## MARINE ZOOPLANKTON OF SOUTHERN BRITAIN

## Part 2:

Arachnida, Pycnogonida, Cladocera, Facetotecta, Cirripedia and Copepoda

## David V.P. Conway



Edited by Anthony W.G. John
Marine Biological Association Occasional Publications No 26

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## Preface

The range of zooplankton species included in this series of three guides is based on those that have been recorded in the Plymouth Marine Fauna (PMF; Marine Biological Association. 1957. Plymouth Marine Fauna, Third edition. Plymouth, Marine Biological Association, 457 pp.) and at Station L4, a zooplankton sampling station off Plymouth where zooplankton has been collected weekly since 1988, but also includes some species that have been recorded from the more general area. The guides were originally conceived solely for local training purposes, but can be used over a much broader region, as the large range of species found off Plymouth actually represent the vast majority of those found over the whole neritic, northern European Shelf area. Taxonomy is mainly based on the World Register of Marine Species (WORMS) scheme, which is constantly being updated, so classifications unfortunately soon become outdated. To avoid copyright issues and costs, many of the illustrations included are from quite old publications, but are still of high quality and accuracy. Full details about the guides are given in Part 1 of the series (Conway, D.V.P. 2012. Marine zooplankton of southern Britain. Part 1: Radiolaria, Heliozoa, Foraminifera, Ciliophora, Cnidaria, Ctenophora, Platyhelminthes, Nemertea, Rotifera and Mollusca. A.W.G. John (ed.). Occasional Publications. Marine Biological Association of the United Kingdom, No. 25, Plymouth, United Kingdom, 138 pp.), available for free download, from the National Marine Biological Library website - http://www.mba.ac.uk/NMBL/ from the "Download Occasional Publications of the MBA" section.

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## PICTORIAL KEY TO ZOOPLANKTON

(Not to scale; numbers in brackets are part numbers of the guide)


Phylum Echinodermata (3)


Phylum Platyhelminthes (1)


Phylum Mollusca (1)


Subclass Prosobranchia
Subclass Prosobranchia
Littorina egg capsules


Order Sepiida
Class Cephalopoda


## CRUSTACEAN ZOOPLANKTON

Phylum Arthropoda - Subphylum Crustacea
Subclass Copepoda (2)


Class Arachnida (2) Class Pycnogonida (2) Order Stomatopoda (3)
Order Isopoda (3)


Suborder Gammaridea


Order Amphipoda (3)
Suborder Hyperiidea


Suborder Corophiidea





Order Mysida (3)


Order Euphausiidae (3)




Suborder Cladocera (2)



## PHYLUM ARTHROPODA

## Subphylum Chelicerata:

## Class Arachnida: Order Acarina: Family Halacaridae:

Order Acarina is a group of primarily terrestrial arachnids, so they are related to spiders, but the majority of one family, Halacaridae, are marine. They are mainly found intertidally, but also below low tide level (sublittoral) to the very deep ocean.
Because of their terrestrial, mite-like appearance, they are unlikely to be confused with any other plankton group. Their bodies are short, oval in shape, outwardly showing little or no division into somites, bearing four pairs of legs, the anterior two pairs directed forwards and the posterior two pairs backwards. Their bodies and legs are sparsely covered in setae. On the anterior body is the gnathostoma that bears the mouth parts and palps. This articulates with the main body.
Halacaridae are occasionally sampled in inshore plankton tows. The PMF records 17 species and an illustration of one that is found off Plymouth is given as an example (Fig. 1).

Copidognathus rhodostigma (Gosse, 1855)


Fig. 1. Example of a halacarid arachnid, Copidognathus rhodostigma (from Fountain, 1953; as Halacarus rhodostigma).

Recorded: PMF, 17 species. L4, only recorded as Halacaridae. All coastal European waters. Size: $\sim 0.34-1.00 \mathrm{~mm}$.
Further information: Lebour, 1945; Fountain, 1953; Green \& MacQuitty, 1987; King \& Pugh, 1995.

## PHYLUM ARTHROPODA: Subphylum Chelicerata:

## Class Pycnogonida:

These are unconventional looking arthropods, called "sea-spiders" because of their resemblance to terrestrial spiders and they are in the same sub-phylum. Bottom living, they typically feed by sucking nutriment from hydroids, bryozoans and other fleshy organisms. They are not planktonic, but some can swim and they occasionally turn up in plankton samples. Around 16 species are recorded in the PMF and one of these is given as an example in Figure 2.

## Morphology

Most pycnogonids are small, but there are some very large species. They have a long, narrow, body, usually divided into several visible somites (Fig. 2A). Anteriorly the body is produced into a cephalon with a proboscis that bears a terminal mouth, either side of which in most species there are two pairs of appendages involved in feeding. Dorsally on the cephalon in most species are two pairs of eyes, one pair pointing forwards, the other backwards. The first body somite is fused with the cephalon and the last somite has an anal process with a terminal anus. There are usually five further pairs of appendages. The first is a pair of ovigerous appendages (ovigers), situated ventrally, used in cleaning the body and courtship, and egg carrying in the male, but often missing in females. There are then usually four pairs of lateral legs used in locomotion, but sometimes fewer in juveniles and five or six pairs in a few species. There can be differences between species and also sexes in number and development of the feeding appendages and ovigers.

## Reproduction and development

When the female lays eggs they are fertilised by the male, then attached to his ovigers (Fig. 2B), dorsally beneath the trunk. When eggs hatch there are four different routes of larval development: a free-living larva that gradually develops into an adult; a larva that completes its development on or in temporary hosts such as hydrozoan medusae, polychaetes and bivalves; a parasitic larva that finds a host e.g. a hydrozoan polyp colony, into which it burrows and encysts, remaining until it emerges as a juvenile (Fig. 2D, E); or a larva that immediately attaches itself to the ovigers of the male, where it will remain until it is ready for a free-living existence. Pycnogonids can reach maturity within 5 months and average life expectancy is typically about a year.

Anoplodactylus pygmaeus (Hodge, 1864)
When the eggs hatch, the larvae (Fig. 2C) burrow into the hydroids of hydrozoans such as Obelia spp., where they encyst and develop (Fig. 2D) before emerging to take up a benthic existence. Typical of many pycnogonids, the emerging larva (Fig. 2E) has only three pairs of limbs.


Fig. 2. Example of a pycnogonid, Anoplodactylus pygmaeus (from Lebour, 1945).
Recorded: PMF, 16 species. L4, not recorded. All coastal European waters.
Size: ~0.6-10 mm, but up to 90 cm .
Further information: King, 1974; King \& Pugh, 1995; Bamber, 2010.

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## PHYLUM ARTHROPODA:

## Subphylum Crustacea:

## Class Branchiopoda: Suborder Cladocera:

Cladocera are small crustaceans, commonly called "water fleas" that can seasonally be very abundant. Cladocera as a taxonomic unit has been dropped by some taxonomists (Fryer, 1987), but the WORMS classification still includes it. Most species are found in freshwater or brackish conditions, with only eight true marine species worldwide. Six of the marine species are found in European waters and all are in Infraorder Onychopoda, Family Podonidae, apart from Genus Penilia which is in Infraorder Ctenopoda, Family Sididae. One brackish water species, from another infraorder, Anomopoda, that is occasionally found in inshore plankton samples, has also been included here, Bosmina (Eubosmina) coregoni.
Marine Cladocera typically have an anterior, single, large compound eye (Fig. 1; front cover). The head bears two pairs of appendages, the antennules that are usually tiny and unsegmented, bearing olfactory setae, and the antennae that are large, segmented and branched, with powerful muscles for swimming. In some species a rostrum projects in front of the antennule. The head may be angled downwards and separated from the rest of the body by a notch (cervical groove). The mouthparts are very small and not very obvious compared to the other limbs. The thorax bears four to six pairs of limbs, each with setae. There is a dorsal carapace that in some species encloses the thoracic region, including limbs, while in others only the dorsal part of the body is enclosed. Dorsally within the carapace of the female is a brood chamber. Cladocera are often found on the surface of samples, which may be due to trapped air inside the carapace.

## Reproduction and development

Eggs, embryos and young stages that are replicas of the adults, are retained in the brood chamber, so there are no free larval stages. The life cycle is dominated by parthenogenesis (asexual reproduction) with occasional periods of sexual reproduction, a process known as cyclical parthenogenesis. When conditions are favourable, reproduction occurs by parthenogenesis for several generations, producing only female clones, and the populations can increase explosively. These population increases are usually followed by production of males, then sexual reproduction. The cause of this change in reproductive behaviour is not always obvious, but may relate to a variety of interacting biological, chemical and physical factors, stressing the population. Following copulation, one or two thick-walled, dormant eggs are produced in the brood chambers. These may be released by the females, or reach the bottom when the female dies. They can survive for long periods in the bottom sediments until conditions favour hatching, forming an egg bank for the next year, or later generations.

## Key to the Cladocera described

1. Carapace covers the thorax and thoracic limbs, free edges serrated; six pairs of thoracic limbs Infraorder Ctenopoda, Penilia avirostris Fig. 6

- Carapace covers the thorax and thoracic limbs, free edges smooth; six pairs of thoracic limbs --------------------------- Infraorder Anomopoda, Bosmina (Eubosmina) coregoni Fig. 7
- Carapace covers only the dorsal brood chamber; the four pairs of thoracic limbs exposed -Infraorder Onychopoda, Family Podonidae 2



3. Exopod of first thoracic limb with one large seta $-\ldots \ldots-\ldots-\ldots$ - Podon leuckartii Fig. 1C, D

- Exopod of first thoracic limb with two large setae ---..---..-..-- Podon intermedius Fig. 2D, E
- Exopod of first thoracic limb with three large setae ---- Pleopsis polyphaemoides Fig. 3C, D

4. Carapace gradually narrows into a point --------------------------------- Evadne nordmanni Fig. 4


PHYLUM ARTHROPODA: Subphylum Crustacea: Class Branchiopoda: Suborder Cladocera:

## Infraorder Onychopoda:

## Family Podonidae:

## Genus Podon:

Antennules short and quite rudimentary (Fig. 1B, 2C); body stout and carapace hemispherical, but shape may be modified by presence of embryos in the brood chamber; deep transverse cervical groove between head and thorax (Fig. 1B); exopods of thoracic limbs with between one and three setae (Fig. 1C). Males can be recognised by presence of a strong hook on the endopod of the first thoracic limb (Fig. 1D) and a pair of copulatory organs on anterior abdomen (Fig. 1B).

Podon leuckartii (G.O. Sars, 1862)
Large body; carapace hemispherical (Fig. 1A, B); caudal furcae long; caudal process quite large; exopods of legs one to four with one (Fig. 1C), one, one and two setae respectively.


