 short, paired spines usually appear in increasing numbers with each moult (Figs. 27-30, 31b, 32-35). As earlier mentioned, very obvious in calanoid nauplii, a pair of fine setae are also present, situated at slightly different levels on the posterior body and pointing in different directions, so easiest seen together in lateral view (e.g. Figs. 33, 34). These diverging setae are missing in N4-N6 of a very small number of calanoids, such as *Metridia lucens*, but their nauplii still have the characteristic calanoid shape. Euchaetidae do not follow the pattern described above, related to their lecithotrophic development (see below). Their N1 has no caudal armature and N2-N5 only have a pair of setae which can be quite thick (Fig. 45), diverging in the later stages. Caudal spines do not appear until N6.

In many species of calanoid nauplii, each side of the caudal region and associated armature is almost the mirror image of the other side (Figs. 25-30), but in some species it can be asymmetric and the spine pairs of different lengths and thicknesses. This is the case in *Anomalocera patersonii* (Fig. 42), *Temora longicornis* (Fig. 46) and *Centropages typicus* (Fig. 47). In families Pontellidae (Fig. 42), Temoridae (Fig. 46), Centropagidae (Fig. 47), and Pseudodiaptomidae the left side is more developed, while in Eucalanidae (Fig. 48) and Rhincalanidae it is the right side (Huys, 2014). Asymmetry of the caudal region in some species appears to be another feature only found in calanoid nauplii.

Fig. 45. *Paraeuchaeta norvegica* N4 dorsal, 0.68 mm.

Fig. 46. *Temora longicornis* N4 ventral, 0.25 mm.

Fig. 47. *Centropages typicus* N6 dorsal, 0.29 mm.

Fig. 48. *Subeucalanus crassus* N3 ventral, 0.51 mm.

Fig. 49. *Paraeuchaeta norvegica,* egg-N6 group.

Fig. 50. *Calanus helgolandicus,* N3-N6 group.

Appendages: Only the first three pairs of functional appendages are present from N1-N3 (Figs. 25-27), but in a few cases, very rudimentary maxillules appear in N3. In live calanoid, nauplii the A1 usually point forwards and their setae are generally long and clearly visible. They are three-segmented, usually with a broad, paddle-shaped distal segment in later stages (Figs. 38-41). A1 setation in most species broadly follows the pattern shown in Table 2 (Ogilvie, 1953).

Many calanoid nauplii gradually acquire the full set of eight appendage pairs by N6, but some have development where particular appendages do not appear, or they are rudimentary. Families Phaennidae and Euchaetidae, including *Paraeuchaeta norvegica* (Figs. 45, 49) are some of the calanoid exceptions. Only the first three pairs of appendages are present until N5, when some rudimentary appendages appear, most of the remaining ones only appearing in N6, but still rudimentary (Nicholls, 1934). This development is typical of deep-living copepods (Kosobokova *et al*., 2007), related to their life history. They are lecithotrophic in all stages, developing from eggs packed with lipid, laid deep in the water column. The nauplii slowly develop as they rise to the surface, so do not require a sophisticated set of limbs. Because of their special development,

there is only a small difference in size between stages and sometimes considerable variation in size within a stage. This makes it difficult to separate stages on size alone (Fig. 49), which is usually possible with non-lecithotrophic nauplii of all orders. Calanoid (and also harpacticoid) nauplii have a slightly different mandible structure compared to cyclopoids and Polyartha. The endopod of the mandible in calanoids has one segment (Fig. 51) while there are two in cyclopoids and Polyartha (Fig. 52). The mandible can often be inspected without engaging in a delicate dissection.

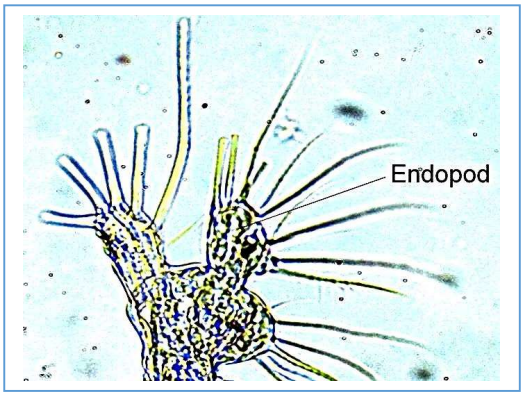

Fig. 51. Calanoida, *Calanus finmarchicus* N6 mandible.

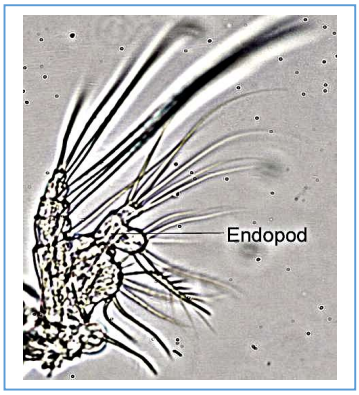

Fig 52. Polyartha, *Longipedia minor* N5 mandible.

Cyclopoida nauplii

There are a limited number of species of pelagic cyclopoid species in the European region, but they and their nauplii can be very numerous in samples. Many cyclopoids are small as adults, so have small nauplii.

Appearance: Cyclopoid nauplii are typically shield-shaped (Figs. 53-61) and more dorsoventrally flattened (Figs. 62, 63) than calanoids. The caudal region only extends slightly beyond the cephalic shield, even in N6 (Fig. 63).

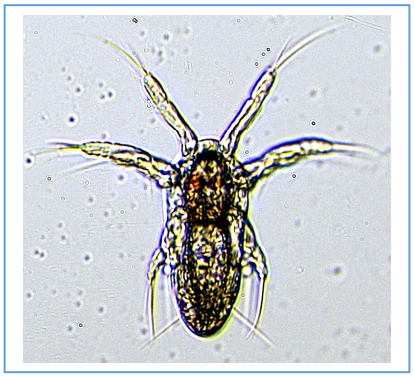

Fig. 53. *Ditrichocorycaeus anglicus* N1 ventral, 0.11 mm, cultured.

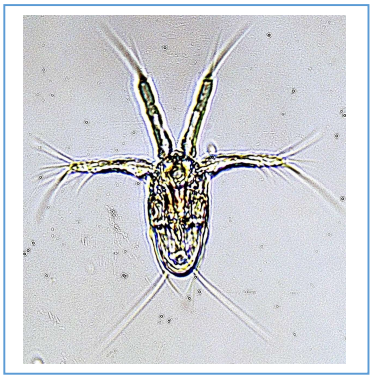

Fig. 54. *Oncaea* sp. N1 dorsal, 0.09 mm, cultured.

Fig. 55. *Oithona similis* N1 dorsal, 0.12 mm, cultured.

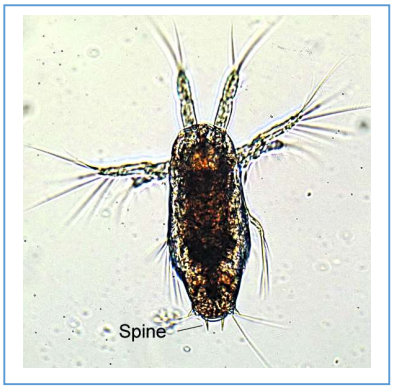

Fig. 56. *Ditrichocorycaeus anglicus* N4 dorsal, 0.31 mm.

Fig. 57. *Oncaea* sp. nauplius ventral, 0.36 mm.

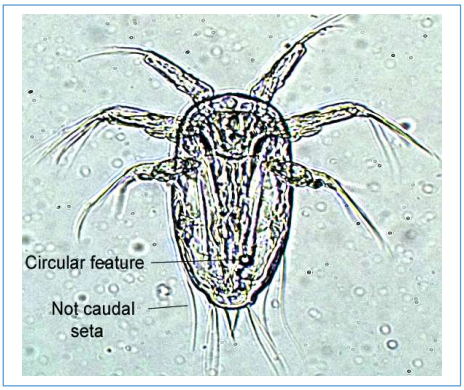

Fig. 58. *Oithona similis* N4 dorsal, 0.16 mm.

Fig. 59. *Ditrichocorycaeus anglicus* N6 ventral, 0.41 mm.

Fig. 60. *Oncaea* sp. late nauplius dorsal, 0.40 mm.

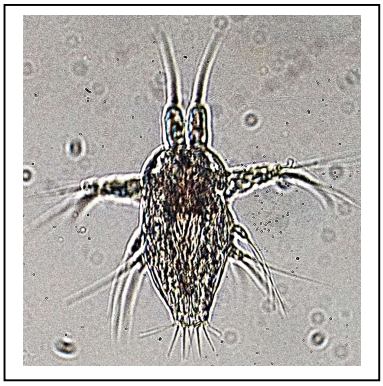

Fig. 61. *Oithona nana* N6 ventral, 0.14 mm.

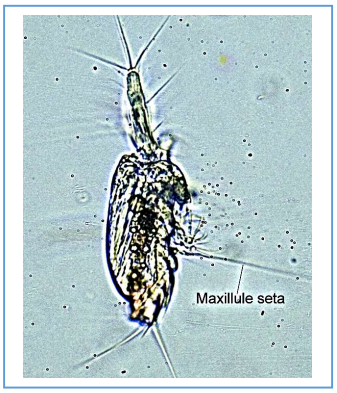

Fig. 62. *Oncaea* sp. early nauplius lateral, 0.20 mm.

Fig. 63. *Oithona similis* N6 lateral, 0.22 mm.

Pigmentation, or lack of it, can sometimes be useful in identification. For example, both *Ditrichocorycaeus* and *Oncaea* spp. are quite colourful nauplii when live, with red pigment in the body and limbs (e.g. Figs. 59, 60). *Oithona* spp. typically lack pigmentation and can have a blueish tinge. Additionally, they often have small circular features inside their hind body, singly (Fig. 58), but often a pair side by side, assumed to be globules of lipid. These may be present in other nauplii, but seem to be particularly obvious in some *Oithona* nauplii.

Caudal region: When assessing the setation of the caudal region, care must be taken to not mistakenly include setae extending down ventrally from the anterior appendages (e.g. Fig. 58).
In N1 and N2, similar to almost all copepod nauplii, there are a pair of fine setae on the hind body (Figs. 53-55), additional setae and spines appearing after subsequent moults (Figs. 56-61). In early nauplii, the caudal setae extend from below the cephalic shield, while in later stages they originate from outside the shield, when the caudal region protrudes slightly. The arrangement of caudal armature is bilaterally symmetrical, each side the mirror image of the other, without any of the paired setae obviously diverging dorsoventrally from one another, although at least the central ones sometimes cross in the same plane (Figs. 58, 61). *Oncaea* and *Ditrichocorycaeus* spp. nauplii appear quite similar. In *Ditrichocorycaeus* from N3-N6, there are two pairs of very long caudal setae and also a pair of slim spines and some tiny spinules distally (Figs. 56, 59; Gibson &Grice, 1977; Koga, 1984). In *Oncaea* spp. there are only two pairs of fine caudal setae (Figs. 57, 60), although a pair of tiny, distal spinules appear from N5 in some species (Koga, 1984). Malt (1982) drew three pairs of long caudal setae in N4 and N5 of one species. .
Oithona spp. nauplii follow a slightly different pattern of development. In N3, there are two pairs of long caudal setae, with a pair of short spinules between. This armature remains the same in N4, but the central pair of spinules become longer, slim spines (Fig. 58; Koga, 1984). In N5 a small pair of spinules may develop between the central pair, but difficult to see. These become longer slim spines in N6, sometimes crossing (Fig. 61). In N5 and N6 there may also be a tiny lateral spinule on each side, to the very outside of the armature.

Appendages: As in all copepod nauplii, only the first three pairs of functional appendages are present from N1-N3. However, in N2 a seta usually appears behind each mandible, representing a rudimentary maxillule. As the maxillules gradually develop at each moult, among the setae each bears is a very long one (Fig. 62) that can extends backwards over the caudal region. Care has to be taken not to confuse these with the caudal setae. The mandible can also bear long setae that extend rearwards.
Compared to calanoids, the distal segment of the A1 is usually not as broad (Figs. 53-63). The setae on the segment are more difficult to count than in calanoids, as they are sometimes tiny, or on the face of the segment rather than the edge. Difficulty in counting these setae is possibly the reason for the rather varied counts given in the literature (e.g. Koga, 1984; Gibson & Grice, 1977). In *Oncaea* and *Ditrichocorycaeus* spp., N1 always appears to have 3 setae on the A1, while in *Oithona* spp. there are three plus apparently a tiny one (Gibbons & Ogilvie, 1933). The endopod of the mandible is of two segments as in Polyartha (Fig. 52), which separates

them from calanoid and harpacticoid nauplii. The maxilla and maxilliped never develop externally during the naupliar phase, only visible as simple cuticular folds, although rudimentary P1 and P2 are usually present in N6 (Dahms *et al*., 2006).

Harpacticoida nauplii

Appearance: Harpacticoids are a morphologically varied group, which is reflected in their nauplii. In ventral view the nauplii body is usually broad and disc-shaped (Figs. 64-66), but in some species more shield-shaped (Figs. 67, 68). Like cyclopoids they are quite dorsoventrally flattened and even in later stages the posterior body usually only protrudes a short distance from below the cephalic shield.

Caudal region: Similar to cyclopoid nauplii, the caudal region is bilaterally symmetrical and the caudal armature identical both sides. It also appears that none of the individual setae pairs diverge dorsoventrally from one another. *Euterpina acutifrons*, usually the commonest pelagic harpacticoid sampled inshore, have a very characteristic nauplius (Figs. 65, 66). There is a narrow, central process projecting from the hind body in N1 (Fig. 65) and N2 (Haq, 1965), blunt with tiny spinules distally. They have quite broad A1, a pair of fine caudal setae in all stages (Figs. 65, 66) and a pair of very robust caudal spines from N3-N6. In N6 there is an additional pair of short, fine setae, just outside the spines, but difficult to see.

Fig. 64. Unidentified harpacticoid nauplius dorsal, 0.31 mm.

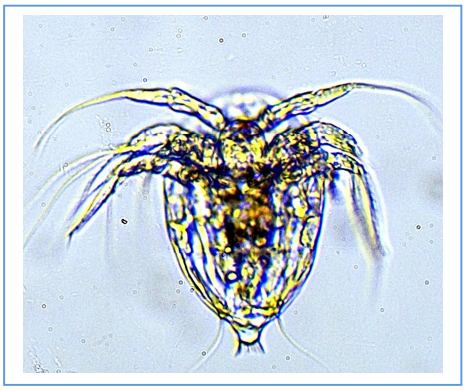

Fig. 65. *Euterpina acutifrons* N1 ventral, 0.11 mm, cultured.

Fig. 66. *Euterpina acutifrons* N6 dorsal, 0.19 mm.

M. norvegica nauplii (Figs. 67-69) can be very abundant in certain areas. They have a very characteristic appearance, especially in lateral view (Fig. 69), their massive labrum very prominent. Their caudal armature, described from Japanese waters by Hirakawa (1974), differs slightly from descriptions from UK waters by Diaz & Evans (1983). Because of the region of capture of the nauplii described here, the latter description has been followed. In N1 and N2 there is a sharp, central caudal process, not blunt as in *E. acutifrons*. In N1 there are no distal caudal setae, but a pair of setae from the rudimentary maxillule project from below the cephalic shield in this and the following two stages, reducing in length by N3. In N2, there are a pair of distal, slim setae and in N3 these are replaced by a pair of long, strong setae with two pairs of finer setae outside them. In N4-N6 (Figs. 67-69), there are two pairs of strong caudal setae, the central pair much longer and two pairs of small, fine setae. Setae projecting rearwards from the anterior limbs often overlay the caudal setae.
M. rosea, a species that also occurs in the area, have very similar nauplii (Björnberg, 1972).

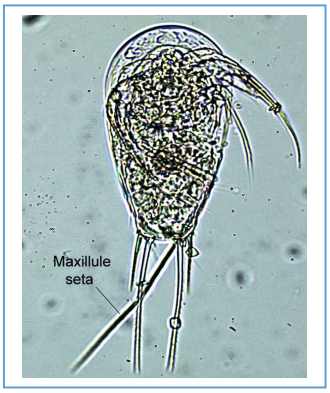

Fig. 67. *Microsetella norvegica* N4 ventral, 0.19 mm.

Fig. 68. *Microsetella norvegica* N6 ventral, 0.23 mm.

Fig. 69. *Microsetella norvegica* N6 lateral, 0.22 mm.

Appendages: As in other orders, only the first three pairs of functional appendages are present from N1. Similar to cyclopoids, in N2 a seta usually appear behind each mandible, which represent a rudimentary maxillule. At each moult, as the maxillules gradually develop, one of the setae they bear can be very long and extend over the hind body (Figs. 67-69). The mandible can also bear long setae that extend over the hind body.
The A1 have a narrow distal segment and are usually held laterally, or back alongside the body. Similar to calanoids (Fig. 51) the endopod of the mandible has only one segment. The maxilla and maxilliped do not generally develop until N6, when the full set of appendages may be present, although some may be very rudimentary.

Polyartha nauplii
Adults of Order Polyartha are often collected in shallow inshore plankton samples, but are really a bottom living group. However, their six naupliar stages are pelagic and sometimes numerous in samples. They have a very characteristic appearance, so are easily identified. The main species found in the northern European area are all from Family Longipediidae, *Longipedia coronata, L. minor* and *L. scotti*.

Appearance: In lateral view the bodies of the above species are quite deep dorsoventrally (Fig. 72). The cephalic shield is broadly rounded anteriorly in all stages (Figs. 73, 74), except in *L. coronata* where it is only rounded in the N1 (Fig. 70), the subsequent stages with a distinctive, forward pointing projection (Figs. 71, 72). Because of its rounded shield, the N1 of *L. coronata* is probably indistinguishable from the N1 of *L. scotti* (Nicholls, 1935).

Caudal region: While the nauplii of at least some of the other families of Polyartha have nauplii very similar to harpacticoid nauplii, Longipediidae are unusual in having from N1 a centrally located, single, strong caudal spine (Figs. 70-74), in some stages serrated like the caudal spine of a cirripede nauplius (Fig. 70). Measurements given in the figures do not include the caudal spine, to make them consistent with the measurements of the other nauplii. In *L. coronata*, while the body shows an increase in length with development, the central spine remains around the same length. In *L. minor* (Fig. 73) the spine increases in length relative to body length with development, while in *L. scotti* (Fig. 74) it decreases in length. Nichols (1935) gives a comparative table of body and spine lengths for the three species. Apart from the central caudal spine, *Longipedia* nauplii also have in N1 (Fig. 70) and N2 a pair of prominent, strong spines, covered in serrations, that emerge anterior to the caudal region and protrude well beyond it. These are precursors of the maxillules and become less obvious from N3, when two-segmented appendages bearing large terminal spines and small, lateral setae develop.

Appendages: Longipediidae nauplii are similar to cyclopoid nauplii in having the endopod of the mandible composed of two segments (Fig. 52).

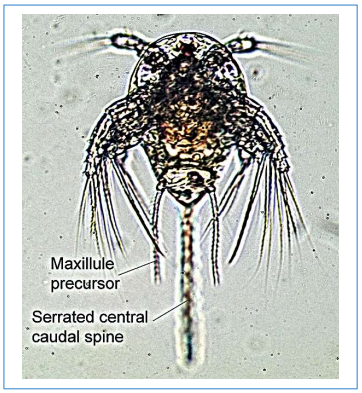

Fig. 70. *Longipedia coronata* N1 ventral, 0.16 mm (ex. spine).

Fig. 71. *Longipedia coronata* N6 ventral, 0.44 mm.

Fig. 72. *Longipedia coronata* N6 lateral, 0.44 mm.

Fig. 73. *Longipedia minor* N6 dorsal, 0.30 mm.

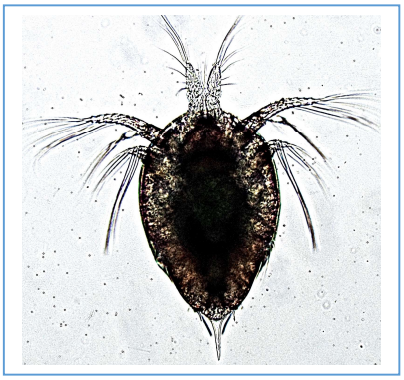

Fig. 74. *Longipedia scotti* N6 dorsal, 0.38 mm.

Monstrilloida nauplii

Monstrilloida are parasites of certain benthic invertebrates and in common with most parasitic copepods, the number of naupliar stages is reduced, in the case of monstrilloids to a single lecithotrophic stage. The nauplii are free-swimming for a very short period so are rarely sampled. From the little information available for a few genera and species, the nauplii are 0.049-0.070 mm in length (Giesbrecht, 1897; Malaquin, 1901; Grygier & Ohtsuka, 1995; personal observations), so will only be caught in finer mesh nets.

Appearance: Very few illustrations of monstrilloid nauplii seem to be available (Malaquin, 1901; Koga, 1984) and the only photographs appear to be of scanning electron microscope images (Grygier & Ohtsuka, 1995; Huys, 2014), which distort the natural appearance. *Monstrilla grandis* nauplii were cultured from females bearing eggs and were simple, flattened and shield-shaped with obvious globules of lipid internally (Figs. 75, 76). The eyes were orange/brown pigmented and X-shaped, which was also illustrated by Malaquin (1901) for *Cymbasoma danae* (as *Haemocera danae*), so this may be a useful identification feature for monstrilloid nauplii.

Caudal region: The caudal armature consists of a pair of fine setae (Figs. 75, 76).

Appendages: In common with the N1 of other copepods, only the first three appendages are present. Unlike most copepod nauplii, the A1 are situated quite far back from the anterior edge of the cephalic shield (Grygier & Ohtsuka, 1995). The endopod of the mandible consists of a single segment as in calanoid (Fig. 53) and harpacticoid nauplii, but this cannot easily be seen. The exopod bears a large, curved claw (Fig. 75), presumed to aid in attachment to, or penetration of the host.

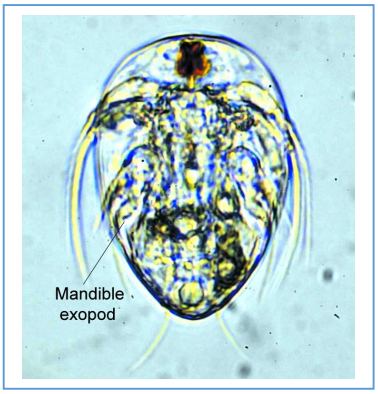

Fig. 75. *Monstrilla grandis* N1 dorsal, 0.07 mm, cultured.

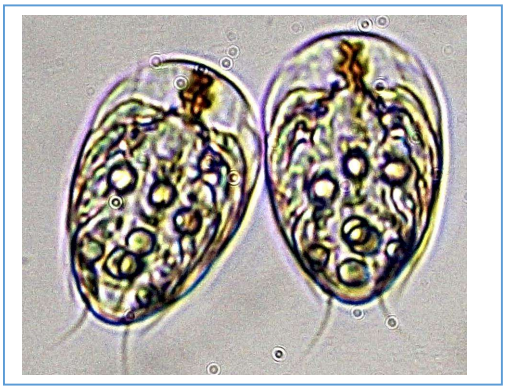

Fig. 76. Pair of *Monstrilla grandis* N1 dorsal, 0.07 mm, cultured.

Siphonostomatoida nauplii

Siphonostomatoida nauplii sampled are mainly of fish ectoparasites and general only found in low numbers inshore. In common with other parasitic copepods, the nauplii are lecithotrophic and the number of stages are usually reduced. *Lernaeocera branchialis*, a common gill parasite of fish, has one stage (Sproston, 1942), while two stages have been described for *Caligus elongatus* (Scram, 2004). However, some species have been reported to have no naupliar stages, the first copepodite stage (C1) hatching directly from the egg (Perkins, 1983). Dahms *et al*. (2006) mention N6, so number appears to range from 0-6. The commonest siphonostome nauplii sampled are usually those of Family Caligidae, which generally seem to have two naupliar stages. There are numerous caligoid species and their nauplii are poorly studied, so they probably can only be identified to species with certainty if cultured. The N1 of *Caligus elongatus* hatched to N2 within 24 hours (Piasecki & MacKinnon, 1995) and this moulted to a C1 in 67 hours, so N1 is less likely to be sampled.

Appearance: The body is characteristically shield-shaped and elongated (Figs. 77, 78), slenderer in the N2 (Schram, 2004). There is a short, blunt projection on the posterior body that is usually more pronounced in the N2. In live nauplii, bands of dark pigment are typically found across the anterior above the eye and across the mid and hind body. The eyes are usually red, but this is difficult to see because of overlying pigment.

Caudal region: Caudal armature typically consists of a pair of long, flattened, latterly directed setae (Fig. 79) that can sometimes be difficult to see.

Appendages: Only the first three pairs of appendages are present during the naupliar phase. In live specimens, all limbs are often held pointing forwards, giving a distinctive profile.

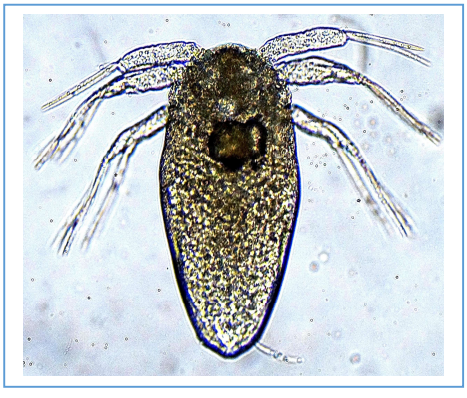

Fig. 77. Caligoid sp. nauplius dorsal, possibly N1, 0.41 mm (one caudal seta missing).

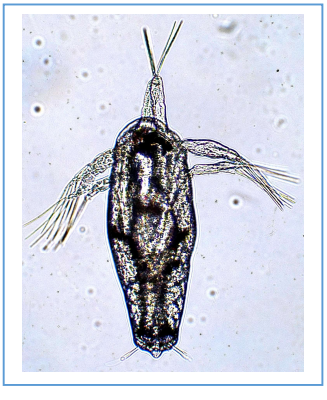

Fig. 78. Caligoid sp. N2 dorsal, 0.46 mm.

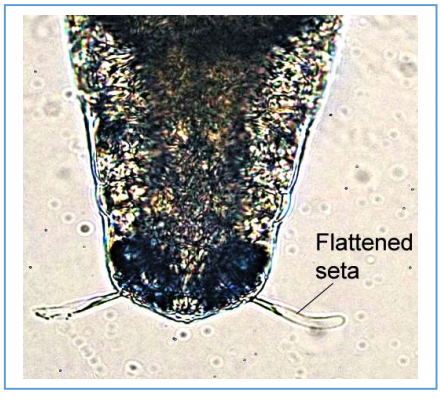

Fig. 79. Caligoid N1 caudal setae.

Adult copepod morphology

Classification of copepods into superorders Gymnoplea and Podoplea is based on the point on the body where it bends (see below). However, before detailing how to separate these superorders and also how to identify their copepodite stages, it is useful to review copepod morphology nomenclature, here using calanoids as the main example. The following information is given in greater detail in Huys & Boxshall (1991), Mauchline (1998), Bradford-Grieve *et al*. (1999) and Wootton & Castellani (2017).

Normal arthropod nomenclature, such as head, thorax and abdomen cannot accurately be applied to copepods, because of the slightly different way parts of the body are fused together and the different function of some of the appendages. Major divisions of the body are termed somites, while divisions of appendages are termed segments. The adult (C6) body is divided into two main parts, prosome and urosome (Fig. 80). Theoretically, the body of all adult copepods is composed of sixteen somites, but not all the somites are visible externally, as during evolution some have become fused or partially fused together. The anterior part of the prosome is termed the cephalosome. It externally appears as a single somite, but bears six paired limbs, A1 to maxillipeds, evidence that it is actually formed from six fused somites (Figs. 80, 81).

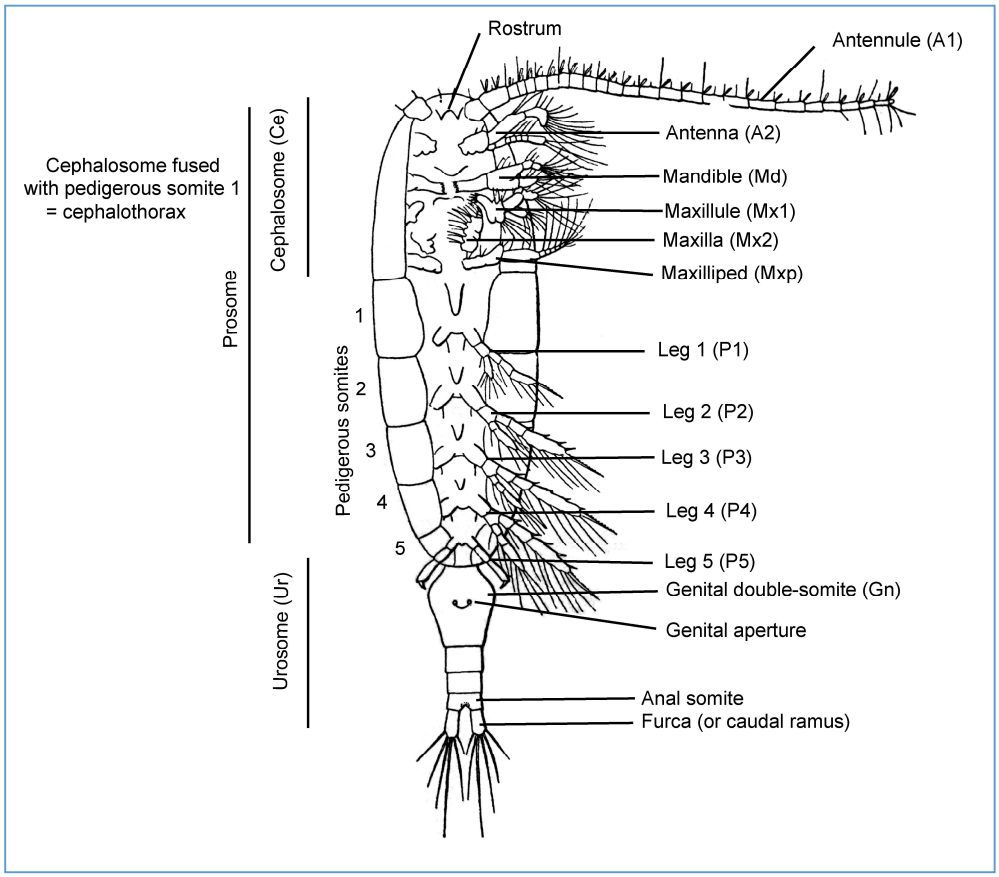

Fig. 80. Morphology of an adult calanoid copepod (Superorder Gymnoplea), ventral view, showing the maximum number of visible somites possible in a female. For clarity, only the appendages on the right side are drawn. Abbreviations commonly used for parts are shown and the legs (P1-P5) and pedigerous somites of the prosome are numbered (from Conway, 2012a; after Rose, 1933).

In calanoids, on the prosome behind the cephalosome are a maximum of five additional somites that may all bear limbs and are called pedigerous somites. In many species, such as *Pseudocalanus elongatus* (Fig. 82), the cephalosome is partially or completely fused to the first pedigerous somite and this whole anterior fused region is then called the cephalothorax. Additionally, in many copepods, including *Pseudocalanus,* the posterior two prosome somites are also fused, so the whole prosome has only four visible somites. In other

calanoids, such as *Temora longicornis* (Fig. 83) and *Acartia* spp., only the last two pedigerous somites are fused, giving five visible somites in the prosome. In Siphonostomatoida, additional fusion of somites can take place. Variation in number of visible somites between species is a useful identification feature.
The group of prosome somites posterior to the cephalosome or cephalothorax is called the metasome, but this term is becoming less used.

Fig. 81. *Calanus helgolandicus* female, prosome lateral.

Fig. 82. *Pseudocalanus elongatus* female, prosome lateral.

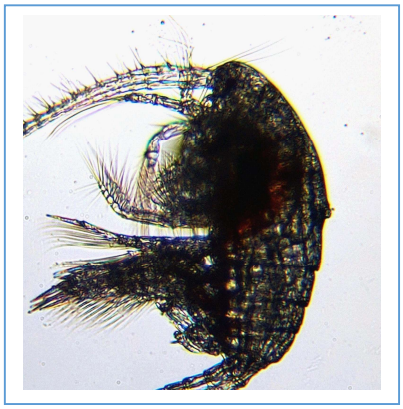

Fig. 83. *Temora longicornis* male, prosome lateral.

Posterior to the prosome is a series of somites called the urosome (Fig. 80). The last somite of the urosome is called the anal somite, as it has the anus located ventrally. On the anal somite are two processes called furcae or caudal rami that bear an array of setae. These are not counted as a somite.
The point where the prosome and the urosome meet is where the body articulates, so the urosome is defined as the series of somites posterior to the articulation (Boxshall & Halsey, 2004). The position of articulation in adult copepods (marked by arrows in Figs. 84-95) separates Calanoida, which are in Superorder Gymnoplea, from all the other orders, which are in Superorder Podoplea. In calanoids, it is located behind the last pedigerous somite, so P1-P5 are all in front of the articulation (Figs. 84, 90). In podopleans, the articulation is typically located between the fourth and fifth pedigerous somites, so the first somite of the urosome usually bears the P5 (Figs. 85-88, 91-94). There are some exceptions to this in the podoplean Order Siphonostomatoida, which includes some important fish parasites. Because of their specialised niche, these have heavily modified bodies. In at least Family Caligidae, the commonest siphonostome adult copepods sampled, the body articulates between pedigerous somites three and four (Boxshall & Halsey, 2004; Figs. 89, 95).
While males and females of the same species typically have the same number of somites in the prosome, this is not the case for the urosome. Because of the position of the articulation, there are theoretically a maximum of five somites in the urosome of adult gymnopleans and six in podopleans and this is true for males, with few exceptions. However, in females of both superorders, at least the two somites behind the last pedigerous somite fuse during the final moult to form a, usually longer, genital double-somite (e.g. Figs. 84, 85) that bears the genital apertures. Females thus usually have at least one less free somite in the urosome than males and in both sexes the first somite in the urosome of calanoids and usually the second in podopleans is the genital somite. In calanoid species such as *Subeucalanus crassus,* females have only three free urosome somites (Fig. 96) due to additional fusion of somites, while in some *Calocalanus* spp. there are only two.

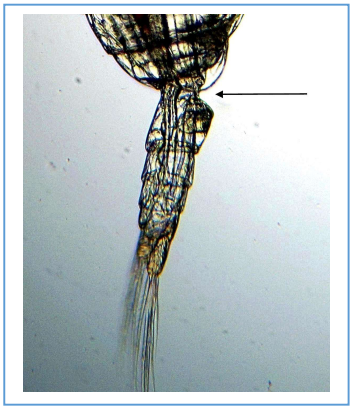

Fig. 84. *Calanus helgolandicus* (Calanoida) female, urosome lateral. Arrow indicates prosome/urosome articulation point.

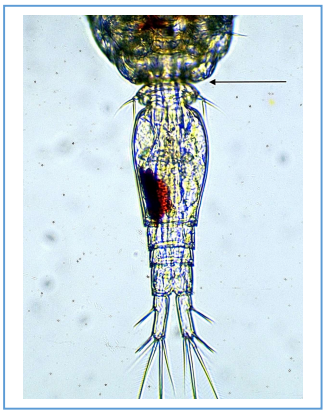

Fig. 85. *Oncaea* sp. (Cyclopoida) female, urosome ventral.

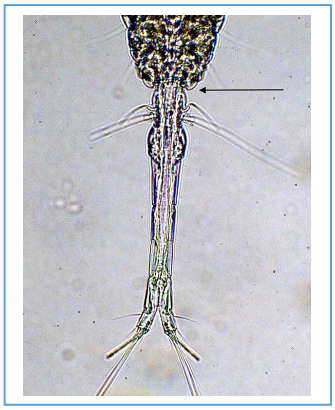

Fig. 86. *Oithona similis* (Cyclopoida) female, urosome ventral.

Fig. 87. *Euterpina acutifrons* (Harpacticoida) female, urosome lateral.

Fig. 88. *Monstrilla grandis* (Monstrilloida) female, urosome lateral.

Fig. 89. *Caligus elongatus* (Siphonostomatoida) female, urosome dorsal.

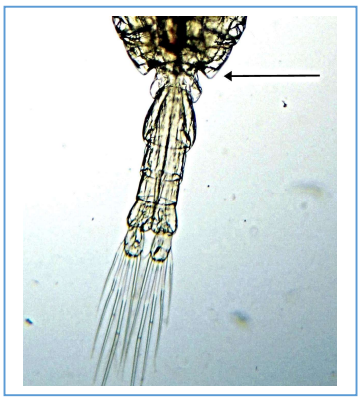

Fig. 90. *Calanus helgolandicus* (Calanoida) male, urosome ventral.

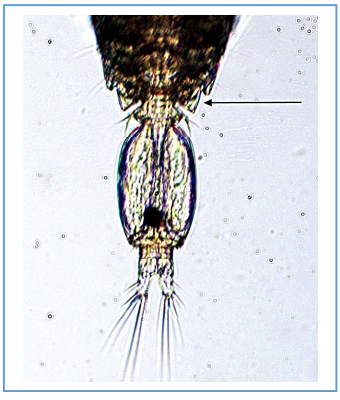

Fig. 91. *Oncaea* sp. (Cyclopoida) male, urosome ventral.