Fig. 1. Podon leuckartii (from Lilljeborg, 1901, as P. leuckarti).
Recorded: PMF (as Podon leuckarti). L4, rare. All European waters, mainly coastal.
Size: Resting eggs 0.21-0.23 mm; female 0.8-1.0 mm; male $\sim 1.0 \mathrm{~mm}$.
Further information: Lilljeborg, 1901; Rammner, 1939; Della Croce, 1974; Onbé, 1999; Gerber, 2000; Larink \& Westheide, 2006 (all as P. leuckarti).

Podon intermedius Lilljeborg, 1853
Large body; female carapace hemispherical to oval-shaped (Fig. 2A; front cover), in male more triangular (Fig. 2B); caudal furcae large; caudal process particularly large (Fig. 2A, B); exopods of legs one to four with two (Fig. 2D), one, one and two setae respectively.


Fig. 2. Podon intermedius (from Lilljeborg, 1901).
Recorded: PMF. L4, common. All European waters, mainly coastal, but also open sea. Size: Resting eggs $\sim 0.27 \mathrm{~mm}$; female $1.1-1.2 \mathrm{~mm}$; male $0.6-1.0 \mathrm{~mm}$.
Further information: Lilljeborg, 1901; Rammner, 1939; Della Croce, 1974; Onbé, 1999; Gerber, 2000.

## Genus Pleopis:

Similar characteristics to Genus Podon, but different number of setae on the thoracic limb exopods.

Pleopis polyphaemoides (Leuckart, 1859)
Small body; female carapace hemispherical (Fig. 3A), male carapace more oblong (Fig. 3B); caudal furcae and caudal process short; exopods of legs one to four with three (Fig. 3C), three, three and two setae respectively.


Fig. 3. Pleopis polyphaemoides (from Lilljeborg, 1901, as Podon polyphemoides).
Recorded: Not recorded from Plymouth, but could occur. Widespread in European waters, mainly coastal.
Size: Resting eggs $0.15-0.21 \mathrm{~mm}$; female $0.3-0.7 \mathrm{~mm}$; male $0.4-0.7 \mathrm{~mm}$.
Further information: Lilljeborg, 1901; Baker, 1938; Rammner, 1939; Della Croce, 1974 (all as Podon polyphemoides); Onbé, 1999; Gerber, 2000; Johnson \& Allen, 2005; Larink \& Westheide, 2006 (all as Pleopsis polyphemoides).

## Genus Evadne:

Body stout; carapace triangular, pointed; no clear cervical groove between head and thorax; antennae smaller than in Podon and Pleopis; four pairs of thoracic limbs, exopods with between one and two setae.

Evadne nordmanni Lovén, 1836
Streamlined body; carapace triangular (Fig. 4), progressively narrowing into a point, but in females carrying many young the body may be swollen and rounded with short point (Fig. 4B). Exopods of thoracic limbs one to four bearing two, two, one and one setae respectively.


Fig. 4. Evadne nordmanni (from Lilljeborg, 1901).
Recorded: PMF. L4, common. All European waters, mainly coastal, but also open sea.
Size: Resting egg $\sim 0.20 \mathrm{~mm}$; female $0.4-1.4 \mathrm{~mm}$; male 0.4-0.8 mm.
Further information: Lilljeborg, 1901; Jorgensen, 1933; Baker, 1938; Rammner, 1939; Della Croce, 1974; Onbé, 1999; Gerber, 2000; Muxagata \& Williams, 2004; Larink \& Westheide, 2006.

Evadne spinifera Müller, 1867
Streamlined body; carapace triangular (Fig. 5), but with terminal point drawn out into long spine. Exopods of thoracic limbs one to four with two, two, two and one setae respectively,


Fig. 5. Evadne spinifera (from Lilljeborg, 1901).
Recorded: Not recorded from Plymouth, but could occur. North Sea. English Channel. Western and southern Ireland. Skagerrak. Western Baltic. Coastal and open sea.
Size: Resting egg size unknown; female 0.7-1.4 mm; male 0.6-1.3 mm.
Further information: Lilljeborg, 1901; Baker, 1938; Rammner, 1939; Della Croce, 1974; Onbé, 1999.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Branchiopoda: Suborder Cladocera:

## Infraorder Ctenopoda:

## Family Sididae:

## Genus Penilia:

Genus description, as for the species below.

Penilia avirostris Dana, 1849
Very transparent species. Carapace covers the thorax and thoracic limbs (Fig. 6); free edge of carapace characteristically serrated, terminating in sharp carapace spine; six pairs of thoracic limbs; abdomen terminating in caudal furcae with spines of different lengths. Antennules moveable, short in females, as long as carapace in adult males; female head with prominent rostral point, round in males. In male first thoracic limb with strong distal hook (Fig. 6B); a pair of copulatory appendages located behind sixth thoracic limbs.
A feature of the strong setae on the thoracic limbs is that they have a spherical, glassy vesicle around halfway along their length (Fig. 6C). This feature does not appear to be found in any of the other cladocera sampled off southern Britain.


Fig. 6. Penilia avirostris (from Trégouboff \& Rose, 1957).
Recorded: PMF, not recorded. L4, small numbers in September 2008. Common in the southern North Sea, but rare in the English Channel, reappearing along the French coast from Brittany to Spain.
Size: Resting egg ovoid/compressed, $0.21-0.29 \mathrm{~mm}$ long by $0.14-0.20 \mathrm{~mm}$ wide; female $0.4-1.2$ mm ; male 0.7-0.9 mm.
Further information: Trégouboff \& Rose, 1957; Della Croce, 1974; Onbé, T. 1999; Johns et al, 2005; Johnson \& Allen, 2005; Larink \& Westheide, 2006.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Branchiopoda: Suborder Cladocera:

## Infraorder Anomopoda:

## Family Bosminidae:

## Genus Bosmina:

This is a brackish water species, but is sometimes found in coastal areas where there is freshwater input. The taxonomy of the genus is rather confused, but they are quite characteristic in appearance and identifiable to at least family or genus. Bosmina (Eubosmina) coregoni is one of the commonest European species and is given as an example.

Bosmina (Eubosmina) coregoni Baird, 1857
Carapace covers the thorax and thoracic limbs; rostrum rounded in female, shorter and blunt in male; antennules long, varying in length seasonally, immovably fixed to head in females, free in males; posterioventral edge of carapace with spine that is sometimes reduced to only a backwards protruding corner of the carapace; free carapace edge smooth. Six pairs of thoracic limbs, the most posterior reduced; hook and long flagellum on first thoracic limb of male. Transparent, sometimes yellowish.


Fig. 7. Bosmina (Eubosmina) coregoni (from Rammner, 1939, as Bosmina coregoni maritima).
Recorded: PMF and L4, not recorded. Baltic. Western Scotland (Bosmina sp.). Southampton (Bosmina sp.). Probably most European brackish water regions.
Size: Female 0.4-0.6 mm; male 0.4-0.45 mm
Further information: Rammner, 1939; Della Croce, 1974; Muxagata \& Williams, 2004.

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## PHYLUM ARTHROPODA: Subphylum Crustacea:

## Class Maxillopoda: Subclass Thecostraca: Infraclass Facetotecta:

Hensen (1887) collected some curious small crustacean larvae from West Indies and equatorial regions of the Atlantic and also the southern North Sea (Bay of Kiel) which, because they could not immediately be classified were named 'y-larvae'. Morphological and recent molecular evidence indicates that they belong to Class Maxillopoda, Subclass Thecostraca, which also includes the barnacles. Similar to barnacles, their development also includes nauplius and cyprid stages. They have been placed in a separate infraclass, Facetotecta, the name deriving from the faceted appearance of their carapace (Figs. 1, 2; front cover). Only larval stages have ever knowingly been found, adults remaining undiscovered.
Facetotectans are believed to be internal parasites of some undetermined invertebrates and their parasitic destiny as adults is supported by recent experiments on hormone-induced metamorphosis of the cyprid stage, when an unsegmented slug-like organism was produced (Glenner et al., 2008), similar to a stage of some parasitic barnacles. Larvae have now been recorded, mainly from inshore locations, from the Arctic to tropical waters of all oceans (Kolbasov \& Høeg, 2003). Because most larvae are small, some $<0.2 \mathrm{~mm}$ in width, they will be poorly sampled unless a plankton net of at least 0.1 mm mesh aperture is used. Their known distribution thus reflects where fine mesh net sampling has been carried out in inshore areas, by researchers who can distinguish the larvae from those of other crustaceans. They are occasionally sampled in quite high numbers, suggesting the adults could have considerable biological importance. Morphological examination of facetotectan larvae at one site in Japan indicated that there were more than 40 different species present (Glenner et al., 2008), an amazing biodiversity. Their presence was only recently recorded at Plymouth, during some fine mesh inshore sampling, but was not unexpected, as they are certainly much more widespread than current records suggest.

## Development

Developmental sequence is similar to barnacles, with a series of naupliar stages (Fig. 1) followed by a cyprid stage that emerges from the final naupliar (metanauplius) stage when it moults. There may be only five naupliar stages, compared to six in free-living barnacles (Kolbasov \& Høeg, 2003). Some parasitic barnacles have even fewer than five stages. The facetotectan naupliar body is oval and typically comprises an anterior part covered by a cephalic shield and a triangular, posteriorly projecting hindbody (Fig. 1 A-C).


Fig. 1. Examples of the naupliar and cyprid stages of a facetotectan (from Bresciani, 1965)

Free-living barnacle nauplii typically have a smooth cephalic shield with prominent frontolateral horns, while in facetotectans there are no horns and the dorsal surface of the whole body is covered in ridges, dividing it into plates, giving it a faceted appearance, reminiscent of the surface of the flotation collar of the parasitic rhizocephalan barnacle Peltogaster paguri. The ridges on the lateral sides of the cephalic shield form particularly elongated plates (Figs. 1B, 2).
Depending on species and stage, there can be differing arrangements of rather rudimentary caudal and other furcal spines on the hindbody (Fig. 1B, C). There are three pairs of anterior limbs (Fig. 1A), uniramous (each one branch) antennules and biramous (each two branches) antennae and mandibles. A flap-like labrum covers the mouth, attached at the anterior edge of the mouth.


Fig. 2. Photograph of a facetotectan nauplius cast ( 0.47 mm long $\times 0.23 \mathrm{~mm}$ wide), dorsal view, from which a cyprid emerged. From culture at Plymouth.

The alimentary system has been described for some early nauplii by Elofsson (1971). These did not have an anus, but the glandular tissue of the labral gland and mid-gut epithelium combined with the muscular oesophagus seem to imply planktotrophic feeding. Feeding nauplii have been noted by Kolbasov \& Høeg (2003), but no evidence of food internally was observed in any of the nauplii sampled at Plymouth, all appearing to have large lipid stores, suggesting lecithotrophy. Lecithotrophy is also suggested by a reduction observed in size following moults, indicating diminishing reserves.
Nauplii have an anterior, central naupliar eye (Fig. 1A) below the cephalic shield and cyprids a naupliar eye and paired lateral compound eyes (Fig. 1D). The cyprid develops internally in the late naupliar stages and in at least one species sampled at Plymouth, naupliar and also cyprid eyes were clearly visible, even in the stage before the final nauplius.
In free-living barnacle cyprids, the body is largely enclosed in a bivalve carapace, but in facetotectans the cephalic shield is not bivalved and only partially covers the body (Fig. 1D, E). The only obvious cephalic appendages are the antennules. 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 limb pairs (Fig. 1E).