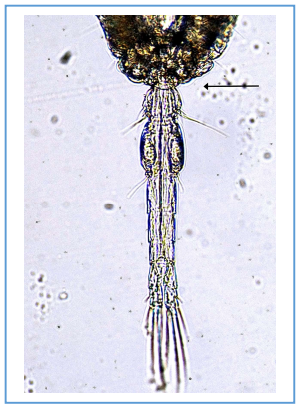

Fig. 92. *Oithona similis* (Cyclopoida) male, urosome ventral.

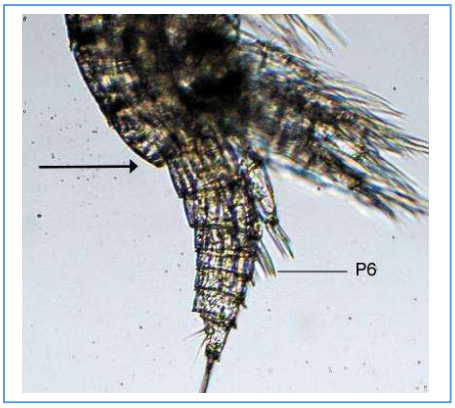

Fig. 93. *Euterpina acutifrons* (Harpacticoida) male, urosome lateral.

Fig. 94. *Monstrilla helgolandica* (Monstrilloida) male, urosome lateral (has no P5).

Fig. 95. *Caligus elongatus* (Siphonostomatoida) male, urosome dorsal.

All male calanoid copepods described here have five free somites in the urosome (Fig. 90), except the three European *Centropages* spp., which have four (Fig. 97), unusual among calanoids. At least some *Centropages* spp. from other areas have five somites. Most male cyclopoids and harpacticoids have six somites in the urosome (Figs. 91-93), sometimes difficult to discern, especially in *Oncaea* sp. where the distal somites can be tiny (Fig. 91). Corycaeidae usually only have three somites in the urosome in both males and females (Fig. 98). The first somite is tiny and difficult to discern, and bears the P5. Monstrilloid males have either four or five (Fig. 94) urosome somites. In Siphonostomatoida of both sexes, fusion of urosome somites can be more extensive than in the other orders (Figs. 89, 95).

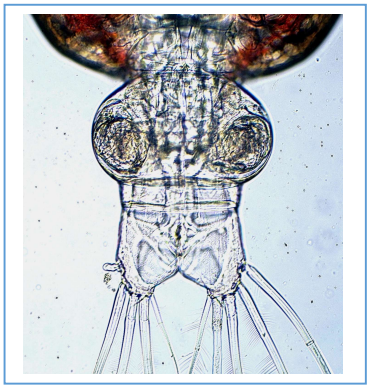

Fig. 96. *Subeucalanus crassus* female, urosome ventral.

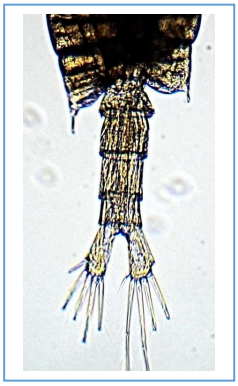

Fig. 97. *Centropages chierchiae* male, urosome dorsal.

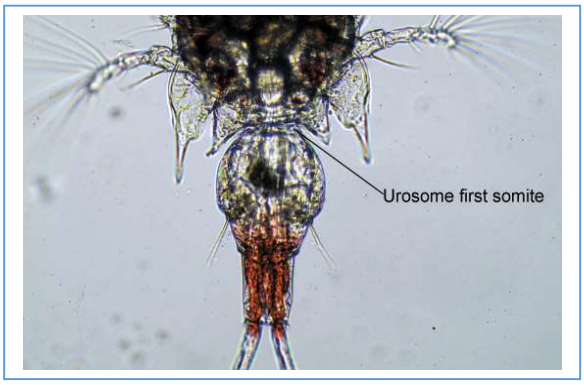

Fig. 98. *Ditrichocorycaeus anglicus* male, urosome ventral.

Copepod appendages

The somites of the cephalosome usually bear paired appendages (Fig. 80). The most anterior appendages are the uniramous A1, which can vary considerably in length between species. In both sexes these bear sensory setae and interspersed among the setae, thin, tubular chemosensory structures called aesthetascs (Fig. 99). In many male copepods, the size and number of aesthetascs often increases at the final moult, related to mate locating. In adult females of all orders, both A1 are identical (Figs. 81, 82). Adult males of some calanoids have both A1 identical, but males in superfamilies' Arietelloidea and Diaptomoidea, one is modified to varying degrees, with swellings, hinges, spines etc. An A1 that is modified is called geniculate (Fig. 100), its structure associated with clasping the female during spermatophore transfer. The geniculation is usually on the right, but in a few calanoids it is on the left, as in *Metridia* spp. In all male podopleans in orders Harpacticoida and Monstrilloida included here, both of the male A1 are geniculate (e.g. Fig. 101). In podoplean Order Cyclopoida,

all adult males in Family Oithonidae have both A1 geniculate (Fig. 102), but males of the other families included here (Oncaeidae and Corycaeidae) lack any geniculation (Fig. 103). Males in some families of Order Siphonostomatoida have weakly double-geniculate A1. In copepod males of all orders that lack any geniculation, there are still at least small differences between sexes in the structure of the A1.

Fig. 99. *Pseudocalanus elongatus* (Calanoida) male, A1 with aesthetascs.

Fig. 100. *Centropages typicus* (Calanoida) male dorsal, geniculate A1.

Fig. 101. *Euterpina acutifrons* (Harpacticoida) male dorsal, geniculate A1.

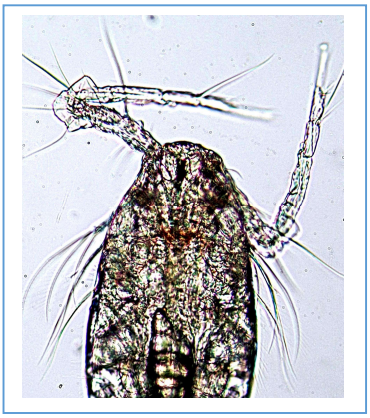

Fig. 102. *Oithona similis* (Cyclopoida: Oithonidae) male dorsal, geniculate A1.

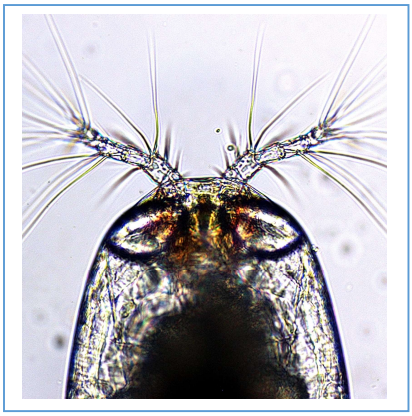

Fig. 103. *Ditrichocorycaeus anglicus* (Cyclopoida: Corycaeidae) male dorsal, non-geniculate A1.

Posterior to the A1 are five pairs of setous feeding appendages. The first three of these, antennae (A2; Fig. 104), mandibles (Md; Fig. 105) and maxillules (Mx1; Fig. 106) are biramous. The first segment (coxa) of the endopod of the mandibles bear internally a multi-toothed gnathobase that lies over the mouth, used to break up food. The final two appendage pairs, maxillae (Mx2; Fig. 107) and maxillipeds (Mxp; Fig. 108) are uniramous. The setation of the feeding appendages varies depending on diet, fine in filter feeders and coarse in carnivores. In large carnivores such as *Paraeuchaeta* spp., the maxillipeds are massively developed for capturing prey or clasping the female (Fig. 2), while in *Candacia* spp. it is the maxillae that are enlarged. In at least some male calanoids, such as *Paraeuchaeta* spp., some of the feeding appendages are greatly reduced, as the males do not feed. Adult monstrilloids of both sexes do not feed, as there sole role is reproduction. They have A1, but completely lack any feeding appendages (Fig. 11).

Fig. 104. *Calanus finmarchicus,* antenna.

Fig. 105. *C. finmarchicus,* mandible.

Fig. 106. *C. finmarchicus,* maxillule.

Fig. 107. *C. finmarchicus,* maxilla.

Fig. 108. *C. finmarchicus,* maxilliped.

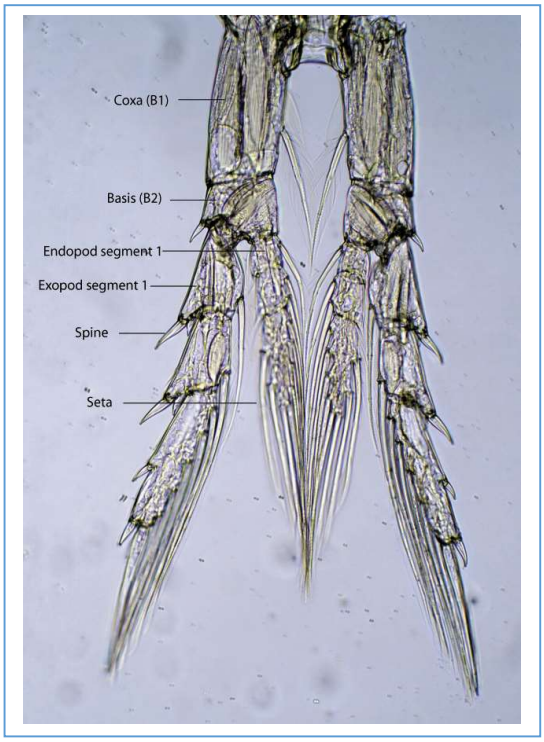

Fig. 109. *C. finmarchicus,* pedigerous leg (P2).

The pedigerous somites (Fig. 80) in adult copepods each bear paired legs (P1-P5) that are rigidly joined at the base (Fig. 109), so they beat simultaneously. At least P1-P4 are quite similar in structure. Each individual leg is biramous and used in swimming, so commonly termed swimming legs. However, the P5 in most copepods, when present, are not used for swimming as they are nor structurally suitable.

All female copepods typically have P5 in which both legs are symmetrical. However, several calanoid species, such as *Pseudocalanus*, *Microcalanus* and *Paraeuchaeta* spp. do not have a P5. Most copepods of both sexes have P5 that are quite individual in structure, making them one of the most useful features for species identification. The P5 in female copepods are bilaterally symmetrical (Figs. 110, 111) and in Family Calanidae and to a lesser extent in Family Centropagidae, are large and quite similar to the other legs. However, in most calanoids they are reduced in size and complexity compared to the other legs (Fig. 110, 111). In female calanoids it is typically the endopod that is most reduced, until it may be completely missing (Fig. 111). In cyclopoid, females the P5 are typically reduced to simple setae (Figs. 85, 86). Harpacticoid females have reduced but well developed P5 (Fig. 87).

Male copepods always have five pairs of legs. In calanoids the P5 in most cases are heavily modified and not bilaterally symmetrical (Fig. 112). The P5 of male cyclopoids are typically symmetrical but very reduced (Figs. 91, 92). In some Monstrilloida, the P5 is missing (Fig. 94).

The genital somite bears evidence of P6 legs, reduced in both sexes to tiny opercular plates that close off the genital apertures. However, in at least some male harpacticoids, the P6 are still quite well developed (Fig. 93).

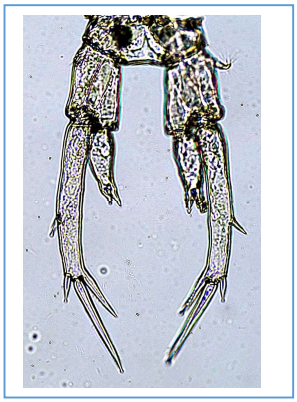

Fig. 110. *Parapontella brevicornis* female, P5.

Fig. 111. *Candacia armata* female, P5.

Fig. 112. *Anomalocera patersonii* male, P5.

Calanoida copepodite stages

In all copepods, following the six naupliar stages (N1-N6) there are typically five copepodite stages (C1-C5) before the final moult to adults (C6) male or female, but some parasitic species have fewer stages. Copepod nauplii and copepodite stages are often found in samples in the process of moulting (Fig. 113). Similar to nauplii (Table 2), sorting of individual copepodite stages of each species is made easier because of the rapid growth that occurs immediately after moulting, often resulting in no or little length overlap between successive stages (Table 3). It is thus usually possible to roughly sort stages of the same species, visually on size alone (Fig. 114). While sizes of each stage can vary in the same sample and also seasonally, the range is usually quite limited.

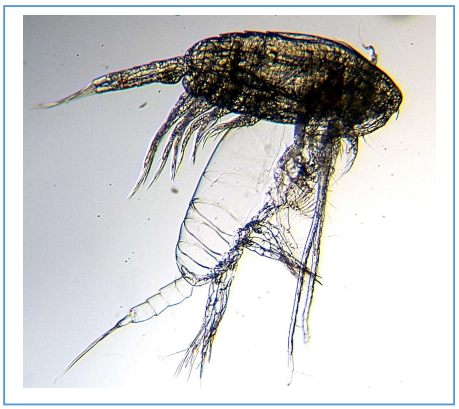

Fig. 113. *Pseudocalanus elongatus* C6 female emerging from moult.

Fig 114. *Calanus finmarchicus* N6-C6 male group.

Table 3. *Calanus finmarchicus.* Developmental details and measurements of copepodites and adults sampled in the northern North Sea in April 1974 (from Conway, 2012b).

	C1	C2	C3	C4	C5	C6
Number of free prosome somites	4	5	6	6	6	6
Number of free urosome somites	2	2	2	3	4	♀4 ♂5
Number of pairs of legs	2 (+1)	3 (+1)	4 (+1)	5	5	5
Mean total length (mm)	0.8	1.1	1.4	1.8	2.4	♀2.7 ♂2.7
Range of total length (mm)	0.7-0.8	1.0-1.2	1.3-1.5	1.7-1.9	2.3-2.6	♀2.4-3.1 ♂2.5-2.9
Mean prosome length (mm)	0.6	0.8	1.1	1.4	1.9	♀2.1 ♂2.1
Range of prosome length (mm)	0.6-0.7	0.7-0.9	1.0-1.2	1.3-1.6	1.7-2.0	♀1.9-2.4 ♂2.0-2.2

+1 in the leg number row indicates that tiny rudimentary leg-buds may be present that will not fully develop until the next moult (See Fig. 117).

An example of the typical, sequential development of somites in a calanoid copepod from C1-C6 is given in Figure 115, in diagrammatic form. Between moults a somite is added, always immediately in front of the anal somite. In the example, the shaded somite in C1 was added between the sixth nauplius stage (N6) and the C1. At the moult into the C2 this somite will be incorporated into the prosome and another somite added in front of the anal somite. This sequence is repeated between the moult from C2 to C3 when the prosome then reaches its full complement of somites. After C3, further somites added are incorporated into the urosome until the final complement of urosome somites is reached in C6. In this example it is five somites in the C6 male and would have been five in the female, but the first two somites of the female urosome fuse during the last moult to form a genital double-somite, typical of female copepods. This results in four free urosome somites

in the female, but fewer in females of some species due to additional somite fusion (e.g. Fig. 96). Prosome somites can also fuse during development, giving interspecific differences in number of free somites.

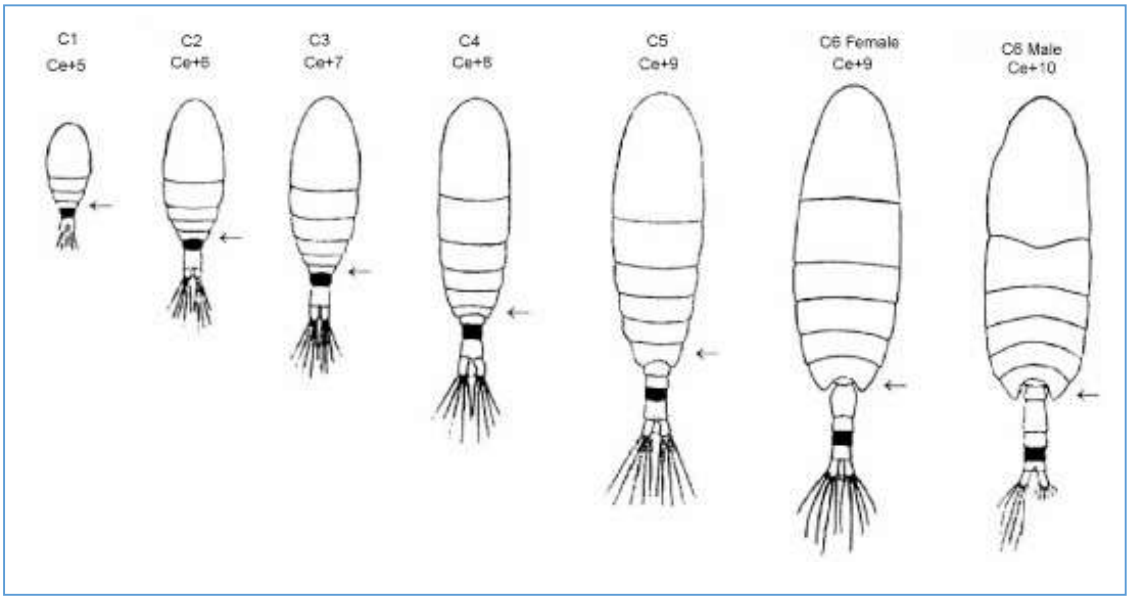

Fig. 115. Sequence of visible somite number change between copepodites C1-C6 of *Calanus* spp. Arrows indicate the last prosome somites. The shaded somite is the one added at the previous moult. Total number of visible somites, additional to the cephalosome (Ce), is noted as e.g. Ce+5. (from Conway, 2012b).

Ventral or dorsal and lateral images of all the copepodite stages of *Calanus helgolandicus* are given in Figures 116-129 to show examples of the appearance of each stage. C1 and C2 are particularly rudimentary in appearance (Figs. 116-119). The features most useful in identifying each stage are the number of pairs of legs and the number of somites in the urosome. Number of legs can sometimes be difficult to count, as they can be pressed close together (e.g. Fig. 127). In all stages, the maxilliped can sometimes be mistaken as a swimming leg, but they often have an obvious forward curve (e.g. Fig. 117) and a clear gap separating them from the P1. Individual urosome somites are sometimes difficult to discern, especially in the early stages, but usually have a much clearer outline in later stages.

The C1 of most calanoid copepods typically have two urosome somites (Table 3) and two pairs of swimming legs. However, several species from C1-C3 sometimes have an additional rudimentary pair of legs (Fig. 117) that do not develop to a functional form until the next moult. Following each moult an additional pair of legs are acquired until the final compliment of five or four pairs is reached in C4, the number depending on whether it is a species destined to have five or four legs in the C6 female. As all C6 male calanoids develop five legs, these will always have five leg pairs in C4.

An obvious feature in many C6 male calanoid copepods is the fusion and thickening of the two proximal segments of the A1, as seen in *Calanus helgolandicus* (Figs. 128, 129).

Tables of the number of body somites, legs and lengths of copepodite and adult stages, compiled from literature sources and from original observations, are given for twenty-six common North Atlantic copepods by Conway (2012b), of which Table 3 is an example.

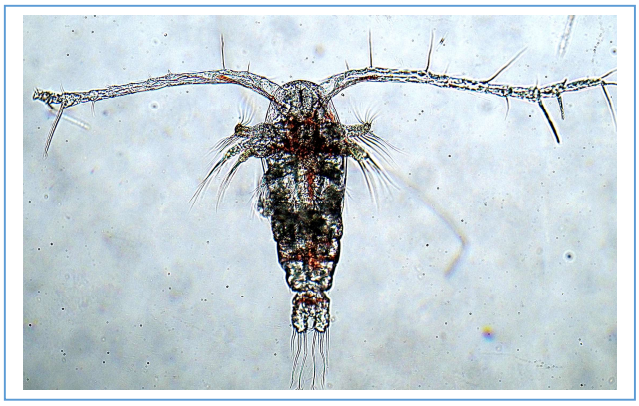

Fig. 116. *C. helgolandicus* C1 ventral, 1.0 mm.

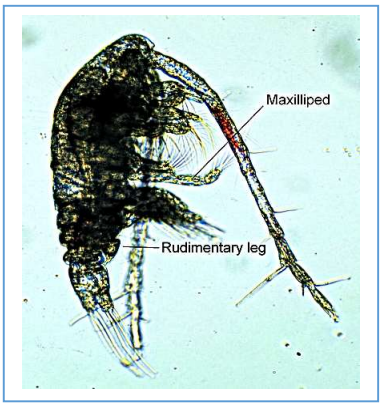

Fig. 117. *C. helgolandicus* C1 lateral, 1.0 mm.

Fig. 118. *C. helgolandicus* C2 ventral, 1.2 mm.

Fig. 119. *C. helgolandicus* C2 lateral, 1.2 mm.

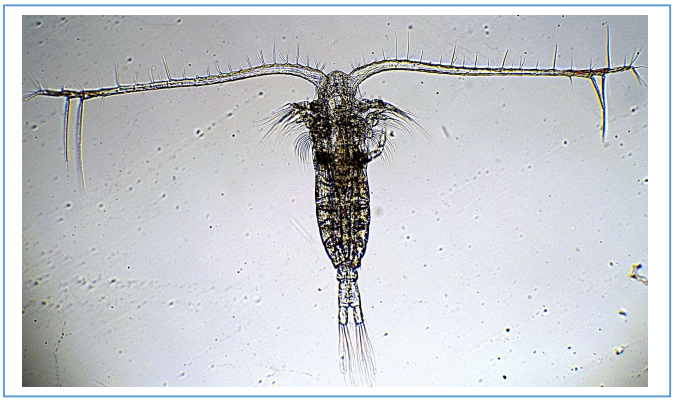

Fig. 120. *C. helgolandicus* C3 ventral, 1.5 mm.

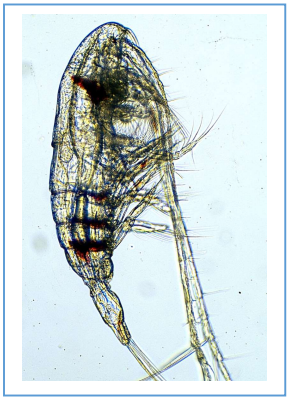

Fig. 121. *C. helgolandicus* C3 lateral, 1.5 mm.

Fig. 122. *C. helgolandicus* C4 dorsal, 2.1 mm.

Fig. 123. *C. helgolandicus* C4 lateral, 2.1 mm.

Fig. 124. *C. helgolandicus* C5 ventral, 2.6 mm.

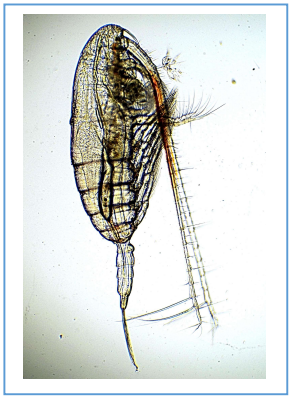

Fig. 125. *C. helgolandicus* C5 lateral, 2.6 mm.

Fig. 126. *C. helgolandicus* C6 female ventral, 2.7 mm.

Fig. 127. *C. helgolandicus* C6 female lateral, 2.7 mm.

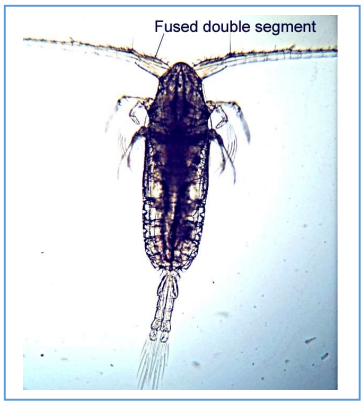

Fig. 128. *C. helgolandicus* C6 male ventral, 2.8 mm.

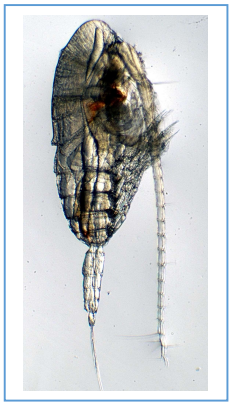

Fig. 129. *C. helgolandicus* C6 male lateral, 2.8 mm.

Identifying calanoid copepods from their immature stages

Included here are a few examples of immature calanoid copepods that have obvious morphological features reminiscent of the adult, which allows them to be confidently identified, at least to family.

In all copepodite stages of *Calanus helgolandicus* the second and third last segments of the A1 each bear a long seta, typical of all Family Calanidae (Figs. 116-129), although they are sometimes damaged.

In *Centropages typicus* and *C. chierchiae,* from C3 (Fig. 130) there are traces of characteristic spines on segments 1, 2 and 5 at the base of the A1, very obvious from C4 (Figs. 131, 132).

A particular feature can first appear in a different stage, depending on species. In *Centropages* spp. in which each side of the posterior prosome somite terminates in a sharp point in C6, the points first appear after the moult from C3 to C4 (Figs. 130, 131) when the final prosome somite is added. The points further enlarge in subsequent stages (Fig. 132). In *Temora stylifera* simple prosome points are present from C1 (Carotenuto, 1999), but in *Eurytemora* spp. C6 females there are no indications of them until C5.

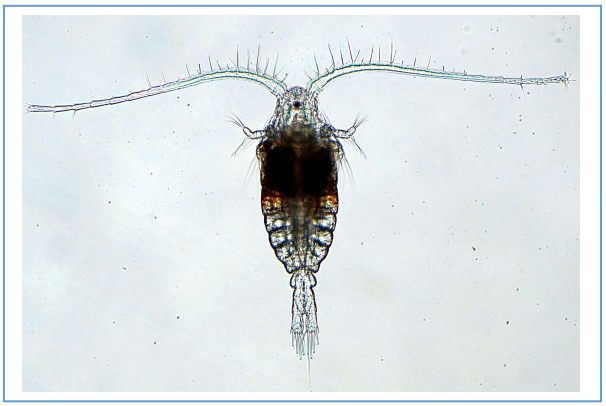

Fig. 130. *Centropages typicus* C3 dorsal, 0.7 mm.

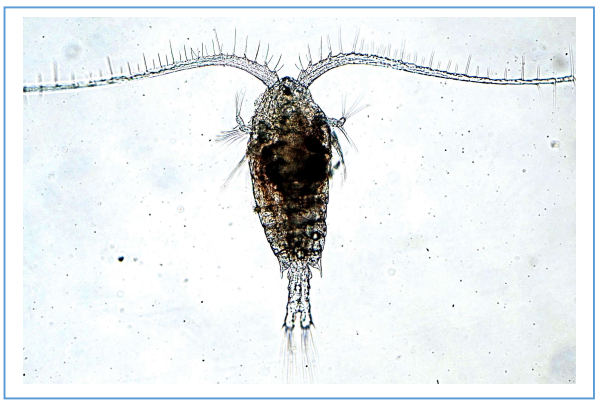

Fig. 131. *Centropages typicus* C4 dorsal, 1.0 mm.

Acartia spp. from C1 (Fig. 133) have the typical coffin-shaped prosome of the adult, prominent dark eye spot, widely-spaced, fine setae on the A1 and an array of fine caudal setae that seem to survive sampling and preservation much better than in most other copepods. *Temora* spp. from C1 have a kite-shaped prosome in ventral view, deep prosome and long caudal furcae (Fig. 134). Euchaetidae spp. from the earliest stages (Fig. 135) have long, widely spaced setae on the A1, powerful maxillipeds that are associated with their carnivorous diet and indication of the anterior projection that becomes developed in later stages. Early stage *Candacia* spp. have powerful maxillae rather than maxillipeds, also associated with carnivory, obvious 'shoulders' on the

anterior prosome and coarsely setose A1 (Fig. 136). They also often have tinges of black pigment between the prosome somites and on the ends of appendages, a distribution of pigment that is well developed in adults.

Fig. 132. *Centropages typicus* C5 ventral, 1.3 mm.

Fig. 133. *Acartia* sp. C1 ventral, 0.5 mm.

Fig. 134. *Temora longicornis* C1 ventral, 0.4 mm.

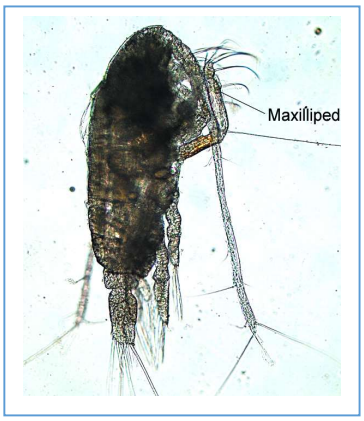

Fig. 135. *Paraeuchaeta norvegica* C2 lateral, 1.3 mm.

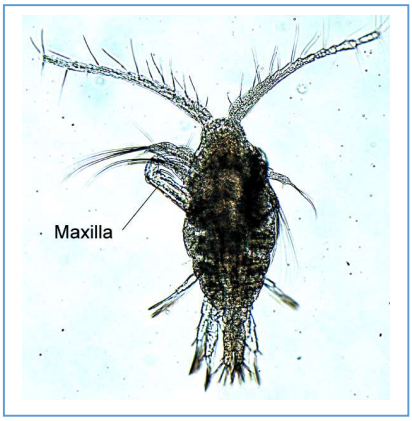

Fig. 136. *Candacia armata* C2 dorsal, 0.8 mm.

Identifying the sex of immature calanoid copepods

The sex of calanoid copepods is easy to determine in C6, because of differences in number of somites between females and males (Conway, 2012a) and the often radical sexual dimorphism. Some of these differences, such as the structure of the A1 and P5, can be indicated in the morphology of earlier stages (e.g. Czaika, 1982).

In calanoids, the last somite of the prosome is added in C3, but a well-developed P5 does not appear on this somite until C4, the earliest that P5 structure could be used in sex determination. Females of some species never develop a P5 (e.g. *Pseudocalanus elongatus*, *Subeucalanus crassus,* Euchaetidae spp.), so from C4, males of the same species will have one more leg pair than females, allowing easy separation. As previously mentioned, the C3 of some species may have a rudimentary P5 (Table 3; Fig. 137), but it is not developed enough to be used for sex determination. In females of species that develop a P5, in adults the structure is always obviously different from that of the males. This difference between sexes can be modest, as in *Calanus* spp. (Figs. 138, 139), where males have a slightly asymmetric P5, but they are quite similar in structure to the female's. Because of this similarity, detailed and time consuming measurements (Grigg *et al*., 1987) or gonad examination (Crain & Miller, 2000) are required to determine the sex of pre-adult *Calanus* spp. In calanoids where the male has strongly asymmetric P5 compared to the female (Figs. 140-142), this is typically reflected in their structure from C4, when these legs first appear, enabling sex determination from this stage.

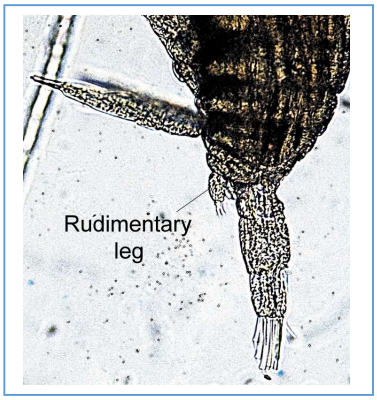

Fig. 137. *Centropages hamatus* C3, urosome lateral.

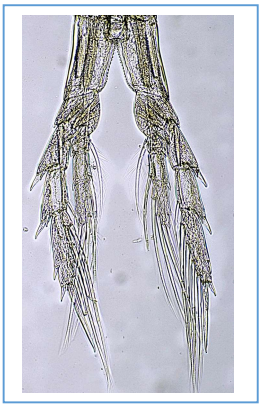

Fig. 138. *Calanus finmarchicus* C6 female, P5.

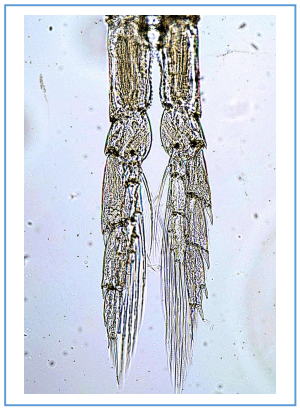

Fig. 139. *Calanus finmarchicus* C6 male, P5.

Fig. 140. *Centropages hamatus* C6 female, P5.

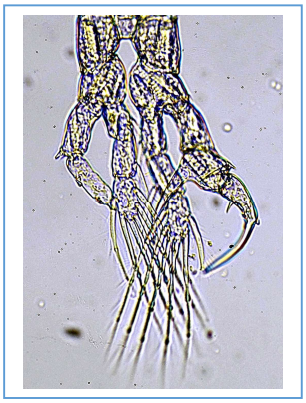

Fig. 141. *Centropages hamatus* C6 male, P5.

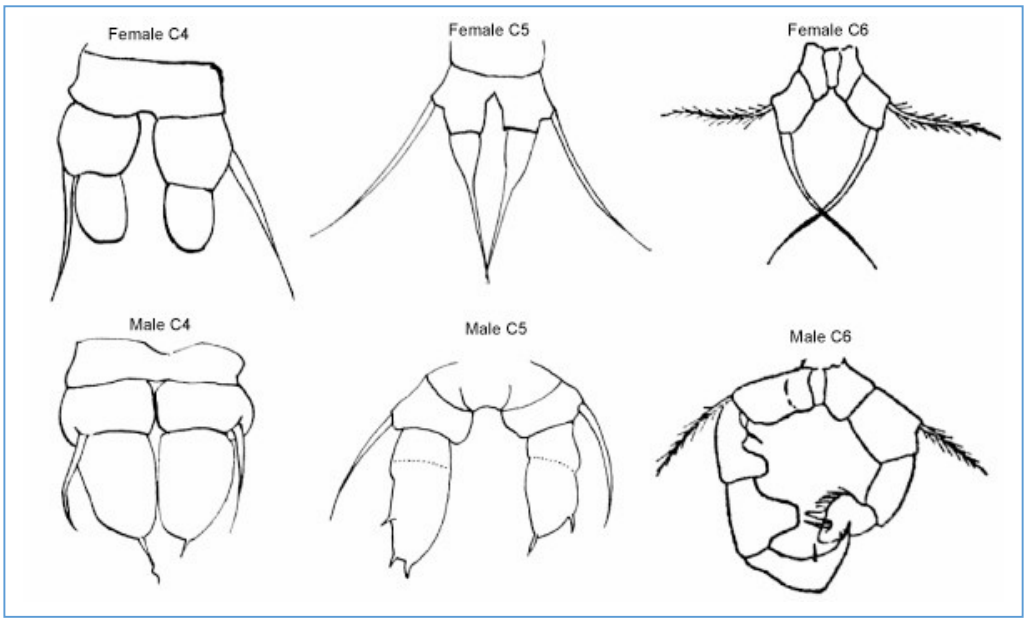

Fig. 142. *Acartia* sp., P5 of female and male copepodite stages C4-C6 (from Conway, 2012a).

Many calanoids, such as *Acartia* spp. have tiny P5 in both sexes (Figs. 142, 147, 148). An example of a genus where both sexes have large P5 and the male P5 has some parts of them quite similar to those of the female's is *Centropages* (Figs. 140, 141), but the sexes in late pre-adults can still be separated. A feature of the C6 female P5 is a strong spine on the inner edge of the second segment of the exopod of both legs, that is only present on the right leg of the C6 male as part of a strong claw. In the C5 female this strong spine is still present (Fig. 143), but is absent in the C5 male (Fig. 144). The male P5 are also slightly asymmetric.
Conway (2012b) and Klein Breteler (1982) separated *Centropages* spp. into males and females from C4, based on the structure of the P5 and the presence of a slightly swollen section on the right A1, the latter a precursor of the male geniculation. C5 males certainly have an obvious swollen section on the right A1 (Fig. 145). In 2024 thirty C4 *C. hamatus* were examined from a sample containing large numbers of C5 and adult males and females, but only individuals with the same type of symmetrical P5 (Fig. 146) were found. Additionally, none of the C4 showed indications of a swollen A1, suggesting that all the C4 were female.

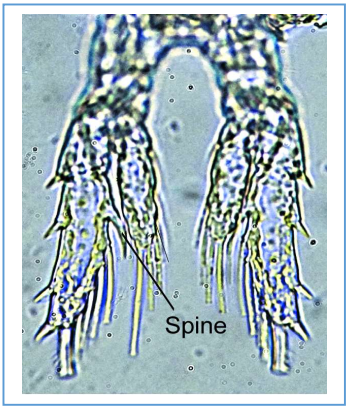

Fig. 143. *Centropages hamatus* C5 female, P5.

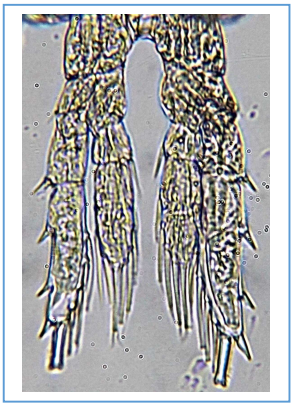

Fig. 144. *Centropages hamatus* C5 male, P5.