Recorded: PMF, not recorded. L4, not recorded. Nauplii first noticed in inner Plymouth Sound in May 2009. Millbay Marina, Plymouth, found all year round since May 2009, numbers lowest December - March. Almost certainly distributed around all European coasts.
Size: Nauplii from Plymouth samples $\sim 0.31-0.49 \mathrm{~mm}$ in length; cyprids 0.31 mm in length.
Further information: Bresciani, 1965; Schram, 1970,1972; Schram, 1986; Grygier, 1991; Kolbasov \& Høeg, 2003; Belmonte, 2005; Glenner et al., 2008; Pérez-Losada et al., 2009; Kirby, 2010.

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PHYLUM ARTHROPODA: Subphylum Crustacea: Class Maxillopoda: Subclass Thecostraca:

## Infraclass Cirripedia:

Adult cirripedes (barnacles) are sessile and found attached to a wide range of inanimate surfaces in the sea, both fixed and free-floating. They can also attach externally to living organisms, e.g. seaweeds, hydroids, crabs, turtles or whales, and some are burrowers or parasites. Adults are particularly common in the intertidal zone and their larvae often dominate inshore plankton during their breeding season. There are three cirripede superorders with members recorded in the PMF:
Superorder Thoracica - Orders Sessilia, Lepadiformes and Scalpelliformes.
Superorder Acrothoracica - Order Lithoglyptida.
Superorder Rhizocephala - Order Kentrogonida.

## Development

Apart from parasitic species, mature cirripedes are typically hermaphroditic, but normally crossfertilise. Embryos develop within the ovaries and are released in high numbers as nauplius larvae (Figs. 1A, 2). In at least some parasitic and Scalpelliformes species, the nauplii are retained and released as the later developmental stage, the cyprid larvae (Fig. 1B). Nauplii superficially resemble copepod nauplii and also moult through a series of naupliar stages, from four to six depending on species, increasing in size between each (Fig. 2). They can easily be distinguished from other crustacean nauplii by the presence of two prominent frontolateral horns on their characteristically rounded cephalic shield (carapace). At least the first nauplius stage (N1) is lecithotrophic, non-feeding, obtaining enough nutriment from the yolk to carry it through to the second stage when it can start feeding in the plankton. However, in some groups all the naupliar stages are lecithotrophic.


Fig. 1. Typical barnacle larval stages (A from Hoek, 1909; B from Burrows et al., 1999).
In N1 the horns are typically folded back against the cephalic shield (Fig. 2B) or extend laterally, pointing in a more anterior direction in later stages. Duration of N1 is very short, so it is less frequently taken in samples. The horns may initially be closed at the tips, opening (sometimes referred to as splitting) in later stages, although some species appear to have open tips from N1. The length and the direction the horns point varies between species. There are other prominent structures that may develop to different degrees, centrally on the posterior of the nauplii. There is typically an upper, dorsal thoracic spine (Fig. 1A) that starts off as part of the cephalic shield, generally separating from the shield in N4 (Fig. 2B, C). Depending on species and stage, a pair of marginal spines may also develop on the posterior of the cephalic shield. Below the thoracic spine is an abdominal process (Fig. 1A, 2C) that extends from the thorax and typically ends in a two furcae or rami. Both the thoracic spine and the abdominal process can be spiny and in lepadiform nauplii the thoracic spine can be very long. Some nauplii can also have one or two small
backwardly directed spines dorsally on the cephalic shield, while some lepadiform nauplii of Superorder Thoracica characteristically have very long single dorsal spines (Fig. 4C). These latter nauplii can also have additional spines on the cephalic shield margin in later stages.
Nauplii typically have a prominent anterior naupliar eye (Fig. 1A). There are three pairs of biramous appendages (antennules, antennae and mandibles) that become increasingly setose at each moult, the progressive setation being useful in stage identification. The shape of the labrum, a muscular lobe covering the mouth, and whether it bears spines is also a useful identification feature.
A cyprid stage with a bivalve carapace (Fig. 1B) develops inside the last nauplius (sometimes termed metanauplius) and is released during the final moult. At least in the parasitic Rhizocephala and Acrothoracica there are separate male and female cyprids. Cyprid are heavily invested with lipid from the nauplius stages and are non-feeding. They superficially resemble an ostracod, but have different limb structure. Most have a pair of obvious, dark, compound cyprid eyes (visible in dorsal view) positioned almost a third of the way down the body, and a separate naupliar eye may also be visible (Fig. 3G). Often protruding ventrally and posteriorly from the valves may be six pairs of thoracic swimming limbs and the caudal furcae (Fig. 1B). A pair of prominent antennules with terminal, flattened attachment discs used for crawling on and exploring the substrate prior to settlement often protrude anteriorly. When a suitable substrate is found the cyprid attaches and develops into the adult.
Identification of the larvae to superorder or order is generally possible, as the different groups are reasonably distinctive, but within these groupings identification to species requires specialist experience and detailed microscopy. Southward (2008; p. 28) lists published sources of descriptions of British barnacle larval stages.

Identification of the individual stages of the commonest barnacle nauplii - Order Sessilia Before a nauplius can be identified to species, the stage (N1-N6) must be determined. Features used in stage identification, at least for Order Sessilia, are given in Figure 2.


Fig. 2. Diagnostic features used to identify the six naupliar stages of Order Sessilia. Numbers identify individual pairs of setae and spines, and indicate their developmental sequence as described in the text (A, B after Korn, 1995; C after Lang, 1980).

Stage identification features used are the sequential development of the three preaxial setae on the antennules (Fig. 2A), from one seta in N3, to three setae in N5 and N6, and the sequential development of spines on the abdominal process (Fig. 2B, C), from one pair in N2, to two pairs and a group of spines in N6.

N1: Only in this stage are the frontolateral horns usually folded back alongside the body (Fig. 2B), in all other stages they extend laterally; furcal rami rudimentary; cephalic shield tapers directly into dorsal thoracic spine.

N2: Cephalic shield still tapers directly into dorsal thoracic spine; abdominal process with the first (distal) pair of spines developed (Fig. 2B, C).

N3: First preaxial seta appears on antennules (Fig. 2A); cephalic shield still tapers directly into dorsal thoracic spine; from at least this stage frontolateral horns have open tips (Fig. 2B); abdominal process still with only the first pair of distal spines present (Fig. 2B, C).

N4: Second preaxial seta appears on the antennules (Fig. 2A); from this stage a distinct posterior border is present on the cephalic shield, separating it from the dorsal thoracic spine (Fig. 2B, C) and a pair of marginal spines may develop on the posterior shield; a second pair of spines (proximal), usually with a small median spine between, appears on the abdominal process.

N5: Third preaxial seta appears on antennules (Fig. 2A); a third pair of spines appears on the abdominal process, between the first and second pairs (Fig. 2B, C).

N6 (metanauplius): Antennules still with three preaxial setae (Fig. 2A); first and third pairs of spines remain on abdominal process, but second (proximal) pair replaced by six pairs of small spines (Fig. 2B, C). One to three days after moulting to this stage the pair of compound cyprid eyes pigment (Fig. 2B).

Further information: Lang, 1980; Korn, 1995; Arnsberg, 2001; Ross et al., 2003.

## Identification of cyprids

Carapace length and height are useful in cyprid identification, as there is wide variation between species, but there is often size range overlap. Elfimov (1995) separated cyprids into carapace length classes of small ( $<0.6 \mathrm{~mm}$ ), medium ( $0.6-1.2 \mathrm{~mm}$ ) and large ( $>1.2 \mathrm{~mm}$ ). In Superorder Thoracica, Orders Sessilia, Lepadiformes and Scalpelliformes have cyprids in all of these size classes, although in Lepadiformes they are mainly in the two larger classes, Sessilia in the two smaller classes and the greatest variability in Scalpelliformes. Cyprids from superorders Acrothoracica and Rhizocephala are mainly in the smallest size class.
Carapace shape can also be a useful tool for at least separating cyprids into their major taxonomic groupings, using mainly lateral, but sometimes also dorsal views (Standing, 1980; Elfimov, 1995; Arnsberg, 2001). However, care should be taken, as deformation can occur following preservation, and shape can vary with age and environmental conditions. Arnsberg (2001) provides a key to some common thoracican cyprids. Pigmentation can also be useful in identification, but is variable (Pyefinch, 1948). Surface ornamentation also varies between groups (Standing, 1980; Elfimov, 1995), but usually requires high magnification to observe.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Maxillopoda: Infra-class Cirripedia:

## Superorder Thoracica:

## Order Sessilia:

Order Sessilia includes the barnacles without stalks (peduncles). In the PMF 14 species are recorded of the $\sim 27$ found around the UK and Ireland (Southward, 2008). Adults are characterised by a low pyramidal structure on a roughly circular base, all formed from calcareous plates. There are two suborders, Balanomorpha with symmetrical arrangement of plates and Verrucomorpha with asymmetrical plates. Rigid wall plates surround an orifice, from which the feeding cirri emerge, protected by four plates in Balanomorpha and two in Verrucomorpha. The casts of the feeding cirri are often sampled inshore. Sessilia are the commonest barnacles found in European coastal areas, attaching in high numbers to rocks and a wide variety of surfaces. Inshore, their nauplii and cyprid developmental stages can seasonally dominate the zooplankton.

## Nauplii

Sessilia nauplii have a rounded cephalic shield with frontolateral horns (Fig. 3). At each moult, limb setation and armature of the posterior processes change as illustrated in Figure 2. In Suborder Balanomorpha, Superfamily Balanoidea, the nauplii have a tri-lobed labrum (Fig. 3A-F), although this feature may not be very obvious in some stages. A pair of marginal spines develop on the rear cephalic shield from N4.


Fig. 3. Examples of Order Sessilia larvae (A-G from Herz, 1933; H-N from Burrows et al., 1999; O from Bassindale, 1936; P from Nilssen-Cantell, 1921; Q, R from Groom, 1894).