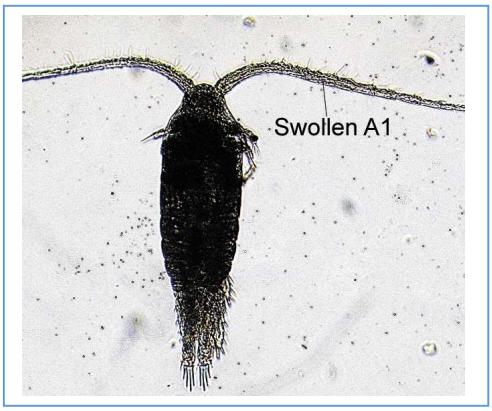

Fig. 145. *Centropages hamatus* C5 male dorsal, 0.8 mm.

Fig. 146. *Centropages hamatus* C4, P5.

C6 calanoid females have a genital somite that in lateral view is swollen ventrally to different degrees, depending on species (Figs. 84, 147). However, It can be sometimes be slightly difficulty to separate female C5 from female C6 of some species such as *Temora*, *Paracalanus* and *Acartia* spp., as the genital somite may also be slightly swollen in the C5 (Fig. 148), while the number of prosome and urosome somites is identical between the two stages. However, the slightly swollen genital somite of the C5 will not have any obvious internal features such as seminal receptacles, although not all copepod families have these (e.g. Centropagidae). Some differences may also be seen between the two stages in how well the P5 is developed and also in the definition of the urosome somites.

Fig. 147. *Acartia bifilosa* C6 female, urosome lateral.

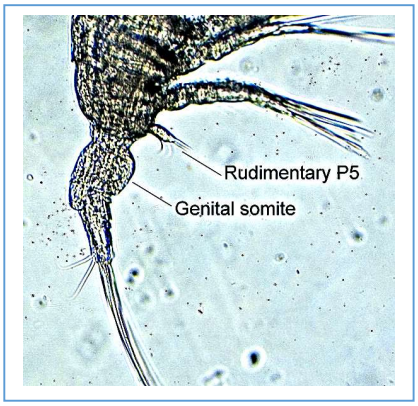

Fig. 148. *Acartia bifilosa* C5 female, urosome lateral.

Many copepods of both sexes have prominent features on their urosome that only appear in the C6. For example, *Centropages hamatus* C5 females have a genital somite that is slightly swollen ventrally (Fig. 149), which in C6 females has a strong dorsal spine and an array of coarse setae (Fig. 150).
Male C5 and C6 copepods have the same number of prosome somites, but apart from a few exceptions such as in some Centropagidae spp. (Fig. 97), C6 males has one more urosome somite. Apart from this, the definition of the urosome somites is much clearer in C6 (Figs. 151, 152) and even on cursory examination, the P5 are obviously much more rudimentary in appearance in C5.

Fig. 149. *Centropages hamatus* C5 female, urosome lateral.

Fig. 150. *Centropages hamatus* C6 female, urosome lateral.

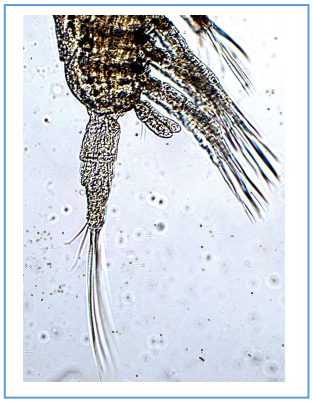

Fig. 151. *Acartia bifilosa* C5 male, urosome lateral.

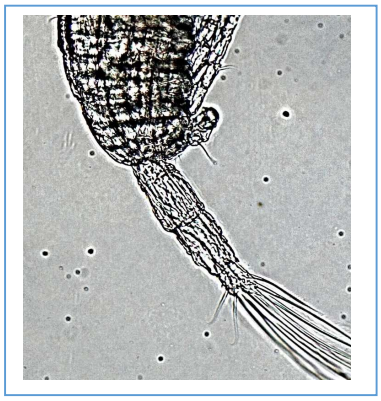

Fig. 152. *Acartia bifilosa* C6 male, urosome lateral.

Intersex copepods

There is often a numerical imbalance between C6 males and females in copepod populations, females usually predominating. Factors suggested for this include differential longevity or mortality of males (e.g. Hirst *et al*., 2010). Another factor causing this imbalance is that ultimate sex, in at least some copepod species, appears to be determined by environmental factors such as food availability at a late stage of development (Gusmão & McKinnon, 2009). A consequence of this late switching of sex from male to female results in a small proportion of intersex individuals with abnormal P5. This is easiest observed in calanoid species such as *Pseudocalanus elongatus*, where the female does not normally develop a P5. Females with a swollen genital somite are occasionally found with a rudimentary P5, often resembling a male P5, but shorter (Fig. 153).

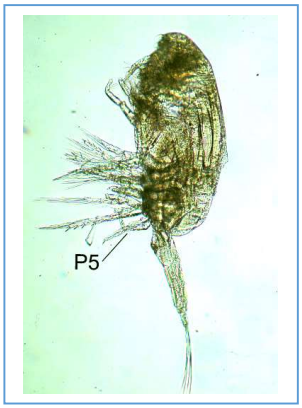

Fig. 153. *Pseudocalanus elongatus,* intersex C6 female with P5, 1.4 mm (damaged).

Cyclopoida and Harpacticoida copepodites

The majority of species in Orders Cyclopoida and Harpacticoida are associated in different ways with the benthic habitat, so pelagic specimens collected in plankton nets are from a very limited species range. However, these can often be very numerous and ecologically important (e.g. Gallienne & Robins, 2001). In northern European seas, the commonest cyclopoid species typically collected are in families Oithonidae, Corycaeidae and Oncaeidae, and the commonest harpacticoids in families Tachidiidae (*Euterpina acutifrons*), Peltidiidae (*Clytemnestra* and *Goniopsyllus* spp.) and Ectinosomatidae (*Microsetella* spp.). These have distinctive copepodite stages and can usually be quickly identified to at least family level. The most challenging sites to identify them from are shallow and inshore, where the copepodites of benthic species may also occur. The same features used to separate the copepodite stages of calanoid copepods (Suborder Gymnoplea) are used with cyclopoids and harpacticoids. Cyclopoids and harpacticoids are classified in a different suborder (Podoplea), because their prosome articulate with the remainder of their body behind the fourth pedigerous somite (Fig. 80) rather than the fifth, so the P5 are on the first urosome somite (Boxshall & Halsey, 2004). Care has to be taken when reading some developmental descriptions, as different interpretations and terminology are sometimes used. The number of visible copepodite body somites found in commonly sampled cyclopoid and harpacticoid families and genera are summarised from literature sources in Table 4. This type of information is published for only a small number of species, so it is possible that the information is not applicable to all species in each of the families and genera included here.

Table 4. Comparative developmental details for each copepodite stage of various families and genera of cyclopoid and harpacticoid copepods (after Conway 2012b; Corycaeidae from Gibson & Grice, 1978).

	Oithonidae	Oncaeidae	Corycaeidae	*Euterpina acutifrons*	*Microsetella norvegica*
Number of legs					
C1	**2**	**2**	**2**	**2+1**	**2+1**
C2	**3**	**3**	**3+1**	**3+1**	**3+1**
C3	**4**	**4**	**4**	**4+1**	**4+1**
C4	**5**	**5**	**5**	**5 ♀** **6 ♂**	**4+1**
C5	**5**	**5**	**5**	**5 ♀** **6 ♂**	**5**
C6	**5**	**5**	**5**	**5 ♀** **6 ♂**	**5**
Number of prosome somites					
C1	**4**	**5**	**4**	**3**	**3**
C2	**5**	**5**	**5**	**4**	**4**
C3	**5**	**5**	**5**	**4**	**4**
C4	**5**	**5**	**5**	**4**	**4**
C5	**5**	**5**	**5**	**4**	**4**
C6	**5**	**5**	**5**	**4**	**4**
Number of urosome somites					
C1	**2**	**1**	**1**	**2**	**2**
C2	**2**	**2**	**2**	**2**	**2**
C3	**3**	**3**	**2**	**3**	**3**
C4	**4**	**4**	**2**	**4**	**4**
C5	**5**	**4 ♀** **5 ♂**	**3**	**5***	**4**
C6 **C6**	**5 ♀** **6 ♂**	**5 ♀** **6 ♂**	**3 ♀** **3 ♂**	**5 ♀** **6 ♂**	**5 ♀** **6 ♂**

+1 indicates a rudimentary leg pair are present that will further or fully develop in the next stage. * Erroneously noted as 4 somites in Conway (2012b).

Cyclopoids and harpacticoids are generally quite small copepods, so it can be difficult to discern the number of body somites and number of legs, especially in early stages. Number of legs at each stage is basically the same in both orders and also very similar to calanoid copepods. Also similar to calanoids, an additional rudimentary pair of legs may be present pre-moult, most obvious in C1-C3 of the harpacticoids *Euterpina* and *Microsetella* spp. (Table 4). As noted earlier, in cyclopoids the P5 are vestigial, reduced to fine setae and the somite on which they are borne is tiny and sometimes difficult to see. In harpacticoids, the P5 are small but well developed in some families. In both cyclopoids and harpacticoids the P5 in both sexes are quite similar and symmetrical, but have differences that can be used to determine sex in the later stages, which can also be done using the comparative structure of the A1.

Cyclopoida copepodite stages

Oithonidae:

Stage characteristics given are based on information for *Oithona brevicornis* from Uchima (1979), which matched those for specimens of *O. nana* and *O. similis* examined here. Oithonidae from the earliest stages have long A1 and urosomes (Figs. 154-162), and fine setae on the A1, characteristics of the adults (Figs. 8, 161). The distal urosome somite is long, particularly in C1-C4 (Figs. 154-157). In C1 there is a fine seta extending either side from the posterolateral corner of the fourth prosome somite, while in C2 there are a pair of setae of different lengths in the same position on the fifth somite, in both cases presumably precursors of legs. In C3, the first urosome somite has a slender seta on the posterolateral corners that becomes in subsequent stages a pair of setae representing the P5 (Figs. 157-162).

Fig. 154. *Oithona* sp. C1 0.25 mm, ventral.

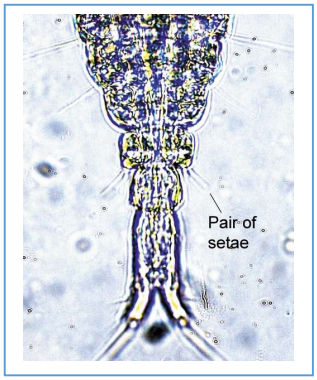

Fig. 155. *Oithona* sp. C2 0.35 mm, urosome.

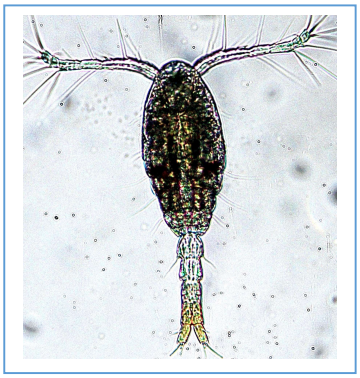

Fig. 156. *Oithona* sp. C3 0.39 mm, ventral.

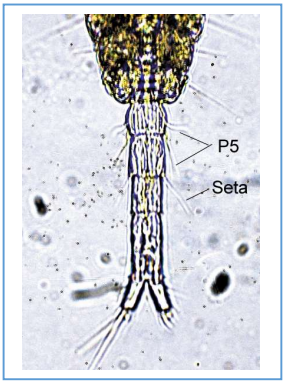

Fig. 157. *Oithona similis* C4 0.45 mm, urosome.

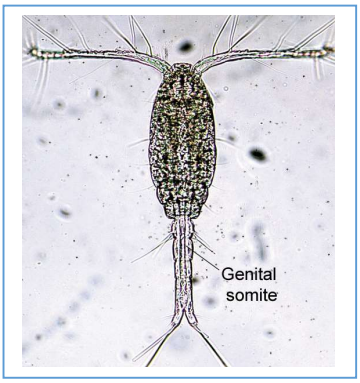

Fig. 158. *O.* similis C5 female 0.72 mm.

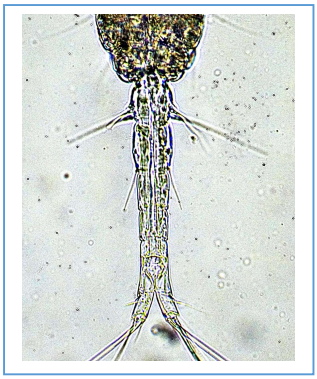

Fig. 159. *O.* similis C5 male 0.70 mm, urosome.

In C4, there is a fine seta either side of the second urosome somite, on the posterolateral corner (Fig. 157). These setae are present in C5 and C6 males (Figs. 159, 161, 162), but missing in females of both these stages (Figs. 158, 160), enabling sex determination from C5. In C5 the genital somite in both sexes has quite parallel sides (Figs. 158, 159), more rounded in the adults (Figs. 160, 162). The A1 in the C6 female are long and very setose (Fig. 8), in the male shorter, double geniculate and often bent (Fig. 161).

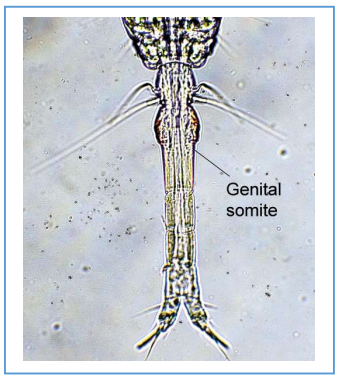

Fig. 160. *O. similis* C6 female 0.80 mm, urosome.

Fig. 161. *O. similis* C6 male 0.82 mm.

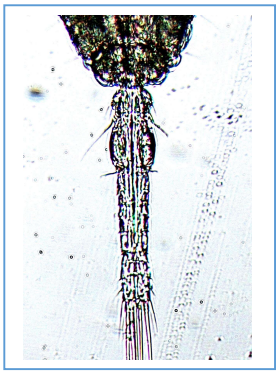

Fig. 162. *O. similis* C6 male 0.82 mm, urosome.

Oncaeidae:

There are currently seven genera in Family Oncaeidae, but their identification is challenging due to their often small size, similarity between species and lack of reliable identification keys (Böttger-Schnack & Schnack, 2009). Oncaeidae and Oithonidae copepodite stages are often found together in samples in high numbers and can initially seem difficult to separate. Both have the same number of legs in all stages (Table 4) and apart from C1 and C5 females, the same number of somites. However, Oncaeidae generally have relatively shorter A1 and urosomes in all stages (Figs. 163-171), their A1 bend between the first and second segments, their prosomes are oval, and the genital somite is broad in C5 and adults. There can be several Oncaeidae spp. of differing adult length in any one sample, making sorting of copepodite stages relative to size unrelated. Information given here is based on descriptions of two *Oncaea* spp. sampled in the same general area as the current specimens (Malt (1982).

No C1 specimens that could confidently be identified as such were sampled. In C2 the last prosome somite bears a few setae (Fig. 163) indicating the rudimentary P4. In all C3 specimens examined, the first somite of the urosome had a fine seta on each posterolateral corner, representing the P5 (Fig. 164), but quite difficult to see. Malt (1982) noted a seta on only one side of this somite.

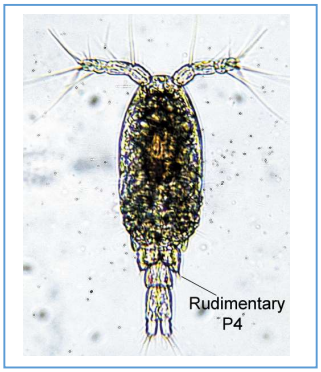

Fig. 163. Oncaeidae sp. C2 0.26 mm, ventral.

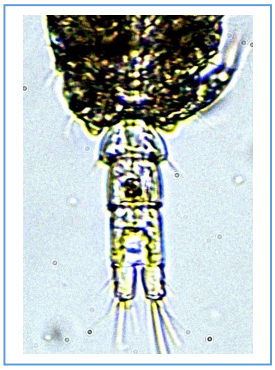

Fig. 164. Oncaeidae sp. C3 0.31 mm, ventral.

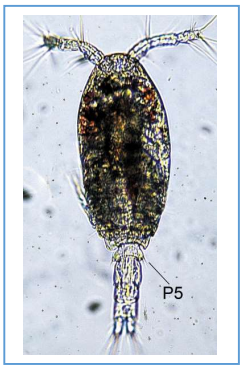

Fig. 165. Oncaeidae sp. C4 0.41 mm, ventral.

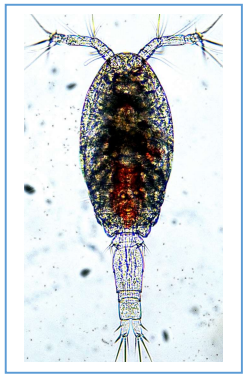

Fig. 166. Oncaeidae sp. C5 female 0.53 mm, ventral.

Fig. 167. Oncaeidae sp. C5 male 0.44 mm, ventral.

Fig. 168. Oncaeidae sp. C6 female 0.60 mm, dorsal.

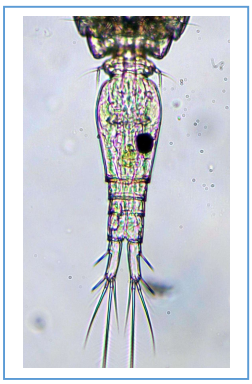

Fig. 169. Oncaeidae sp. C6 female 0.60 mm, urosome.

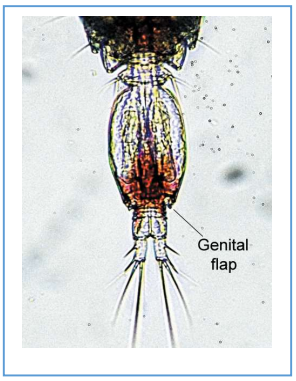

Fig. 170. Oncaeidae sp. C6 male 0.49 mm, urosome.

Fig. 171. Oncaeidae sp. C6 female 0.54 mm, slender species.

In C4 the urosome has four somites, the distal one sometimes not very clearly defined (Fig. 165). The P5 is represented by a pair of simple setae on each side of the tiny first urosome somite.
C5 females also have four somites in the urosome, but their P5 are obviously more developed (Fig. 166). There may be an additional seta present beside each of them, but on the dorsal surface (Malt, 1982). The genital somite is also longer and much broader than in the C4, and has a tiny lateral setule situated centrally each side, which is sometimes difficult to see. C5 males have five somites in the urosome (Fig. 167). The genital somite is broad and long, and the following two somites very short.
In C6 females there are five clearly defined somites in the urosome (Figs. 168, 169). The lateral setules on the genital somite are replaced by a two pairs of tiny setules on the dorsal surface. In the C6 male, there are six somites in the urosome. The genital somite is broad with pointed genital flaps distally each side (Fig. 170) that can be large in some species. The third to fifth somites are tiny. Not all Oncaeidae spp. have broad prosomes and genital somites, some are slenderer and more elongate (Fig. 171).

Corycaeidae:
Gibson & Grice (1978) gave a comprehensive description of the developmental stages of an undetermined Corycaeidae sp., from which the information given here is based. Corycaeidae are immediately recognisable by their paired, anterior cuticular lenses, parallel-sided prosome and very short A1. In all stages, the number of prosome somites are similar to other cyclopoids, but from C3 the number of urosome somites are less (Table 4). *Ditrichocorycaeus anglicus* is the commonest Corycaeidae species found in northern European waters (Figs. 172-186).

The cuticular lenses and typical body shape are less obvious in C1 (Fig. 172). The lenses are just visible internally and the prosome is ovoid. There are four somites in the prosome (Table 4), the last rudimentary and expanded laterally. There is a single, long urosome somite.
In C2 (Figs. 173, 174) the final prosome somite is added, which is expanded laterally and may bear some setae, indicating a rudimentary P4. A narrow, short first urosome somite is also added, which remains tiny in all subsequent stages. The second urosome somite remains long until C4 (Figs. 173-178). The caudal furcae are long, increasing in length through the stages.
In C3, the last three prosome somites are expanded into angular lappets laterally (Fig. 175) but not as obviously as in later stages. The urosome is similar to that of the C2, with a tiny first somite and a long second that is swollen dorsally (Fig. 176). The P4 are now fully present.

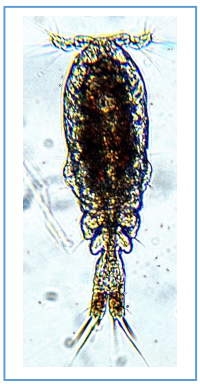

Fig. 172. *Ditrichocorycaeus anglicus* C1 0.28 mm, ventral.

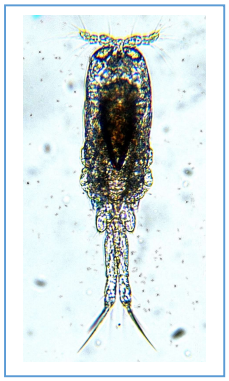

Fig. 173. *D. anglicus* C2 0.33 mm, ventral.

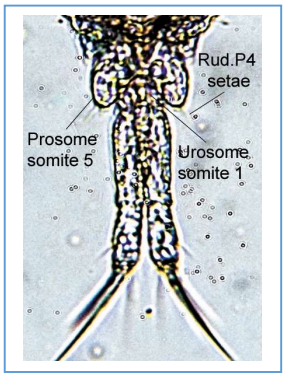

Fig. 174. *D. anglicus* C2 0.33 mm, urosome.

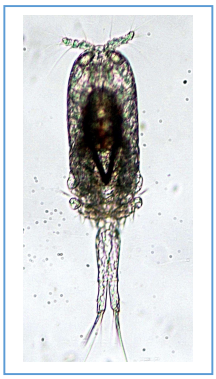

Fig. 175. *D. anglicus* C3 0.36 mm, ventral.

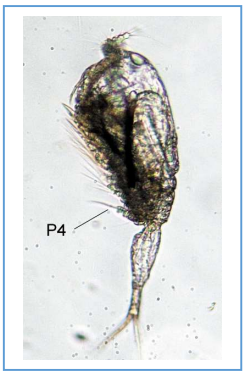

Fig. 176. *D. anglicus* C3 0.36 mm, lateral.

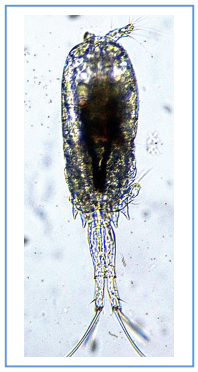

Fig. 177. *D. anglicus* C4 0.53 mm, ventral.

C4 (Fig. 177) has the same number of somites as C3, but the last three prosome somites, particularly the last two, are more obviously expanded laterally into sharp lappets. The urosome has a fine ventrolateral spine situated centrally on each side of the second somite, angled slightly backwards (Fig. 178), but these can be difficult to see, may be damaged or one missing. Gibson & Grice (1978) did not mention the presence of P5 on the first, tiny urosome somite, but these were observed here, represented by a single tiny seta each side.
In C5, the lateral lappets on the fourth prosome somite extend beyond those on the fifth, down alongside the urosome (Fig. 179). The second urosome (genital) somite is swollen laterally and ventrally (Figs. 179-181). A third somite has been added to the urosome, the indistinct division situated immediately behind the genital swelling. P5 are present on the tiny first urosome somite, represented by a single seta each side (Fig. 181). There is a spine, ventrolaterally on either side of the genital somite, angled rearwards, but these are sometimes

broken. These presumably represent the eventual P6. The C5 male has a swollen base to the terminal spine of the A2, distinguishing them from females.

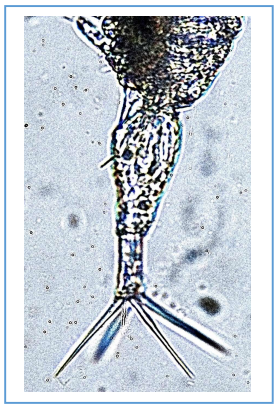

Fig. 178. *D. anglicus* C4 0.53 mm urosome, lateral.

Fig. 179. *D. anglicus* C5 0.74 mm, ventral.

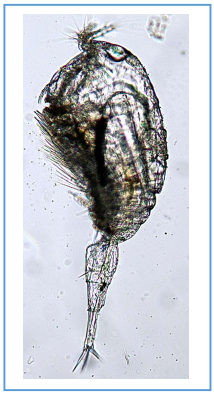

Fig. 180. *D. anglicus* C5 0.74 mm lateral.

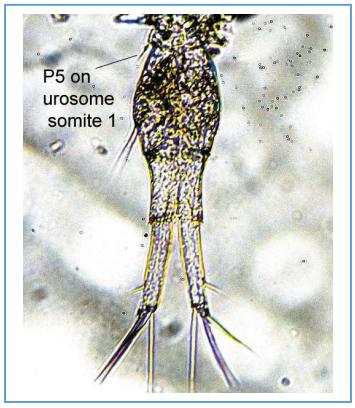

Fig. 181. *D. anglicus* C5, urosome. One genital spine missing.

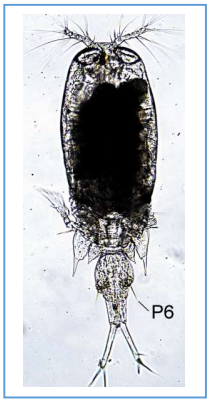

Fig. 182. *D. anglicus* C6 female 1.10 mm dorsal.

Fig. 183. *D. anglicus* C6 female 1.10 mm, lateral.

Adults are transparent, typically with localised patches of orange/red pigment. In the C6 female, the lateral lappets on the fourth prosome somite are wide and extend to the middle of the genital somite (Fig. 182). The A2 terminate in a short, curved hook. The P5 comprise a pair of unequal setae, either side of the tiny first urosome somite, but are difficult to see. P6 are represented by a single, plumose spine on the dorsolateral urosome, on each of the two genital operculae. There is a pointed projection, visible laterally on the face of the genital somite (Fig. 183). The furcae are typically widely divergent (Fig. 182).

Fig. 184. *D. anglicus* C6 male 0.90 mm, ventral.

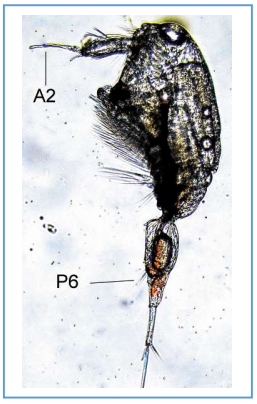

Fig. 185. *D. anglicus* C6 male 0.90 mm, lateral.

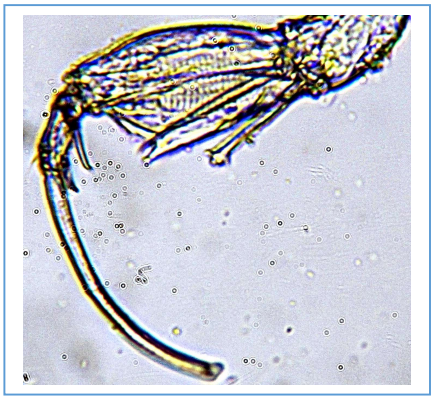

Fig. 186. *D. anglicus* C6 male A2 claw.

Males are quite similar to females, but have slightly larger cuticular lenses (Fig. 184). The lateral lappets on the fourth prosome somite are less pronounced and the A2 more robust (Fig. 185), with a much longer and straighter hook distally (Figs. 186). They also have a pointed projection on the ventral face of the genital somite (Fig. 185) The P5 are similar to the female's and the P6 are represented by a long and a very short spine, ventrolaterally on each of the genital operculae (Razouls, 1974). The furcae are typically scarcely divergent (Fig. 184).

Harpacticoida copepodite stages

***Euterpina acutifrons*:**

Euterpina acutifrons has a cosmopolitan distribution in inshore, shelf and oceanic waters and can be very abundant in northern European coastal waters. They are distinctive in appearance, so easy to identify, but can be difficult to examine, as they curl their bodies when not swimming or dead, making accurate measurements difficult. Adults of both sexes (Figs. 205, 209) have a distinct boundary between prosome and urosome, a prominent rostrum that tapers to a blunt point and A1 that are short, around half the length of the first prosome somite. These feature can be seen in all the copepodite stages. Copepodite developmental information was obtained from El-Maghraby (1964) and Haq (1965), summarised in Table 4. From C2-C5 El-Maghraby (1964) rather puzzlingly noted one more somite in the body than is visible, which has been ignored. In C1-C3, additional to the functional legs, a pair of tiny rudimentary legs that will develop into functional legs at the next moult are present. Depending on stage, there are spinules along the rear edges of the urosome somites that can be quite large and could be confused with parts of developing legs. Copepods collected inshore, particularly cyclopoids and harpacticoids, are often infested with epibionts of different types (Fig. 187), sometimes in considerable numbers.

In C1 there are three prosome somites, two urosome somites and two pairs of functional legs (Table 4; Fig. 187). The rudimentary P3 are visible as a few setae projecting from the last prosome somite. The A1 have three visible segments (Fig. 188; El-Maghraby, 1964). Haq (1965) illustrated an additional tiny, basal segment on the A1 of all stages. However, this cannot easily be seen in routine examination, so while being aware of this additional segment it is convenient to count just visible segments, which has been done here.

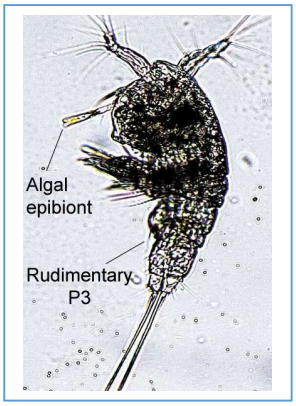

Fig. 187. *E. acutifrons* C1 0.27 mm, lateral.

Fig. 188. *E. acutifrons* C1 A1.

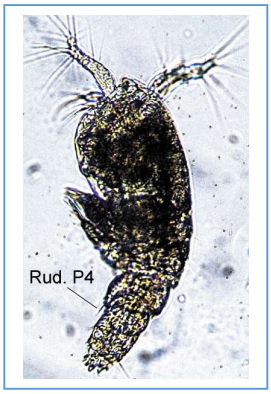

Fig. 189. *E. acutifrons* C2 0.31 mm, lateral.

In C2 there are three pairs of functional legs (Fig. 189). The fourth, final prosome somite has been added and bears a rudimentary P4, represented by a few setae. The number of urosome somites remains at two and there are four segments in the A1 (Fig. 190).

In C3, the fourth pair of functional legs are now present on the last prosome somite (Fig. 191). There are three somites in the urosome, the first of which protrudes dorsally slightly and bears a few setae representing the rudimentary P5. The A1 have five segments.

In C4 the A1 are six-segmented. The sexes can be separated from this stage, as in C4 females the proximal three visible A1 segments are obviously narrower than in the C4 male (Figs. 193, 195). Both sexes have four urosome somites (Figs. 192, 194). The P5 are small, but of the same basic structure as in the following two stages. They are situated centrally, on the distal edge of the first urosome somite and in C4 female are a scale-like projection with a small cleft between the limbs. Each limb carries four large spines on the posterior margin and a smaller lateral spine pointing outwards. The P5 of C4 males has only two spines on the posterior margin and also a lateral spine. The P6 in all copepods are typically reduced to tiny plates covering the genital openings, but in *Euterpina* C6 males and some other harpacticoids they are still quite well developed, so those C4 destined to be males have a rudimentary P6 on the posterolateral edge of the second somite of the urosome. These are difficult to see and are represented by a small bulge each side, bearing a pair of tiny spines.

Fig. 190. *E. acutifrons* C2 A1.

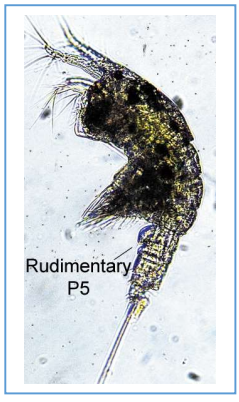

Fig. 191. *E. acutifrons* C3 0.37 mm, lateral.

Fig. 192. *E. acutifrons* C4 female 0.50 mm, lateral.

Fig. 193. *E. acutifrons* C4 female A1.

Fig. 194. *E. acutifrons* C4 male 0.51 mm, lateral.

Fig. 195. *E. acutifrons* C4 male A1.

In C5, both sexes have five urosome somites (Figs. 196, 201). C5 females still have six segments in the A1 (Fig. 197), but as in the C4, they are narrower than in the C5 male (Fig. 202). In C5 females, the second urosome somite (genital somite) is short, around the same length as the first (Fig. 198). In both sexes the P5 have increased in size (Figs. 199, 203, 204) and are the same basic structure as in the C4. The innermost P5 spine in females is sometimes smaller than the others (Fig. 199). In males, the P6 have also retained the same structure and have also increased in size. Because of their lateral position on the urosome, one of the spines protrudes laterally, visible in dorsal and ventral view (Figs. 200, 203). The A1 in males have only four segments (Fig. 202) because of fusion during the moult

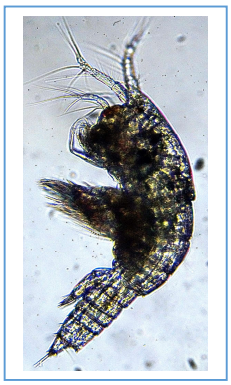

Fig. 196. *E. acutifrons* C5 female 0.54 mm, lateral.

Fig. 197. *E. acutifrons* C5 female A1.

Fig. 198. *E. acutifrons* C5 female urosome, lateral.

Fig. 199. *E. acutifrons* C5 female P5, damaged.

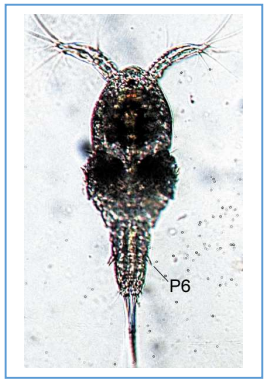

Fig. 200. *E. acutifrons* C5 male 0.43 mm, ventral.

Fig. 201. *E. acutifrons* C5 male 0.41 mm, lateral.

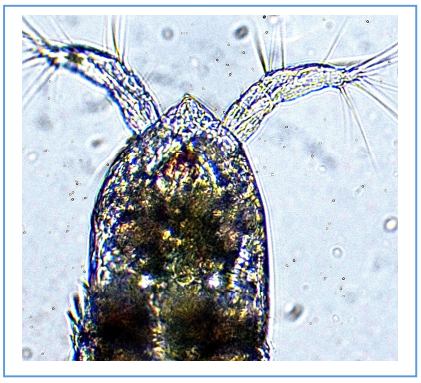

Fig. 202. *E. acutifrons* C5 male A1.

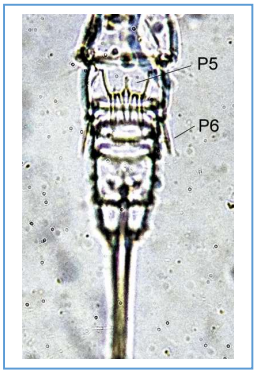

Fig. 203. *E. acutifrons* C5 male urosome, ventral (cast).

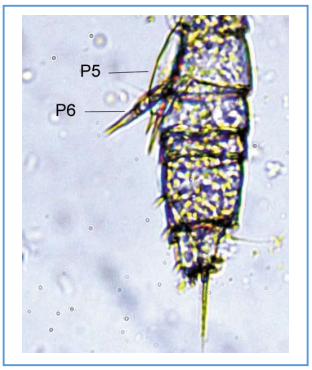

Fig. 204. *E. acutifrons* C5 male urosome, lateral.

In C6 females an additional segment has been added to the A1 making it seven-segmented. The urosome still has five somites (Table 4; Figs. 205, 206). The genital somite is longer than in the C5, around the same length as the following two somites together. This is due to the process during the final moult of a somite being added and then fusing to give a double somite, typical of female copepods. Each limb of the P5 is a flattened plate with a deep division between (Fig. 207). They are longer than in the male, one-segmented and still have four distal spines. The innermost spine may be smaller than the others, or crossed with the spine on the opposite limb. There is a fine seta and a short spine on the outer margin. The spine has a fine setule emerging from near the base.

Fig. 205. *E. acutifrons* C6 female 0.8 mm, lateral.

Fig. 206. *E. acutifrons* C6 female urosome, lateral.

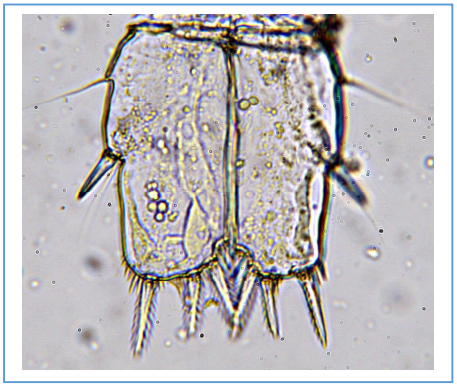

Fig. 207. *E. acutifrons* C6 female P5.

In the C6 male, both A1 are indistinctly five-segmented and strongly geniculate (Figs. 208, 209). The fourth segment is particularly wide making identification easy. Males have six urosome somites. The P5 are simple and symmetrical, each limb a single plate with a short notch between (Fig. 210). Each limb bears two distal spines and similar to the female, on the outer margin a fine seta and a short spine with a fine setule emerging from the base, usually difficult to see. The P6 comprises two lobes, each situated laterally on the distal margin of the second urosome somite (Fig. 211), each bearing two spines. The outer of the spines is longer and projects beyond the sides of the urosome, visible in both ventral and dorsal view (Fig. 208), as in the C5.