In Balanomorpha, Superfamily Chthamaloidea, nauplii have a labrum with a single lobe (Fig. 31-M) and also differ from Balanoidea in having teeth on the end of the labrum from N2 onwards (Burrows et al., 1999), two particularly large terminal teeth from N3 onwards. The latter authors did not draw a labrum in N1 nauplii of Chthamalus stellatus or C. montagui (Fig. 3H), but Miller et al. (1989) drew smooth rounded labrums in N1 two closely related Chthamalus species, so C. montagui N1 may actually have a labrum? Chthamaloidea nauplii do not develop marginal spines on the posterior cephalic shield. The dorsal thoracic spine and abdominal process are much shorter than the cephalic shield and in N5-N6 the abdominal process is longer than the dorsal thoracic spine.
There is very little information on Verrucomorpha nauplii. The only local species, Verruca stroemia (Fig. 30), resembles Chthamaloidea in having a uni-lobed, toothed labrum (Ross et al., 2003). They resemble Order Scalpelliformes (Fig. 5) in shape of cephalic shield, rounded without posterior marginal shield spines. The frontolateral horns are of medium length and the abdominal process long in comparison to the dorsal thoracic spine, which it exceeds in length in later stages.
Keys to the identification of the nauplii of several common UK species of Order Sessilia are given by Lang (1980) and Ross et al. (2003)

## Cyprids

Standing (1980), Elfimov (1995) and Arnsberg (2001) give comparative information on identification of the cyprids of Order Sessilia. In Suborder Balanomorpha the shell profile is typically elongated, the ventral edge is straight or slightly convex, and the anterior and posterior ends are narrowly rounded or pointed (Fig. 3G). In some balanomorph species there are slight anterioventral projections, indicating remains of the frontolateral horns (Fig. 3R).
Chthamalus spp. cyprids have a short carapace with convex dorsal and ventral margins (Fig. 3N), the highest point of the dorsal curve mid-carapace. Either both the anterior and posterior ends are narrowly rounded, or the anterior one is pointed. The cyprid of the only species in Suborder Verrucomorpha recorded locally, Verruca stroemia (Fig. 3P), has an elongated carapace with narrowly rounded or slightly pointed anterior and posterior ends, and a dorsal border that is practically straight posteriorly.

Recorded: PMF, adults of Verruca stroemia O.F. Müller, 1776; Chthamalus stellatus (Poli, 1795); C. montagui Southward, 1976; Megabalanus tintinnabulum (Linnaeus, 1758)(as Balanus tintinnabulum); Balanus spongicola Brown, 1844; Balanus crenatus Bruguière, 1789; Amphibalanus amphitrite (Darwin, 1854)(as Balanus amphitrite); Perforatus perforatus Bruguière, 1789 (as Balanus perforatus); Semibalanus balanoides (Linnaeus, 1758)(as Balanus balanoides); Solidobalanus fallax (Broch, 1927); Amphibalanus improvisus (Darwin, 1854)(as Balanus improvisus); Acasta spongite (Poli, 1795); Megatrema anglicum (Sowerby, 1823)(as Pyrgoma anglicum); Elminius modestus Darwin, 1854. L4, cirripede larvae only recorded as nauplii and cyprids. MarLIN, adults of Balanus balanus (Linnaeus, 1758). Most of these species widely distributed around European coasts.
Size: Nauplii $\sim 0.3-0.8 \mathrm{~mm}$ (includes carapace and dorsal thoracic spine); cyprids $\sim 0.4-1.2 \mathrm{~mm}$.
Further information: Groom, 1894; Herz, 1933; Bassindale, 1936; Pyefinch, 1948; Knight-Jones \& Waugh, 1949; Norris \& Crisp, 1953; Jones \& Crisp, 1954; Crisp, 1962; Southward, 1976, 2008; Standing, 1980; Lang, 1980; Branscomb \& Vedder, 1982; Korn, 1995; Burrows et al. 1999; Arnsberg, 2001; Ross et al., 2003; Muxagata \& Williams, 2004; Southward et al., 2004; Larink \& Westheide, 2006.

## Order Lepadiformes:

Adult Lepadiformes have a naked stalk that anchors them to the substrate and holds the head (capitulum), which bears five plates, at varying distances from their point of attachment, hence their common name "stalked barnacles". They are typical of warmer waters, but currents often carry them to western European shores on floating debris and they can also be introduced on the hulls of ships etc.
There are seven species recorded in the PMF, of the 12 species that have been found around the UK and Ireland (Southward, 2008). Some adults were noted as being in breeding condition, so while larvae have not been recorded at Plymouth, they could potentially be sampled, as evidenced by the record of a larva thought to be of Conchoderma auritum, collected at Southampton (Muxagata \& Williams, 2004).

C) Dosima fascicularis, nauplius 6

D) Lepas sp nauplius 6



F) Lepas sp., cyprid lateral

G) Conchoderma auritum, cyprid lateral


Fig. 4. Lepadiform nauplii and cyprids (A, E from Hoek, 1909; B-D, F from Trégouboff \& Rose, 1957; G after Dalley, 1984).

## Nauplii

At least some of the features of the setation etc. used in identifying the naupliar stages of Order Sessilia nauplii (Fig. 2) also apply to this order. One difference is that late lepadiform nauplii have two, rather than three, preaxial setae on the antennules. They differ from most of Order Sessilia in having a labrum that is a single lobe and bears spines. However, they are more easily distinguishable from other groups because of their unique shape (Fig. 4A-D). Their frontolateral horns are usually much longer than in other groups. In N1 the horns are folded close to the body (Fig. 4A), similar to balanomorph N1, but the horns are almost as long as the nauplius. In this stage the limbs, abdominal process and dorsal thoracic spine are rudimentary. From N2 a dorsal thoracic spine develops that is more than twice the body length (Fig. 4B, C). From N3 the cephalic shield develops spines on the margins. The shield margin becoming progressively more ornate in later stages and a large dorsal spine also appears (Fig. 4C, D). The three pairs of limbs bear very long setae that are generally covered with setules. From N4 the cephalic shield is freed from the tail process, similar to Sessilia. The nauplii tend to be transparent and very large, increasing around ten times in length between N1 and N6.

## Cyprids

The lepadiform cyprid is large and not remarkably different from those of other cirripede groups (Fig. 4E-G). In some species there are slight anteriolateral projections, indicating remnants of the frontolateral horns, while Lepas pectinata has very prominent anteriolateral horns. Most have a lateral profile characterised by a lack of angularity and points, except at the posterior end. The front is straight or rounded, the dorsal margin evenly convex and the ventral margin straight or sinuous (Elfimov, 1995). Lepas and Conchoderma have very different shapes of carapace. The frontal edge of Lepas is broadly rounded (Fig. 4F), the convex dorsal edge has a slight angle in its posterior part and the posterior part is pointed. Conchoderma (Fig. 4G) has an almost straight frontal edge, a slightly convex dorsal edge and a narrowly rounded posterior end.

Recorded: PMF, adults of Dosima fascicularis Ellis \& Solander, 1786 (as Lepas fascicularis); Lepas anatifera Linnaeus, 1758; L. anserifera Linnaeus, 1767; L. pectinata Spengler, 1793; L. hilli Leach, 1818; Conchoderma auritum (Linnaeus, 1758); C. virgatum Spengler, 1789. L4, not recorded. Most likely to occur on western European coasts.
Size: Nauplii $\sim 0.3-6.0 \mathrm{~mm}$ (includes carapace and dorsal thoracic spine); cyprids $\sim 1.2-2.0 \mathrm{~mm}$. Further information: Hoek, 1909; Trégouboff \& Rose, 1957; Broch, 1959; Bainbridge \& Roskell, 1966; Dalley, 1984; Moyse, 1987; Elfimov, 1995; Arnsberg, 2001; Muxagata \& Williams, 2004; Southward, 2008.

## Order Scalpelliformes:

Adults have a short stalk covered with tiny plates and more than five plates on the capitulum. Scalpellum scalpellum (Linnaeus, 1767) is found attached to hydroid and bryozoan colonies etc. and is the only species native to the southern UK. A warmer water scalpellid species, Pollicipes pollicipes, has occasionally been found around southern UK and southern Ireland (Southward, 2008), but colonies may not survive long out of their normal range. This species is harvested around Spain and Portugal and consumed in restaurants as "percebes".

## Nauplii

Adult Scalpelliformes fall into the category of "stalked barnacles", but the nauplii do not have spiny cephalic shields like lepadiform nauplii, more closely resembling Sessilia or Acrothoracican nauplii. Some scalpellids release larvae as cyprids, but both the species described here have six free naupliar stages that spend more than ten days in the plankton (Buhl-Mortensen \& Høeg, 2006). Nauplii have rounded, convex cephalic shields, which in most stages are as wide as they are long (Fig. 5A). In P. pollicipes the cephalic shield becomes freed from the dorsal thoracic spine from N4 (Fig. 5C-H), similar to Sessilia. However, Figure 5A appears to show that in S. scalpellum there is no dorsal thoracic spine on the carapace, the abdomen emerging from below the carapace, similar to Acrothoracican nauplii, but this may not be the case. Most scalpellid nauplii are thought to be lecithotrophic and have features related to this type of development, such as retention of swimming appendages and reduction of feeding ones. This is certainly the case with the N1 of S. scalpellum (Fig. 5A), which has reduced labrum and limb setae (Korn, 1995; Nilssen-Cantell, 1978). However, $P$. pollicipes has been observed feeding from N2 (Molares et al., 1994) and the labrum is well developed. The labrum is a single lobe and in P. pollicipes is armed with one pair of teeth from N2 and two pairs in subsequent stages. In $P$. pollicipes N1-N3, the abdominal process is shorter than the dorsal thoracic spine, of similar length in N4, and longer in N5 and N6 (Fig. 5C-H). This is an unusual developmental sequence.


Fig. 5. Scalpelliform larvae (A from Bassindale, 1936; B outline of image from Kaufmann, 1965; C-I from Molares et al., 1994, as Pollicipes cornucopia)

## Cyprids

In Scalpellum scalpellum the cyprid carapace in lateral view is highest towards the anterior, quite rounded dorsally and straighter ventrally (Fig. 5B). Anteriorly it is rounded and comes to a blunt point posteriorly. In Pollicipes pollicipes the shape is quite different (Fig. 5I). The anterior margin is broadly rounded and the posterior end narrowly rounded. The dorsal and ventral edges are convex and the carapace reaches its highest point towards the anterior. There is a large, visible cyprid eye, but no obvious groups of oil droplets as seen in some of the balanomorph cyprids.

Recorded: PMF, adults of Scalpellum scalpellum. L4, cirripede larvae only recorded as nauplii and cyprids. S. scalpellum widespread in Europe. MarLIN, adults of Pollicipes pollicipes in southwest UK and southern Ireland.
Size: Nauplii $\sim 0.25-0.70 \mathrm{~mm}$ (includes the carapace and dorsal thoracic spine); cyprids $\sim 0.40-$ 0.70 mm .