Fig. 208. *E. acutifrons* C6 male 0.59 mm, ventral.

Fig. 209. *E. acutifrons* C6 male 0.59 mm, lateral.

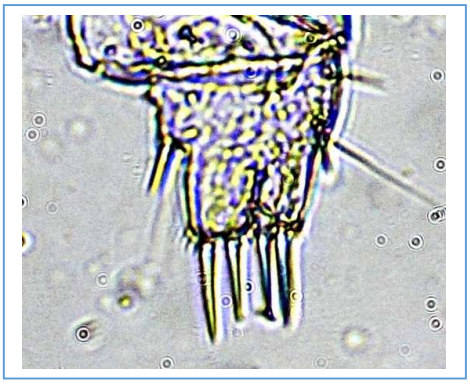

Fig. 210. *E. acutifrons* C6 male P5.

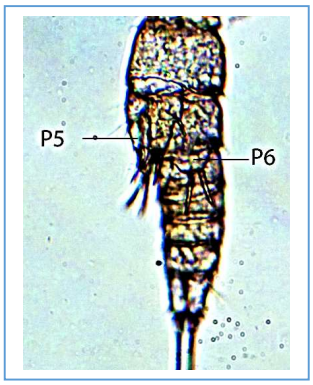

Fig. 211. *E. acutifrons* C6 male urosome,

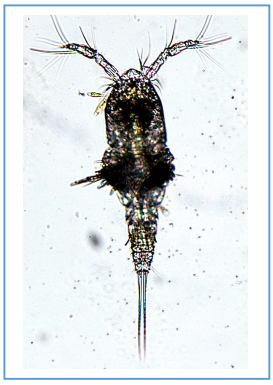

Fig. 212. *E. acutifrons* C6 small male 0.41 mm, ventral.

Fig. 213. *E. acutifrons* C6 small male 0.43 mm, lateral.

It is not unusual in copepod populations to find individuals of the same developmental stage present in two obviously different size classes. This dimorphism is particularly obvious in males of *Euterpina* (Figs. 212, 213), for which reason they have been studied by several authors (e.g. Haq, 1965; D'Apolito & Stancyk, 1979). Apart from size there is reported to be slight variation, between large and small males, in setation of some of the limbs (Haq, 1965), but no difference in the gross morphology. Haq (1972) also found differences in breeding behaviour between small and large males, but the whole topic would benefit from further research.

***Microsetella norvegica*:**

There are two *Microsetella* spp. found in northern European waters, *M. rosea* (Fig. 214) and *M. norvegica* (Figs. 215, 216), both of which have cosmopolitan distributions. *Microsetella* spp. have streamlined, cigar-shaped bodies and conspicuously long furcal setae in all stages, making them easily identifiable copepods. Excluding furcal setae, adult *M. rosea* are around twice the length of *M. norvegica.* In all stages of *M. rosea*, their longest furcal setae are around twice the length of the body, while in *M. norvegica* they are around the same length. There are two long setae on each furca, one around half the length of the other, but because they are positioned closely together they typically appear as one (Figs. 216, 217). Some short, fine setae are also present distally on the furcae. The furcae may be positioned together or splayed slightly apart.

Fig. 214. *M. rosea* C6 female 0.8 mm (excluding setae),

Fig. 215. *Microsetella norvegica* C6 female 0.6 mm,

Fig. 216. *M. norvegica* C6 female ventral.

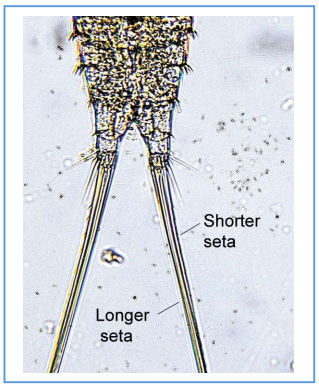

Fig. 217. *M. norvegica* C6 female urosome ventral.

Fig. 218. *M. norvegica* C6 female left

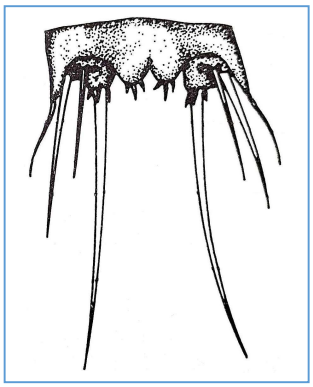

Fig. 219. *M. norvegica* C6 male P5 (after Diaz & Evans, 1983.

Copepodite developmental information for *M. norvegica* was obtained from Hirakawa (1974) and (Diaz & Evans (1983), summarised in Table 4. The stages of *M. rosea* appear to share the same developmental features (Björnberg, 1972). *Microsetella* spp. are not common in the Plymouth plankton, so C1-C5 stages were not available to photograph. Instead, drawings of *M. norvegica* from Hirakawa (1974) have been included here (Fig. 220).

Changes in the segmentation of the A1 may be helpful in identifying stages. In C1 there are three segments, four in C2 and C3, five in C4 and C5, six in C6 females and five in C6 males. In C6 males the A1 are both geniculate and in some individuals sampled may be bent at the hinge (Fig. 220). Similar to *Euterpina*, C1-C3 *Microsetella* have in addition to their fully developed legs, a pair of smaller, more rudimentary legs that will not fully develop until the next moult (Table 4; Fig. 220). These are better developed than the corresponding very rudimentary legs found in calanoid copepods. In C4 the P5 are short, with only one long seta each side. These setae become longer and additional long setae are added in C5 and C6.

In *Euterpina,* the sexes can be distinguished from C4, but Diaz & Evans (1983) considered that the sexes in *M. norvegica* could not be differentiated until they were adult. However, Björnberg (1972) noted that in *M. rosea,* females could be distinguished from C4, as compared to males they had a more developed P5 in this and subsequent stages. The illustrations of the P5 of male and female *M. norvegica* by Diaz & Evans (1983) and Hirakawa (1974) differ somewhat, possibly because of regional or environmental variation, but the sexes are still easily distinguishable by the general structure and setation (Figs. 218, 219).

The number of urosome somites noted for C5 *M. norvegica* was four (Table 4), which is one less than usually found in harpacticoids and the same as in C4. This indicates that the male gains two somites in the final moult, which is unusual. The C6 female genital somite is much longer than the other urosome somites (Fig. 220), as it is a fused double somite.

From *M. norvegica* specimens examined by Diaz & Evans (1983), in all stages the distal edge of at least the last three somites is ringed with spinules (Fig. 217), with additional fine setae/spinules on the surface of some somites. Not all authors have mentioned these, so there may be regional variations.

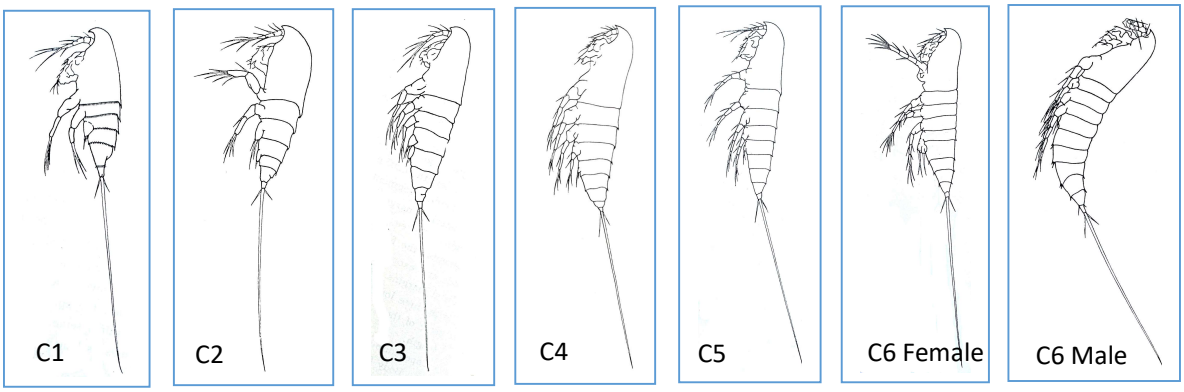

Fig. 220. *Microsetella norvegica* copepodite developmental stages (after Hirakawa, 1974; images not to same scale).

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Subclass Facetotecta

In the late 1800's some curious small crustacean larvae, reminiscent of copepod nauplii, were described from plankton samples taken in the southern North Sea and also from West Indian and equatorial Atlantic waters (Hensen, 1887; Hansen, 1899). Initially called y-larvae, molecular studies have established that they are closely related to barnacles (Pérez-Losada *et al*., 2009), which are in arthropod Class Thecostraca, Subclass Cirripedia. Cirripedes have a series of naupliar stages in their life cycle (Figs. 1, 2), then a final settlement stage, the cyprid (Fig. 3). Y-larvae (Figs. 4, 5) follow a similar nauplii/cyprid developmental sequence and have been placed in a sister-group to Subclass Cirripedia, in Subclass Facetotecta. Their name is derived from the faceted appearance of their carapaces (Figs. 6, 7), created by a network of plates fringed by ridges. It is now known that facetotectans are distributed worldwide in all oceans, sometimes numerous in inshore samples. Current knowledge of the group has been comprehensively reviewed by Dreyer *et al.* (2023a). There are presently only around seventeen species formally described, all placed in a single genus, *Hansenocaris* (Itô, 1985). Molecular studies in Japan and Taiwan (Dreyer, 2023b) indicated that there were up to 127 species between just these two locations, suggesting a large number of undescribed species worldwide.

Intriguingly, only larval facetotectan stages have ever knowingly been found, adults remaining undiscovered. They are thought to be internal parasites, probably of some undetermined invertebrates (Glenner *et al*., 2008). This life style is suggested, based on observations made during hormone treatment experiments on cyprids, which were induced to produce an unsegmented, worm-like ypsigon stage. The ypsigon, while independently evolved, resembles the vermigion stage of the Rhizocephala, a parasitic infraclass of Cirripedia. Rhizocephalans are mainly parasitic on crustaceans such as shrimps and crabs. Their cyprid releases a kentrogon stage, inside which the vermigion develops and this is them injected through the host cuticle (Glenner, 2001).

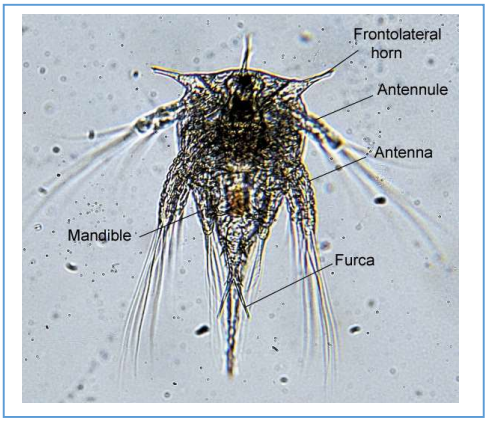

Fig. 1. Cirripede thoracican nauplius 0.8 mm, ventral.

Fig. 2. Cirripede rhizocephalan nauplius (*Peltogaster paguri*) 0.4 mm, dorsal.

Fig. 3. Cirripede thoracican cyprid 0.7 mm, lateral.

Morphology and development

Cirripede nauplii, both free-living and parasitic, are easy to distinguish from other crustacean nauplii by their characteristic frontolateral horns on the cephalic shield (Figs. 1, 2). Only a few thecostracans have a faceted exoskeleton like facetotectans (Dreyer et al., 2023a), and no copepod nauplii. Some cirripede rhizocephalan nauplii have a thin, dorsal 'flotation collar' that is reinforced by a network of ridges (Fig. 2) that appears similar Most facetotectans seem to have five naupliar stages, compared to six in many free-living crustaceans, a reduction in numbers of stages typical of many parasitic species, but up to seven stages have been described (Kolbasov *et al*., 2021). The anterior naupliar body is covered by the cephalic shield (Figs. 4-10). There is a dark, naupliar eye situated anteriorly below the cephalic shield (Figs. 4, 5). Ventrally, the cephalic region bears three paired limbs, comprising uniramous antennules and biramous antennae and mandibles (Fig. 6). Between the limbs, a flap-like labrum covers the mouth, attached at the anterior edge. Some nauplii have been observed to be planktotrophic (Kolbasov & Høeg, 2003), but most appear to be lecithotrophic. Nauplii considered

planktotrophic have feeding related development of the antennae and mandibles, extension of the labrum over the mouth, a functional gut and no egg yolk (Dreyer *et al*., 2023a).

The exoskeleton is divided into many plates of different shapes, fringed by ridges, in a pattern particular to each species, easiest seen in the casts (Figs. 6, 7) or in dead individuals (Fig. 8). The plate pattern changes between moults, but there can be intraspecific variability in pattern in each stage (Kolbasov *et al*., 2021), which could pose taxonomic challenges. On the thorax are six short somites and on the abdomen two to four, all without limbs (Fig. 6). The hind body generally terminates in a strong dorsocaudal spine that, depending on species, projects slightly dorsally (Fig. 7), or close to right angles to the abdomen (Fig. 9). In the latter case the spine is not profiled in dorsal view (Fig. 10).

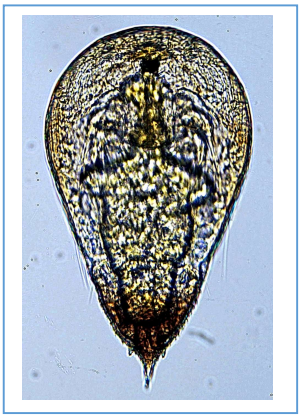

Fig. 4. Facetotectan nauplius, 0.48 mm dorsal.

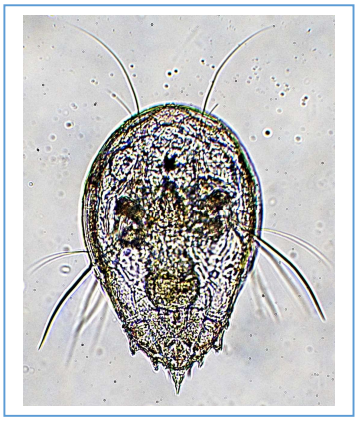

Fig. 5. Facetotectan nauplius with strong posterolateral spines, 0.31 mm dorsal.

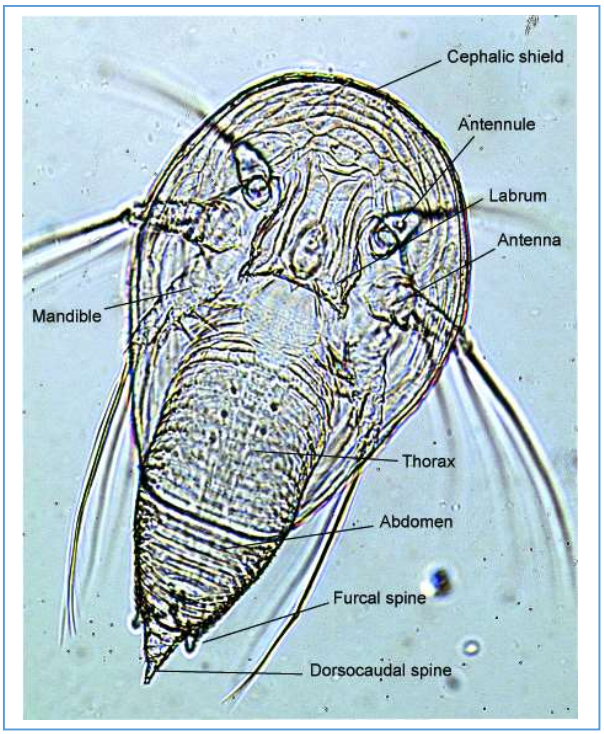

Fig. 6. Facetotectan nauplius intact cast, 0.42 mm dorsal.

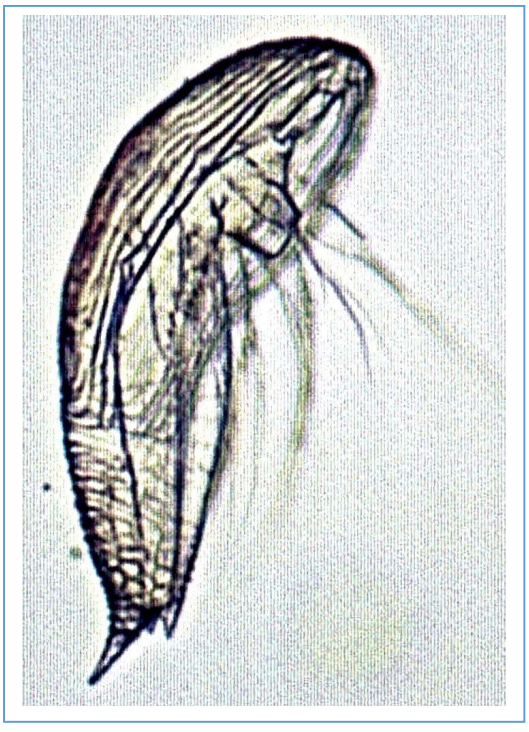

Fig. 7. Facetotectan nauplius intact cast, 0.47 mm lateral.

Ventrally in some species, anterior to the dorsocaudal spine, is a protruding dorsocaudal organ (Figs. 9, 10) whose function is unknown. It overlies a circular feature that lies flush to the exoskeleton, obvious in the casts (Fig. 11). Distally on the abdomen is typically a pair of furcal spines (Figs. 6, 9). The cuticular ridges on the edges of the hind body protrude, appearing like small spines (Figs. 4, 6, 10), but in some species there are large, posterolateral spines (Figs. 5, 8).

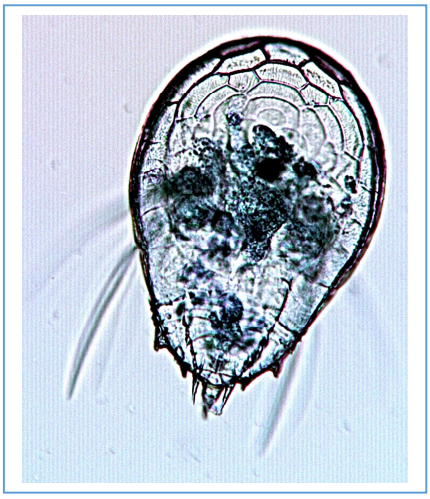

Fig. 8. Facetotectan nauplius with strong posterolateral spines, 0.31 mm, dorsal (dead).