Further information: Bassindale, 1936; Broch, 1959; Kaufmann, 1965; Moyse, 1987; Molares et al., 1994 (as Pollicipes cornucopia); Elfimov, 1995; Korn, 1995; Arnsberg, 2001; Muxagata \& Williams, 2004; Buhl-Mortensen \& Høeg, 2006; Southward, 2008.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Maxillopoda: Infra-class Cirripedia:

## Superorder Acrothoracica:

## Order Lithoglyptida:

Adults are tiny parasites that never develop the typical barnacle plates; the body is instead covered in chitinous teeth. The sexes are separate and only the adult female can feed. The immature adult female burrows into gastropod mollusc shells, or shells inhabited by hermit crabs, using chemicals and also their carapace (Gotelli \& Spivey, 1992), then occupies the burrow. Tiny male cyprids enter the female burrow, attach to the surface of the female ovarian disc and moult into adults, reaching sexual maturity within a few days of attachment. Most species brood their larvae and release them at the cyprid stage, but Trypetesa lampas Hancock, 1849, the only species recorded in the PMF, releases a nauplius. Complete development is very short, six to ten days (Turquier, 1967). $T$. nasseroides Turquier, 1967 is the only other species from this order that has been recorded around the UK and Ireland (Southward, 2008) and this also releases a nauplius (Turquier, 1967).

## Nauplii

There are only four naupliar stages before the cyprid and these are quite characteristic in appearance (Fig. 6A-E). They are lecithotrophic, and as they do not feed there is no mouth or labrum. They have short frontolateral horns that are open at the tip from N1. Spines do not develop on the posterior carapace, which is rounded. The abdomen in all stages is extended into a long point, corresponding to the abdominal process. It is covered in small spinules, except at the base, with two strong, slightly curving spines ventrally near the base.

## Cyprids

The carapace is very narrow laterally and in lateral view has a spindle or elongated, oval shape with an anterior rounded end (Fig. 6F), and a narrower, pointed posterior end (Kolbasov \& Høeg, 2007). The dorsal edge is curved, the ventral margin slightly concave. The shape is reminiscent of rhizocephalan cyprids (Fig. 7E). Cyprid and also naupliar eyes are usually visible.


Fig. 6. Acrothoracican larvae. Trypetesa lampas (from Kühnert, 1934).
Recorded: PMF adults and nauplii of Trypetesa lampas Hancock, 1849 (as Alcippe lampas). L4, cirripede larvae only recorded as nauplii and cyprids. Probably most European coasts.
Size: T. lampas nauplii $\sim 0.45-0.60 \mathrm{~mm}$; cyprid $0.60-0.65 \mathrm{~mm}$.
Further information: Kühnert, 1934 (as Alcippe lampas); Turquier, 1967; Schram, 1986;
Arnsberg, 2001; Muxagata \& Williams, 2004; Kolbasov \& Høeg, 2007; Southward, 2008.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Maxillopoda: Infra-class Cirripedia:

## Superorder Rhizocephala:

There are two orders in Superorder Rhizocephala, Kentrogonida and Akentrogonida, but only species from the former have been recorded in the PMF, seven of the 22 species that have been recorded from around the UK and Ireland (Southward, 2008). Høeg (1995) has reviewed the complex biology and life cycle of the Rhizocephala.

## Order Kentrogonida:

Kentrogonidan barnacles mainly parasitise crustaceans such as shrimps and crabs, their morphology and life cycle making these perhaps the most spectacular and unusual of parasitic organisms. Depending on species, either nauplius or cyprid larvae are released. Where nauplii are released there is traditionally thought to be four stages before the cyprid, but up to six have been suggested (Rybakov et al., 2002). While at least some species have a high reproductive potential, nauplii are usually only sampled in low numbers.
Only the free-living stages show any resemblance to non-parasitic barnacles. The female cyprid larva typically attaches to its crustacean host via its antennae. It metamorphoses into a larva called a kentrogon, which produces embryonic cells that penetrate throughout the host forming root-like branches called the sacculina interna. A large mass without appendages and containing the genital system develops externally. When this is mature it is called the sacculina externa. This attracts male cyprids for fertilisation. These become implanted as dwarf males and nauplii are subsequently released. There are three families in Order Kentrogonida: Sacculinidae, Peltogastridae and Lernaeodiscidae.

## Nauplii

All stages of Kentrogonida are lecithotrophic, so as is usual in these circumstances, they have reductions in the labrum, in the setation on the appendages and lack a mouth.
Sacculinidae nauplii appear to go through four stages and show some of the typical barnacle nauplius features (Fig. 7A, B). The labrum is simple with a pore opening at the tip. The frontolateral horns were drawn as open at the ends in the N1 by Delage (1884; Fig. 7A), but Collis \& Walker (1994) considered they were closed with a spine protruding. N1 has two short, pointed projections on the posterior carapace and the body is quite rounded, but later stages are more elongate. From N2 the frontolateral horns are open and the posterior projections are longer, covered in small spinules. There are also areas of spinules on the ventral and dorsal body cuticle (Fig. 7B). In N3, paired and also single spines appear on a process that is probably a vestigial ventral thoracic process (Fig. 7C), the spines even more evident in N4 (Fig. 7D). The cyprid thoracic limbs develop within the N4, the ends of their setae squashed together into the ventral process.
Peltogastridae and Lernaeodiscidae nauplii have features of other cirripede nauplii (Fig. 7F, J, K), but differ in having an oval collar around the body from N2 (Fig. 7G, H, K, L) in all species investigated by Høeg et al. (2004). This collar is situated above the carapace and consists of an exceedingly thin transparent cuticle, rounded anteriorly and more pointed posteriorly. The collar is connected to the general body cuticle along a continuous narrow ridge. In nauplii of some species e.g. Peltogaster paguri (Fig. 7G; front cover), the collar is very large $\sim 0.57 \mathrm{~mm}$ long and 0.36 mm wide in the N4, its surface ornamented by a very conspicuous reticulated pattern of ridges (Veillet, 1943; Schram, 1972; Høeg et al., 2004). Transmission electron microscopy shows that the collar is formed in an unexpanded state beneath the old cuticle and it must therefore be inflated at or immediately after each moult (Høeg et al., 2004). The collar must have a considerable influence on the flotation properties of the nauplius, both when swimming and passively sinking. In Triangulus galatheae (Fig. 7K, L) the collar is smaller, with a smooth surface, making it difficult to see under a light microscope.

## Cyprids

Rhizocephalan cyprids are small compared with free-living cirripede cyprids and males are usually larger than females. They have a shape reminiscent of acrothoracican cyprids. The carapace in lateral view has a spindle or elongated, oval shape (Fig. 7E, I), with an anterior bluntly pointed end and a much narrower posterior end. The carapace of the cyprids of both Sacculina carcini and Peltogaster paguri are sparsely covered with quite long, backwardly directed, fine setae (not drawn in Fig. 7), particularly in the latter species. They do not appear to have cyprid eyes, but some have
a naupliar eye (Glenner et al., 1989). Delage (1884) drew a naupliar eye in S. carcini (Fig. 7E), but Glenner et. al. (1989) stated that neither it nor $P$. paguri have one?


Fig. 7. Rhizocephalan larvae (A, B, E from Delage, 1884; C, D after Collis \& Walker, 1994; F from Nilsson-Cantell, 1921; G, H, J-L from Veillet, 1943; I outline of photograph from Glenner et al., 1989).

Recorded: PMF, adults parasitic on various crustaceans: Sacculinidae - Sacculina carcini Thompson, 1836; Drepanorchis neglecta (Fraisse, 1877); Peltogastridae - Galatheascus striatus Boschma, 1929; Peltogaster paguri Rathke, 1842; Peltogaster curvatus Kossmann, 1873; Peltogastrella sulcata (Lilljeborg, 1859)(as Chlorogaster sulcatus and Peltogaster socialis); Lernaeodiscidae - Triangulus galatheae (Norman \& Scott, 1906)(as Lernaeodiscus galatheae). L4, Peltogaster paguri nauplii. Millbay Marina, Plymouth, Sacculina carcini nauplii, even in winter. Most European coasts.
Size: Nauplii $\sim 0.2-0.6 \mathrm{~mm}$; cyprids $\sim 01-0.4 \mathrm{~mm}$.
Further information: Delage, 1884; Veillet, 1943; Schram, 1972; Glenner et al., 1989; Collis \& Walker, 1994; Høeg, 1995; Høeg \& Lützen, 1995; Arnsberg, 2001; Høeg et al., 2004; Muxagata \& Williams, 2004; Larink \& Westheide, 2006; Southward, 2008.

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PHYLUM ARTHROPODA: Subphylum Crustacea: Class Maxillopoda:

## Sub-class Copepoda

Copepoda is one of the most diverse and studied marine zooplankton groups, so more information on it is provided than for other groups. Descriptions of adult copepods included here are mainly for planktonic species (including some brackish water species), but also a few bottom-living and parasitic species that are sometimes sampled; also a few species that have not been recorded off southern Britain, but have been found in adjacent sea areas. The developmental stages of copepods found in the plankton (eggs to adults) are often studied, so these are also described.

## Classification

The marine species of Sub-class Copepoda are currently divided into eight orders:
Infraclass Progymnoplea, containing only Order Platycopioida.
Infraclass Neocopepoda, which is divided into two superorders containing seven orders.
Superorder Gymnoplea - Order Calanoida.
Superorder Podoplea - Orders Cyclopoida, Harpacticoida, Misophrioida, Monstrilloida, Siphonostomatoida and Mormonilloida.

The WORMS classification lists a further podoplean order, Poecilostomatoida. However, current evidence shows that these should be merged within Order Cyclopoida (Boxshall \& Halsey, 2004) and this classification has been followed here.
Some Order Platycopioida species are recorded from the Norwegian (Sars, 1911) and French coasts (Brylinski, 2009) and Mormonilloida from deep water west of Ireland (Rose, 1933), but are rare and have not been found off southern Britain, so these orders are not included here. Misophrioida are not pelagic, living in the bottom sediments, so are unlikely to be sampled, but the only species recorded in northern Europe is included. There are only a few species of the parasitic Monstrilloida recorded off southern Britain and most are included. The free-swimming stages and adults of the parasitic Siphonostomatoida are rarely sampled, so only some examples are given.

## Developmental stages

In many zooplankton studies it can be important to be able to identify the various developmental stages of copepods, from eggs to adults, and for many species stage descriptions are available (e.g. Koga, 1968, 1984; Björnberg, 1972; Izawa, 1987; Ferrari, 1988; Mauchline, 1998; Conway, 2012). However, if descriptions are not available, it is possible, at least in simple copepod communities, to identify and separate out the stages of the species you are interested in and compile descriptions. Eggs can often be identified by size and appearance. Separation of copepod nauplii and copepodite stages is made easier because of the crustacean characteristic of regular moulting and rapid growth between stages, often resulting in no overlap in length between successive stages, so it is usually possible to roughly sort them just on size. While sizes can vary in the same sample and also seasonally, the range is usually quite limited.

## Copepod egg identification

Copepod development starts from an egg (Fig. 1), which can be spherical e.g. Calanus helgolandicus, spherical in a large gelatinous case e.g. Subeucalanus crassus or, spherical but covered in spines e.g. Centropages typicus, etc.


Fig. 1. Examples of a selection of free-spawned calanoid copepod eggs: 1, Calanus finmarchicus; 2, C. finmarchicus variant; 3, C. helgolandicus; 4, C. hyperboreus; 5, Undinula vulgaris; 6, Temora discaudata; 7, Labidocera acuta; 8, Pontellopsis yamadae; 9, Eucalanus elongatus; 10, E. elongatus central egg; 11, Subeucalanus crassus; 12, S. crassus central egg; 13, Centropages hamatus; 14, C. tenuiremis (as C. yamadai; 15, C. abdominalis; 16, C. furcatus; 17, Tortanus discaudatus ventral; 18, T. discaudatus lateral (after Koga, 1973).

Some of the eggs in Figure 1 are those of non-European or oceanic species, included to show the variability in appearance. Size is crucial information for identifying eggs. Egg diameters of some common European copepods are given in Table 1. Chiba (1956) lists the diameters of 55 species of copepods, but mainly ones not found in northern European waters.

Table 1. Diameter of the eggs of some copepod species recorded from the Plymouth area.

| Species | Egg diameter $(\mu \mathrm{m})$ | Source |
| :--- | :---: | :---: |
| CALANOIDA |  |  |
| Metridia lucens | $170-200$ | ? |
| Calanus finmarchicus | $135-180$ | Bainbridge \& McKay (1968); Valentin (1972) |
| Calanus helgolandicus | $153-191$ | Own measurements |
| Calanoides carinatus | $190-225$ | Hirche (1980) |
| Pseudocalanus elongatus | $100-133$ | Corkett \& McLaren (1969); Frost, (1989) |
| Paracalanus parvus | $50-70$ | Valentin (1972); Pillar (1984) |
| Acartia clausi | $72-84$ | Valentin (1972); Uye (1982); Castro-Longoria (2001) |
| Candacia armata | $170-190$ | Bernard (1964, 1965) |
| Centropages typicus | 70 | Own measurements |
| Centropages hamatus | $62-80$ | Chen \& Marcus (1997); Lindley (1990) |
| Temora longicornis | $76-86$ | Corkett \& McLaren (1970); Castellani \& Lucas (2003) |
| Temora stylifera | 80 | Valentin (1972) |
| Eurytemora velox | $90-110$ | Conway et al. (1994) |
| Eurytemora affinis | $73-98$ | Conway et al. (1994) |
| CYCLOPOIDA |  |  |
| Oithona similis | 56 | Own measurements |
| Oncaea venusta | $40-60$ | Conway et al. (1994); Izawa (1987) |
| Corycaeus anglicus | $54-60$ | Conway et al. (1994) |
| HARPACTICOIDA |  |  |
| Euterpina acutifrons | $54-73$ | Conway et al. (1994) |
| Microsetella norvegica | 40 | Own measurements |

Depending on the copepod order and genus, eggs may be spawned directly into the sea, held in single or paired egg sacs, an egg mass without an enclosing membrane, or in a matrix supporting the eggs. Large numbers of small eggs may be carried, or a few large ones. Fine-mesh zooplankton nets usually catch many eggs, some of which may be free-spawned, detached enclosed in sacs, or individually detached from the female.
Appearance of the egg can change as it develops. In Calanus helgolandicus the newly laid egg is squeezed out like a drop of oil and then quickly becomes spherical. It is pale golden with a fine granular yolk and once the cells start dividing it becomes darker and more granular in appearance. Matthews (1964) described the eggs of Xanthocalanus fallax G.O. Sars, 1903, a species found in Norwegian waters, as being long and thin when laid, with irregular ends where they had been broken off the string of extruded eggs. Within two minutes they were spherical and a membrane was forming. Surface ornamentation develops in some species after the eggs are laid. Initially they may have a smooth surface, but then develop spines e.g. Candacia armata (Bernard, 1965). Few copepod eggs seem to be sampled at a late stage of development, perhaps because egg development time is very short (typically within 24 hours), or possibly because late development eggs damage easily and the nauplius emerges prematurely.
An interesting characteristic, of at least some copepod eggs, is that the chitinous egg membrane protects them from digestion (Conway et al., 1994), the eggs remaining viable even after several hours passing throught the guts of larval fish (front cover), a remarkable survival capability.

## Copepod nauplius stages

When the egg hatches a nauplius stage emerges, which is the typical crustacean larva. The commonest non-copepod nauplii sampled are usually those of barnacles (Cirripedia), but barnacle nauplii have obvious fronto-lateral horns on the carapace, readily distinguishing them (Page 24). A typical calanoid nauplius is shown in Figure 2A as an example of their morphology. For clarity, in many figures in identification texts, some appendages, or components of the appendages such as setae, are often not drawn, and where paired appendages are identical, often only one pair is drawn, which sometimes confuses people. The morphology of the nauplii developmental stages of the main free-living species all follow a generally similar pattern.
As with other crustaceans, the nauplius has an external skeleton that is moulted between each stage. The nauplii of most free-living copepods typically moult five times until they reach the final sixth stage (stages N1-N6). The sixth nauplius stage moults into the first copepodite stage (Co1),
the stage from which the adult features progressively develop. Some copepods, even a small number of Calanoida, have fewer than six nauplius stages, but it is mainly parasitic species that deviate from the norm (e.g. Snodgrass, 1956), to the extent that in some species there are none, the Co1 hatching directly from the egg (e.g. Perkins, 1983). Nauplii of parasitic species are often non-feeding, their development sustained by lipid reserves (lecithotrophic nauplii) and this is often associated with lack of a mouth, anus and some appendages, and by abbreviated development (Dahms et al., 2006). Some calanoid copepod nauplii also appear to be non-feeding. The nauplii of Xanthocalanus fallax hatches with a large enough yolk reserve to sustains all the nauplii stages until the Co1 (Matthews, 1964). Probably all free-living copepods found off southern Britain have six nauplius stages. Lovegrove (1956) states that there are usually only five nauplius stages in harpacticoids, but this is not correct.
The N1 body is composed of a small number of undefined somites (the term somite is used for major body divisions, while segment is used for divisions of appendages). There does not appear to be an established terminology for different regions of the nauplius body, so a very simple, descriptive scheme (e.g. posterior body) is used here. The nauplius body is largely covered by a cephalic shield (Fig. 2A), at least in early stages (Dahms et al., 2006), while in later nauplii the posterior body may extend to differing distances beyond the shield, depending on the copepod order. On hatching, the N1 typically has three pairs of appendages. The anterior pair are the antennules (A1), each of which are uniramous (single branched). The second and third pairs are the antennae (A2) and mandibles (Md), each limb of which is biramous (two branches). The body is not visibly partitioned into somites, but the presence of three pairs of appendages indicates that at least three are present. Additional somites and pairs of appendages appear in the later stages, although in some orders no further appendages develop. Nauplii with three pairs of appendages are sometimes termed orthonauplii and then metanauplii when additional ones appear. A single median naupliar eye is usually present and a ventral flap-like labrum that covers the mouth.
In N1-N3 only the first three pairs of appendages are present and these acquire further setae and or segments at each moult, while in the caudal region additional setae or spines appear. A spine is defined as a more or less rigid element that tapers throughout its length, while a seta is flexible and usually thinner than a spine, with edges more or less parallel throughout its length. From N4-N6 the remaining paired appendages, maxillules ( $\mathrm{M} \times 1$ ), maxillae ( $\mathrm{M} \times 2$ ) and maxillipeds ( $\mathrm{M} \times \mathrm{p}$ ), additional somites of the posterior body and two pairs of rudimentary swimming legs (P1 and P2) usually progressively appear.


Fig. 2. Schematic calanoid nauplius and antennule (A after Koga, 1984; B after Mauchline, 1998).

The naupliar appendages develop successively only if all are destined to be present, as typical of most calanoids and some harpacticoids (Dahms et al., 2006). One calanoid exception is the oceanic species Rhincalanus nasutus, where 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. P1 and P2 are usually present in N6 of all species, but in Cyclopoida and Siphonostomatoida, although P1 and P2 are usually present in N6, the maxilla and maxillipeds never develop externally during the naupliar phase.
In calanoid nauplii at least, the posterior body is sometimes separated by a cleft into two caudal lobes or rami (Faber, 1966; Dahms et al., 2006), as found in later stages of Temora spp. (Fig. 3A). It should be noted that Björnberg (1986) suggested that environmental conditions may alter the morphology of individual naupliar stages.
Each of the naupliar stages can thus be recognised by developmental changes between moults. The number of setae on the distal segment of the A1 (Fig. 2B) can be used in identification (see Table 2), as there is an increasing number in progressive developmental stages. A setal formula has sometimes been used for staging nauplii (e.g. Ogilvie, 1953; Klein Breteler, 1982), which gives the number of setae either side of a thinner or aesthetasc seta (Fig. 2B). However, in some species this aesthetasc seta may not be present or obvious and sometimes spines rather than setae may also be present, so this technique has problems. It is difficult and time consuming counting setae in later stages when there are many, so most researchers base their nauplii identification on a combination of A1 setae number in the early stages (when they are few and easy to count), the progressive appearance, from N4, of appendages additional to the initial three, and number and also arrangement of the caudal spines (Faber, 1966).

## Identifying nauplii of orders Calanoida, Cyclopoida and Harpacticoida

It can be difficult in mixed samples to positively identify to which species a copepod nauplius belongs unless females are isolated and their eggs hatched, but nauplii can usually be identified, at least to the order level, just by their overall appearance (Fig. 3). Mauchline (1998) lists some 83 species of calanoid nauplii that have been described. Oberg (1906), Ogilvie (1953), Lovegrove (1956), Björnberg (1972), Koga (1984) and Li \& Fang (1990) give illustrations of a large range of different nauplii. Individual nauplii have also been described in many papers, but there have been a limited number of papers giving any information on how to discriminate between the nauplii of the main orders. Izawa (1987) has described the features of the eggs and nauplius stages of some cyclopoid copepods. Fornshell (1994) lists the individual features of calanoid, cyclopoid and harpacticoid nauplii and Fornshell (2005) gives a key to the main orders and stages of copepod nauplii. Dahms et al. (2006) gives a key to separate the nauplii of a range of crustaceans, including the main copepod orders. All this information is collated below.