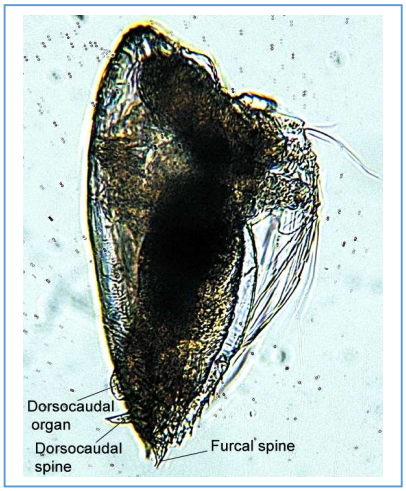

Fig. 9. Facetotectan nauplius from deep water west of Ireland, 0.48 mm, lateral (preserved).

Fig. 10. Facetotectan nauplius from west of Ireland, 0.48 mm, dorsal.

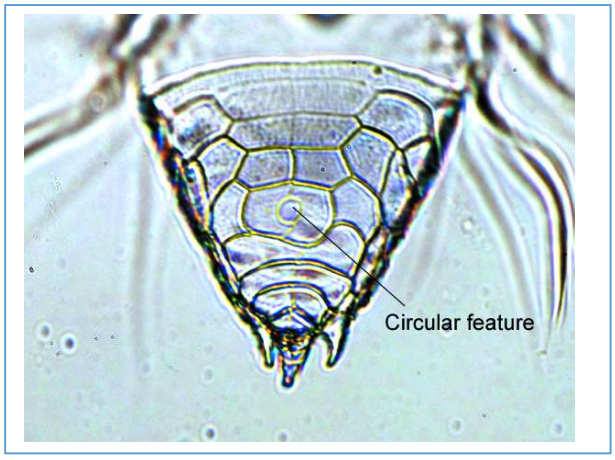

Fig. 11. Facetotectan nauplius cast, 0.45 mm abdomen dorsal.

The exoskeleton sometimes remains in one piece on moulting (Figs. 6, 7), but typically separate into two parts (Figs. 12-15), the cephalic shield and the remainder of the exoskeleton, the faciotrunk. Observations by Grygier *et al*. (2019) and Kolbasov *et al*. (2021) have indicated that nauplii exit dorsally when moulting and the moult generally breaks in two, but in the final moult the cyprid exits anteriorly, when the moult generally remains intact. In support of these observations, cyprids emerged from the intact casts in Figures 6 and 7.

Fig.12. Facetotectan nauplius moulting, 0.47 mm dorsal.

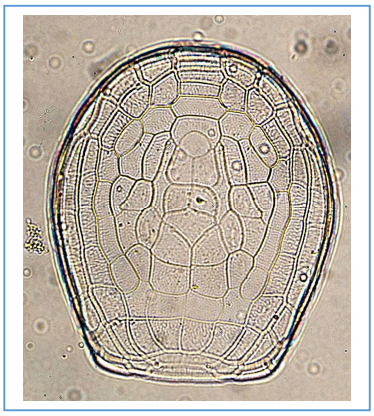

Fig. 13. Facetotectan nauplius cephalic shield cast, dorsal.

Fig. 14. Facetotectan nauplius faciotrunk cast, ventral (remainder from Fig. 13).

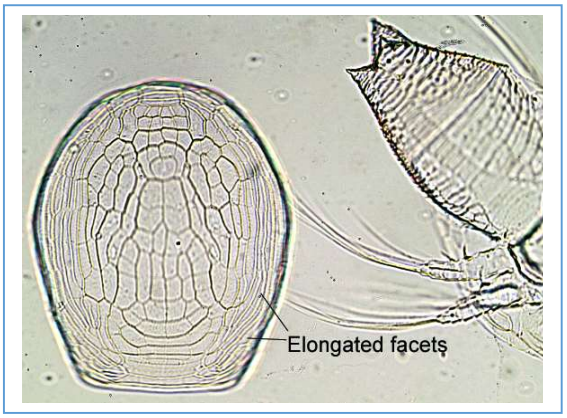

Fig. 15. Facetotectan nauplius cast, cephalic shield dorsal, faciotrunk ventral.

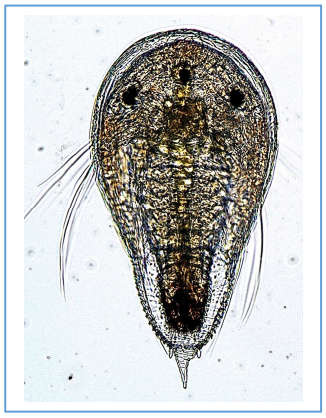

Fig. 16. Facetotectan metanauplius, 0.48 mm dorsal.

Fig. 17. Facetotectan metanauplius, 0.46 mm lateral.

In the final nauplius stage (metanauplius) the cyprid is clearly visible inside (Figs. 16, 17) with an obvious gap between the body and the cast. In lateral view, swimming limbs (thoracopods) are also visible on the thorax. In addition to the naupliar eye, a pair of cyprid eyes are present, sometimes also visible in the stage before the metanauplius.

The single cyprid stage (Figs. 18, 19) emerges from the metanauplius. In free-living barnacle cyprids, the body is largely enclosed in a bivalve carapace (Fig. 3), but in facetotectans the cephalic shield is not bivalved and only covers the anterior body. The rear of the cephalic shield comes to a blunt point ventrally. Similar to the nauplii, the exoskeleton is covered in plates and ridges. Cyprids are lecithotrophic, heavily invested with clearly visible globules of lipid and never feed. Large, lateral compound eyes are very noticeable. The normal crustacean feeding appendages are absent, the only obvious cephalic appendages being the antennules that have four segments and may protrude anteriorly. Behind the antennules and lateral to the labrum are two pairs of simple projections that probably represent the vestiges of the antennae and mandibles. Each of the six thoracic somites bear biramous thoracopod limb pairs. The abdomen comprises two or four somites.

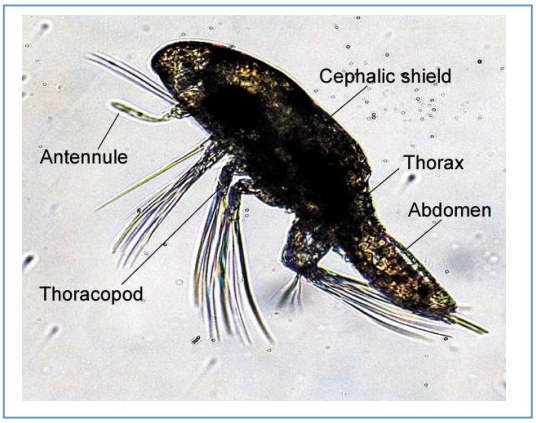

Fig. 18. Facetotectan cyprid, 0.45 mm lateral.

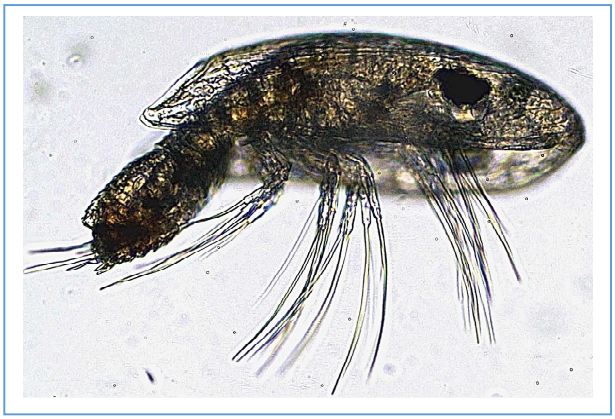

Fig. 19. Facetotectan cyprid, 0.47 mm lateral.

Facetotectan sampling at Plymouth

For anyone wishing to sample facetotectan larvae, information on how they were collected and cultured at Plymouth may be of interest.

Plankton samples were taken in Millbay Marina over a 43-month period (Fig. 20), primarily to obtain general zooplankton for photography, but samples were also carefully searched for facetotectan larvae. The advantage of sampling in a marina with floating pontoons is that collections can be carried out in any weather or state of tide. The plankton net used was a ½ metre hand net of 0.1 mm mesh aperture, towed a standard distance, just below the surface alongside a pontoon. It was towed on a rope from the end of a short pole to hold the net away from the side of the pontoon. It was not feasible to use a flowmeter due to the low towing speed, so volume filtered was calculated based on the dimension of the net and distance towed, assuming 100% filtration. While sampling protocol was standardised as far as possible, the volume filtered will not be absolute, but gives a comparative indication of changing numbers of nauplii over time. Because many facetotectan larvae are small, some <0.2 mm in width, they may not be quantitatively sampled unless a plankton net of at least 0.1 mm mesh aperture is used. For logistical reasons, a net mesh aperture of 0.2 mm is commonly used by researchers during routine plankton surveys, so not all larvae will be retained.

Because of their small size and low numbers, nauplii are laborious to sort from live samples. They appeared to be rather poor swimmers, as most were generally found in the residue in the bottom of the sample beaker, bobbing characteristically on their backs with their anterior down. A very small number of cyprids were also collected.

Sorted nauplii were individually cultured in unfiltered seawater in square (4x4 cm), solid watch glasses covered by petri dishes. They were kept at a temperature of ~12 ^{0}C, usually without any water changes and exposed to a subdued day/night light regime. Because one naupliar type and all cyprids that emerged had a long survival period (see below), most of the seawater these were in was carefully removed by fine pipette and replaced with fresh unfiltered seawater every five days. When the nauplii moult (Fig. 12), the discarded casts are easy to recover with a fine pipette, under a microscope.

Facetotectan larvae found at Plymouth

For convenience, sampling was concentrated in Millbay Marina, but from occasional other sampling, nauplii were found to be widely distributed in low numbers throughout the general Plymouth area. Of the two obviously different naupliar types found, one was small (0.29-0.32 mm) with conspicuous posterolateral spines (Figs. 5, 8), similar in morphology to some of the nauplii sampled by Schram (1972) in Oslofjord, Norway. These nauplii were cultured in unfiltered seawater for up to 33 days, until they died without moulting. The other nauplii type (0.33-0.49 mm) lacked strong posterolateral spines and had only fine ridge spines on the abdomen. These generally moulted once, sometimes twice, in a 24-hour period, and up to a total of five times before cyprid release. The distal abdomen of these nauplii was tinged dull red and there appears to be at least two species, although detailed examination was not carried out. Some individuals had very coarse facets (Figs. 11-14) others finer (Figs 6, 7, 15-17). In later stages it appeared that the peripheral facets on the cephalic shield

transformed into a series of elongated facets (Figs. 6, 7, 15). Emerging cyprids survived for up to 27 days on their food reserves before dying.

Seasonal numbers of facetotectan nauplii at Plymouth

Nauplii were found throughout the year (Fig. 20), usually in very low numbers, with occasional peaks that were possibly related to tidal and mixing conditions. As sampling was only at the surface, no information is available on depth distribution. The nauplii with strong posterolateral spines were sampled in lowest numbers and not found between March and May. Nauplii with only fine abdominal ridge spines occurred in all months. Total numbers were lowest from January to May, coinciding with the lowest sea temperatures (Fig. 21).

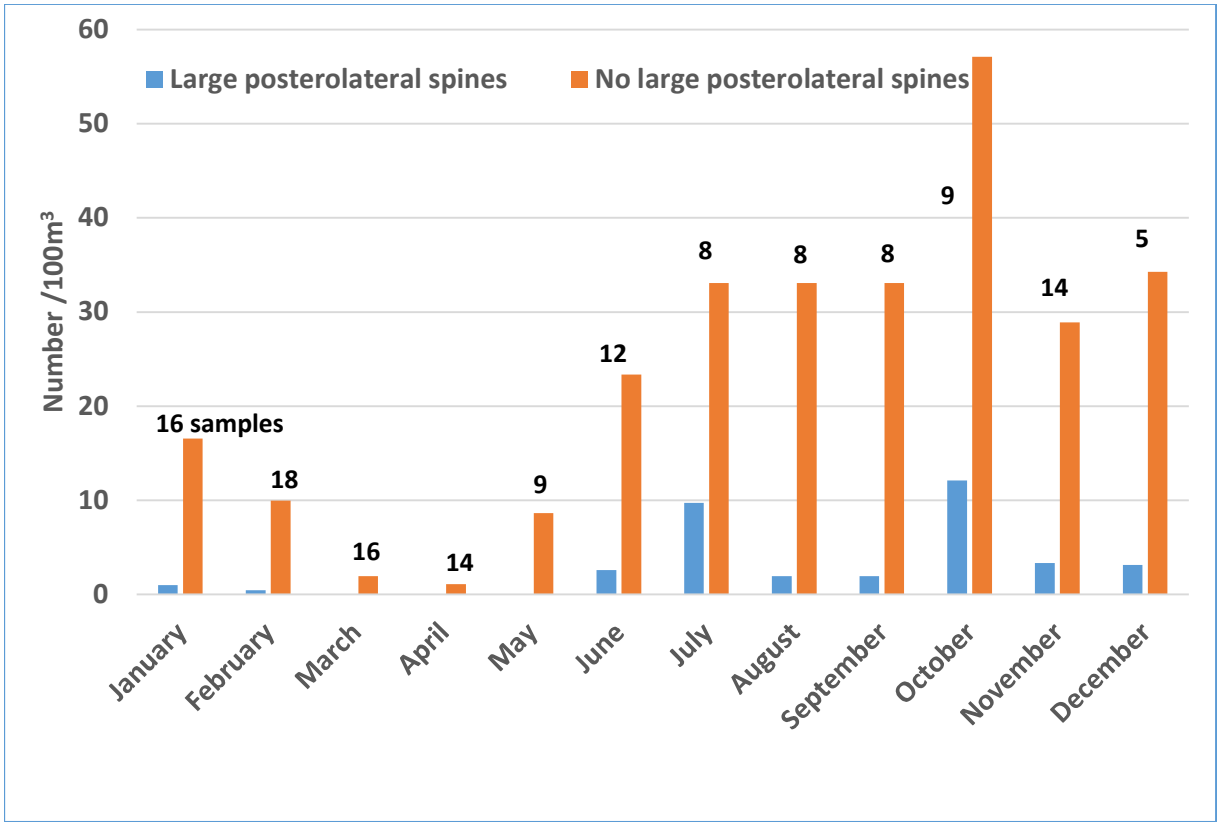

Fig. 20. Monthly mean numbers of the two different facetotectan naupliar types over the sampling period 12/11/2011 – 19/05/2015. Number of samples taken in each month is also shown.

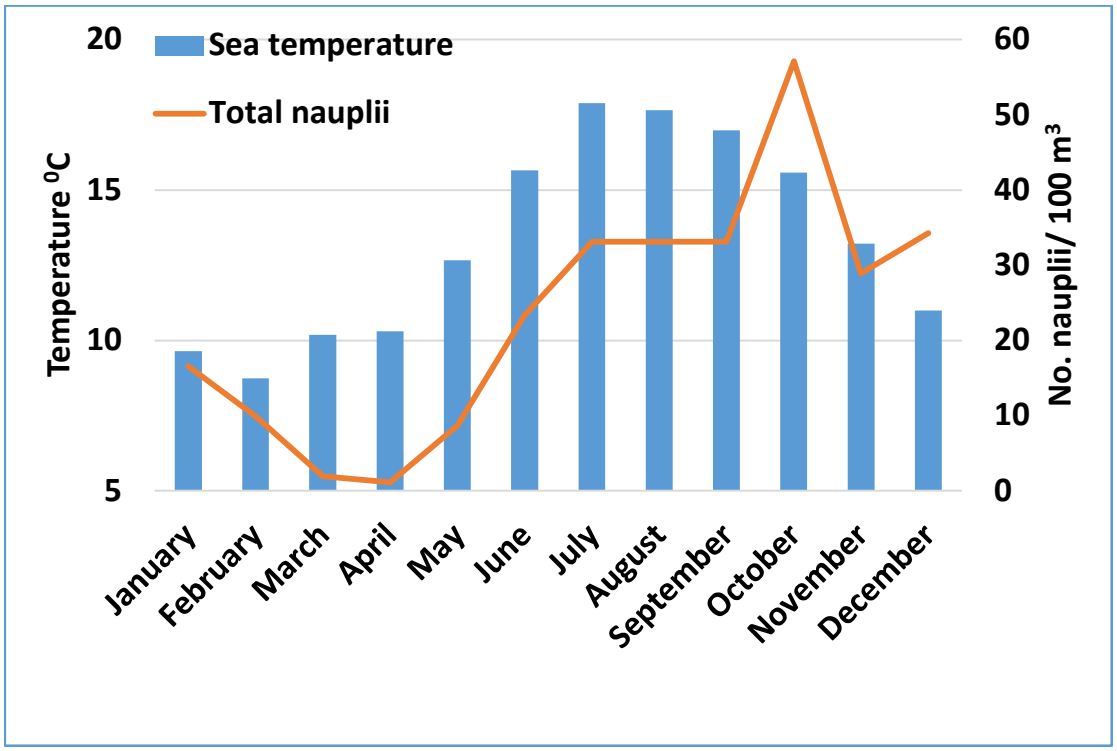

Fig. 21. Monthly mean sea temperature in Millbay Marina and mean numbers of total facetotectan nauplii collected over the sampling period 12/11/2011 – 19/05/2015.

Eventual identification of adult facetotectans

The close phylogenetic relationship between rhizocephalan barnacles and facetotectans, and apparent convergence in features of their infective stages (Glenner *et al*., 2008), suggests that facetotectans may share a similar type of endoparasitic life cycle. Rhizocephalan barnacles mainly parasitise other crustaceans, particularly anomuran and brachyuran decapods, but also carideans, pericarids, stomatopods and even balanomorphan cirripedes. It is likely that facetotectans will also have a restricted range of host organism types, with a widespread distribution and which are present throughout the year. Rhizocephalans are internal parasites, but during their life cycle also show external evidence of their presence on their host, such as the large, sac-like females that emerge from the brood pouch of crabs. This suggests that adult facetotectans may be an anonymous internal lump, with no obvious external part. They perhaps may also only be found in organisms not commercially exploited, so not subjected to close examination. Naupliar diversity, high numbers at some locations (Dreyer at al. 2023b) and extended seasonal presence in the plankton, also suggests that facetotectans should be an ecologically important group.

One potential experimental method to discover the source of facetotectan nauplii could be to collect a range of organisms from an area where high numbers of nauplii are found and individually keep them in aquaria, while regularly filtering the water to see if any nauplii are released. As a starting point, any current aquarium systems could be tested. However, the source of the nauplii might eventually be identified using laboratory analytical techniques. Recently developed sequencing technologies, employed as part of initiatives, such as the Tree of Life Programme, aiming to produce reference genome sequences for all described eukaryotic species (Laumer *et al*., 2019), might eventually lead to detection of the adults in other organisms. Alternatively, as most facetotectan nauplii are lecithotrophic, the lipids they contain, originating from the adults feeding on their host, biochemical methods such as stable isotope or lipid analysis could potentially provide a nutritional pathway back to the host.

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