## Calanoid nauplii

Shape: The cephalic shield is deep, rounded dorsally in lateral view and the posterior body characteristically increasingly protrudes beyond the cephalic shield, becoming more elongated with each moult, e.g. Temora sp. (Fig. 3A). The posterior body is particularly long in species in which the adult is elongated, such as Subeucalanus crassus (Fig. 50E), but is very short in a few species, e.g. Acartia sp. (Fig. 3B). It is often bent ventrally, especially in later stages (apart from species with short bodies).
Caudal region: In dorsal view the caudal region varies from being reasonably bilaterally symmetrical (Fig. 3B) to being quite asymmetrical (Fig. 3A). The caudal armature initially consists of long, fine setae, later short spines and sometimes also setae. The arrangement of armature is usually bilaterally symmetrical, but the spines/setae are often of different sizes on each side and corresponding setae sometimes point in different directions (Fig. 3A).
Appendages: The A1 are generally directed forwards, three-segmented with a broad or long distal segment. The endopod of the mandible is one-segmented (Fig. 4A). The labrum is large and develops spinules. Most calanoid nauplii develop the full set of appendages by N6.

## Cyclopoid nauplii

Illustrations are given of two cyclopoid nauplii, Oithona sp. and Corycaeus sp. (Fig. 3C, D).

Shape: In ventral view usually ovoid or pear-shaped and dorsoventrally flattened, the posterior body hardly protruding beyond the cephalic shield in all stages. They are mainly small as adults, so their nauplii are also mainly small, with generally less robust appendages than calanoid nauplii.
Caudal reaion: The caudal region is bilaterally symmetrical, as is the caudal armature in arrangement of setae and spines and these are usually of identical sizes on both sides, the setae often long and fine.
Appendaqes: Compared with calanoids, the A1 usually point forwards less often. The endopod of the mandible has two segments (Fig. 4B, C). The maxillae and maxillipeds never develop externally during the naupliar phase, although at least rudimentary P2 and P3 are present in N6.


Fig. 3. The six naupliar developmental stages and some individual stages of a range of copepod orders (A-E from Koga, 1984; F from Diaz \& Evans, 1983; G from Nicholls, 1935; H from Gurney, 1930; I from Gurney, 1933a; J from Malaquin, 1901; K from Schram, 2004).

## Harpacticoid nauplii

There are relatively few pelagic harpacticoid copepods and non-pelagic species are usually only sampled in shallow waters, but the nauplii of both can be pelagic and thus collected in nets.
Shape: In ventral view the body is usually broad, disc-shaped and dorsoventrally quite flattened (Fig. 3E, F). Similar to cyclopoids, the posterior body usually hardly protrudes beyond the cephalic shield.
Caudal reaion: The caudal region is bilaterally symmetrical, as is the caudal armature in most harpacticoids (Fig. 3E, F), but in two non-pelagic families (Canuellidae and Longipediidae) there is a centrally located, unpaired, strong caudal spine. Two species of Canuellidae and two species of Longipediidae have been sampled off Plymouth. Longipedia minor Scott, 1893 has the typical central spine of these two families and the anterior carapace is rounded in all stages (Fig. 3H), while L. coronata Claus, 1863 also has the central spine, but in lateral view from N 2 , also has a conspicuous, curving forward projection of the cephalic shield (Fig. 3G).
Appendages: A1 often held back alongside the body. The endopod of the mandible has only one segment (Fig. 4D). The maxillae and maxillipeds do not generally develop until N6, when the full set of appendages may be present, although some may be very rudimentary. Many have specialized features on their A2 or mandibles, adaptations to their particular niche.


Fig. 4. Mandibles of calanoid, cyclopoid and harpacticoid nauplii, to compare segmentation of the endopod. (A, C from Björnberg, 1972; B from Uchima, 1979; D from Diaz \& Evans, 1983).

Identifying nauplii of orders Misophrioida, Monstrilloida and Siphonostomatoida
Adults of all these orders are usually rare in plankton samples, so their nauplii will be correspondingly sampled in low numbers. Additionally, many species have a reduced number of naupliar stages, or the nauplii are only free-swimming for a very short period, which will enhance their rarity. While the simple, early stage nauplii of other orders can be difficult to identify to order, nauplii in these three orders are lecithotrophic, their bodies characteristically packed with lipid.

Misophrioida: The only misophrioid species that has been sampled at Plymouth, and the only European species, is Misophria pallida, which lives in and close to the sea bottom. The female carries two to four large eggs for a considerable time before they hatch and the nauplii that emerge (Fig. 31) are non-feeding and moult directly into Co1 within a day (Gurney, 1933a). Only the first three pairs of appendages develop. The A2 and mandibles are large and the endopod of the mandible has two segments. Caudal armature consists of a pair of sub-distal long setae and a further shorter distal pair. No mouth or naupliar eye is reported and the body contains much yellow lipid.

Monstrilloida: Very few illustrations (Malaquin, 1901) or photographs (Grygier \& Ohtsuka, 1995) of monstrilloid nauplii seem to be available. There appears to be only a single, free nauplius stage before invasion of the polychaete or gastropod host. The nauplii are simple, flattened and ovoid (Fig. 3J). They have a naupliar eye and only develop the first three appendages. The exopod of the mandible consists of a single segment and the caudal armature of a pair of long setae. They are non-feeding, having no mouth or anus and contain obvious globules of stored lipid.

Siphonostomatoida: Ivanenko et al. (2001) noted that there are four morphologically distinguishable nauplius stages in siphonostomatoids, but Piasecki (1996) and Scram (2004) described two for Caligus elongatus. Perkins (1983) described a species without a nauplius stage, Izawa (2010) a species with five stages and Dahms et al. (2006) mention N6, so number appears to vary between zero and six. Only the first three pairs of appendages are present during most of the naupliar phase (Fig. 3K), but rudimentary P1 and P2 may appear in the last stage. The body may be ovoid or shield-shaped and elongated, sometimes with a blunt projection on the posterior margin. Caudal armature consists of a pair of long oar-shaped setae, which are sometimes difficult to see. Two additional shorter pairs of setae may develop in the last stage (Izawa, 2010). In live nauplii dark patches or bands of pigment are often found (Novales et al., 2009; Schram, 2004). They are non-feeding and heavily invested with lipid when they hatch.

## Identifying individual Calanoida nauplii stages

The six nauplius stages of Calanus helgolandicus, one of the largest nauplii sampled off southern Britain, are described here as an example of typical calanoid naupliar development (Fig. 5; Table 2), although there can be slight variations in this pattern in other calanoids (e.g. Ogilvie, 1933).

Nauplius 1: This has three setae on the A1 and they tend to be long, although sometimes damaged in preserved specimens. There are two caudal setae. This arrangement of setae appears to be typical of the N 1 in all copepod species. The posterior body is very short. There are three pairs of appendages on the body, A1, A2 and mandibles.


Fig. 5. Nauplius stages of Calanus (after Marshall \& Orr, 1955). For clarity, not all appendages are drawn.

Nauplius 2: This has four long setae on the A1. Similar to the N1, there are three pairs of appendages on the anterior body and two caudal setae.
Nauplius 3: This is also easy to identify, as there are seven setae on the A1, obviously sparse and widely spaced compared to later stages. There are still only three pairs of appendages on the anterior body, but caudal spines in addition to setae have developed. This stage can sometimes be quite transparent. Lebour (1916) noted that N3 C. helgolandicus (called C. finmarchicus in her
paper, as the two species had not been separated at that time) tended always to be the commonest stage in the samples, suggesting a longer duration of this stage.
Nauplius 4: This can be distinguished by the eleven setae on the A1 and the arrangement of caudal spines. It can easily be distinguished from the N3, as an additional pair of appendages are present, rather rudimentary maxillules bearing fine setae.
Nauplius 5: In this stage the rudimentary maxillae first appear and also the first pair of rudimentary swimming legs. The various appendages are often held close to the body in preserved samples and the body may be quite opaque, giving an almost insect pupal appearance.
Nauplius 6: In this stage tiny maxillipeds appear and a second rudimentary pair of swimming legs.
Table 2. Calanus helgolandicus nauplii. Number of anterior appendages and swimming legs, length range and number of setae on the A1 distal segment. Measurements from formaldehyde preserved nauplii, cultured at the Plymouth Marine Laboratory (PML) in February 2003.

| Naupliar <br> stage | Number of anterior <br> appendages $/$ <br> swimming legs | Total length range <br> $(\mathbf{m m})$ | Number of setae on <br> the A1 distal <br> 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 |

## Copepod copepodite developmental stages

Adult copepod morphology:
Before detailing how to identify copepodite stages, it is useful to review copepod morphology and nomenclature, using calanoids as the main example. The following information is given in greater detail in Huys \& Boxshall (1991), Mauchline (1998) and Bradford-Grieve et. al. (1999).
Normal arthropod nomenclature, such as head, thorax and abdomen cannot accurately be applied to copepods, because of the slightly different way the somites are fused together and the different function of some of the appendages. The adult (Co6) body (Fig. 6) is basically divided into cephalosome (Ce), metasome (Me) and urosome (Ur), the cephalosome and metasome together termed the prosome (Pr). Theoretically, the body of all adult copepods is composed of 16 somites, but all the somites are not visible externally (free), because some fuse together, the amount of fusion differing between species and sexes.
The cephalosome in all copepods is formed from six fused somites, five cephalic somites and what is actually the first thoracic somite, all outwardly appearing as one somite. These somites each bear paired limbs, which is evidence for the fusion of six somites. Many copepod species also have the seventh somite (first pedigerous or leg-bearing somite) partially or completely fused to the cephalosome, and this whole anterior fused region is then called the cephalothorax. Many calanoid species also have the last two pedigerous metasome somites fused together.
The urosome in all copepod orders is defined as the series of body somites posterior to the major body articulation (bending joint). The position of this articulation in adult copepods differs by one somite between calanoids, which are in Superorder Gymnoplea, and all the other orders that are described in this guide (Cyclopoida, Harpacticoida, Misophrioida, Monstrilloida and Siphonostomatoida), which are in Superorder Podoplea. The articulation in calanoids is located behind the fifth pedigerous somite, so all swimming legs are in front of the articulation (Fig. 6). In podopleans the articulation is located behind the fourth pedigerous somite, so the first somite of the urosome bears the P5. Because of the position of the articulation, there are theoretically five somites in the urosome of adult calanoids and six in podopleans, but in females of both superorders the two somites behind the fifth pedigerous somite fuse during the final moult to form a genital double-somite, so females usually have at least one less free somite in the urosome compared to males. However, in females of all orders, except Misophrioida, some species only have three free urosome somites, including several of the calanoids described in this guide, occasionally two, due to additional fusion of somites.

All male calanoids described here have five free somites in the urosome, except Centropages spp. (Figs. 38-40), which have four, unusual among calanoids. Male misophrioids have six urosome somites and most cyclopoids and harpacticoids described here have six, apart from a few species with three. Monstrilloid males have either four or five urosome somites. In Siphonostomatoids of both sexes, fusion of both prosome and urosome somites is more extensive than in the other orders.
The genital somite, the first somite in the urosome of calanoids, the second in podopleans, has the genital apertures in both sexes. The last somite of the urosome has the anus located ventrally and is termed the anal somite. On the anal somite are two structures, often articulated, called furcae, or caudal rami. These are not counted as a somite.

## Copepod appendages:

The six somites of the cephalosome each bear a pair of appendages (Figs. 6, 7). The anterior somite bears the antennules (A1), which are sensory and each is uniramous (single branch). The following five somites bear the feeding appendages: antennae (A2), mandibles (Md), maxillules ( $\mathrm{M} \times 1$ ), maxillae ( $\mathrm{M} \times 2$ ) and maxillipeds ( $\mathrm{M} \times \mathrm{p}$ ) and each of these is biramous (two branches). The terms proximal and distal are often used when discussing appendages and segments, identifying the part closest and furthest away from the point of attachment (or origin) respectively (Fig. 7E).


Fig. 6. The external morphology and appendages of an adult female calanoid copepod, ventral view. The example shows the minimum possible fusion of somites. Abbreviations commonly used for parts are shown and the swimming legs (P1-P5) and pedigerous somites of the metasome are numbered (after Giesbrecht \& Schmeil, 1898).

There are five pedigerous somites in adult copepods, some of which may be fused to other somites, each bearing paired appendages (P1-P5; Fig. 6), commonly termed swimming legs (Fig. 7F), but in several calanoid genera the females lack the fifth pair (e.g. Pseudocalanus elongatus; Fig. 18). In most copepods of all orders, only the first four pairs of legs of both sexes could actually be used for swimming, as the fifth is usually too small, rudimentary, or in other ways structurally unsuitable for this purpose. In calanoids the P5 are usually involved in reproductive activities. Leg pairs are typically rigidly joined together at the base, so they beat simultaneously. At least P1-P4 are quite similar in structure and each individual limb is biramous, but the P5 are extremely variable in structure between species, making them one of the most useful features for species identification, certainly in calanoids. In most female copepods the P5 are reduced in size and
complexity (e.g. Metridia lucens; Fig. 13), in some cyclopoids to simple setae (e.g. Oithona similis; Fig. 55). Male calanoid copepods have five pairs of swimming legs, the two limbs of the P5 usually heavily modified and morphologically different, while the P5 of male podopleans are typically reduced, but symmetrical. In adult calanoids of both sexes, the P5 are often so reduced or modified from the basic leg pattern shown in Figure 7F, that it mav not be immediatelv obvious which parts are exopods or endopods etc. The genital somite bears remnants of P6 legs, reduced in both sexes to tiny opercular plates (still quite large in some harpacticoids) that close off the genital apertures.
In adult females of all orders, both A1 are identical. Adult males of some calanoids have both A1 identical, these differing from, but generally resembling the female A1, but in other calanoid males one of the A1 may be modified to varying degrees, with swellings, hinges, spines etc. An A1 that is modified is called geniculate. The geniculation is usually on the right, but in a few calanoids it is on the left (e.g. Metridia lucens; Fig. 13). In all male podopleans in orders Misophrioida, Harpacticoida and Monstrilloida included in this guide, both male A1 are geniculate. In podoplean Order Cyclopoida, all adult males in Family Oithonidae have both A1 geniculate, while in the other cyclopoid families (Oncaeidae, Lubbockiidae and Corycaeidae) they lack any geniculation. Some males in orders Siphostomatoida included here have a double geniculate A1. While some copepods may lack any geniculation, there is still sexual dimorphism in the structure of the A1.


Fig. 7. Example of some calanoid prosome appendages (after Rose, 1933). Abbreviations used for parts are shown.

Copepod moulting and development:
An example of the typical sequential development of somites in a calanoid copepod (Calanus sp.) from Co1-Co6 is given in Figure 8. Between moults a somite is added, always immediately in front of the anal somite. In the example in Figure 8, the shaded somite in Co1 was added between the sixth nauplius stage ( N 6 ) and $\mathrm{Co1}$. At the moult into Co 2 this somite will be incorporated into the metasome and another somite added in front of the anal somite. This sequence is repeated between the moult from Co 2 to $\mathrm{Co3}$, the stage at which the final metasome number is reached. After $\mathrm{Co3}$, further somites added are incorporated into the urosome, until the final complement of urosome somites is reached in C06. In this example it is five somites in the $\mathrm{Co6}$ 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 all female copepods. This results in four free urosome somites in the female, fewer in females of some species due to additional somite fusion. In species that have sharp points on the posterior metasome in Co6, these can first appear in Co4
(e.g. Centropages typicus; Fig. 38), the stage after the final metasome somite is produced, but in other species may not appear until the Co6. In Temora stylifera (Fig. 46) evidence of points are present from Co1. Because fusion of both prosome and urosome somites sometimes takes place during development, there are interspecific differences in number of free somites.
The Co1 of most copepods typically have two urosome somites. There are two pairs of swimming legs, but several species sometimes have a third rudimentary pair that do not develop to a functional form until the following moult (e.g. Calanus spp. and Microsetella norvegica). Following each moult an additional pair of legs are acquired, until the final compliment of five or four pairs, depending on sex and species, is reached in Co4. While the final metasome somite appears in Co3, the P5 does not appear on this somite until Co4. Number of pairs of swimming legs is the most useful feature for identifying the stages of early copepodites.


Fig. 8. Sequence of body somites increase between copepodites $\mathrm{Co1-Co6}$ of Calanus sp . Arrows indicate the last metasome somites. The shaded somite is the one added at the previous moult. Number of free somites, in addition to the cephalosome (Ce), is noted as e.g. Ce+5. (after Mauchline, 1998).

Tables of the number of body somites, swimming legs and lengths of copepodite stages, compiled from literature sources and from original observations, are given for some common North Atlantic copepods by Conway (2012). An example is given in Table 3.

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

|  | Co1 | Co2 | Co3 | Co4 | Co5 | Co6 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| No. of free prosome somites | 4 | 5 | 6 | 6 | 6 | 6 |
| No. of free urosome somites | 2 | 2 | 2 | 3 | 4 | $\begin{aligned} & 94 \\ & 85 \end{aligned}$ |
| No. pairs of swimming legs | $2(+1)$ | $3(+1)$ | $4(+1)$ | 5 | 5 | 5 |
| Mean total length (mm) | 0.77 | 1.06 | 1.37 | 1.81 | 2.44 | $\begin{array}{r} 92.70 \\ 62.66 \\ \hline \end{array}$ |
| Range of total length (mm) | 0.73-0.84 | 1.01-1.15 | 1.29-1.46 | 1.66-1.94 | 2.25-2.61 | $\begin{array}{r} q 2.44-3.08 \\ 22.50-2.85 \end{array}$ |
| Mean prosome length (mm) | 0.60 | 0.83 | 1.09 | 1.44 | 1.90 | $\begin{array}{r} 92.11 \\ 02.07 \\ \hline \end{array}$ |
| Range of prosome length (mm) | 0.56-0.67 | 0.73-0.90 | 1.01-1.18 | 1.29-1.55 | 1.74-2.03 | $\begin{array}{r} \text { q1.86-2.44 } \\ \text { 11.97-2.15 } \end{array}$ |
| Mean prosome width (mm) | 0.21 | 0.25 | 0.31 | 0.41 | 0.54 | $\begin{aligned} & 90.64 \\ & 0.61 \end{aligned}$ |
| Range of greatest prosome width (mm) | 0.20-0.23 | 0.23-0.28 | 0.28-0.34 | 0.37-0.45 | 0.46-0.58 | $\begin{array}{r} 90.58-0.76 \\ 60.58-0.64 \\ \hline \end{array}$ |

[^0]Sex determination in late calanoid copepodite stages:
As already mentioned, in calanoids there is considerable difference in the morphology of the P5 between the sexes. The P5 appear at Co4, apart from in females that do not develop a P5. They do not have the adult form in Co4, but are initially quite rudimentary, becoming more complex in Co5 and fully formed after the moult into Co6. Both sides of female calanoid P5 are usually symmetrical from Co4, while most male P5 are usually very asymmetrical and also often longer than those of the female (Fig. 4), the same morphological differences as typically found in the adults. With practise and experience, these differences make separation of the sexes from Co4 relatively simple. In cyclopoids and harpacticoids the P5 are similar and symmetrical in both sexes, so the same method of separation of the sexes is not possible. In calanoid species where the female does not develop a P5, from Co4 a copepodite with five legs should be a male. However, because of the numerical imbalance between males and females often observed among adult copepods, females usually predominating, it is thought that ultimate sex, in at least some copepod species, may be determined by environmental factors e.g. food availability, at a late stage of development (Gusmão \& McKinnon, 2009). This late switching of sex from male to female is thought to result in a small proportion of abnormal, intersex individuals with intermediate types of legs, and also females that should only have four pairs of legs, with a rudimentary fifth. This could, in probably only a small number of cases, make sex determination difficult, in at least Co4 and Co5.







Fig. 9. Swimming legs of female and male stage Co4 to Co6 copepodite stages of Acartia spp. (AB, D-E from Björnberg, 1972; C, F after Sars, 1903).

## Sexual dimorphism in calanoid copepods

While there are morphological differences between the sexes (sexual dimorphism) in all copepod orders, these differences are particularly obvious in most calanoid copepods. It has already been mentioned that in calanoid copepods the body of the female is usually bilaterally symmetrical, while males often show considerable asymmetry in their geniculate A1 ( $\sim 60 \%$ of the species described here), their P5, last metasome somites and urosomes (e.g. Anomalocera patersoni; Fig. 44). In male copepods with a geniculate A1 it is usually the right that is geniculate, but in the genera Paramisophria (Figs. 11, 12) and Metridia (Fig. 13), it is the left. Asymmetry in appendages and somites is species specific, but usually similar in the same genus or larger taxonomic grouping. Sexual dimorphism is also manifest in the reduction, or atrophy of mouthparts in non-feeding males, observable in several species described here (e.g. Subeucalanus crassus; Fig. 50). The initial impression of this dimorphism is to ponder why this vast diversity of bizarre, morphological male features, that initially appear structurally incapable of being used for any useful function, have developed; presumably to serve similar functions in different species. They probably represent
'key-and-lock' mechanisms, developed to reproductively isolate species. Ohtsuka \& Huys (2001) have reviewed sexual dimorphism in calanoid copepods and their observed and suggested functions are briefly summarised here.

Differences between males and females must relate to mate location, recognition and copulatory activities that, given the limited visual capabilities of most copepods, will mainly depend on senses other than vision. The naupliar eye can be shown to be light sensitive, particularly obvious in Acartia spp., which can be separated from mixed zooplankton by attracting them to one side of a beaker using a light source, then pipetting out an almost pure sample. It is suggested that eyes may be used in mate recognition in Family Pontellidae, which are brightly coloured and generally live in well lit surface waters. These have highly developed eyes, usually larger in the males (e.g. Labidocera wollastoni; Fig. 43). Additionally, Family Metridinidae and a large number of species in a few other calanoid families have at least parts of their bodies that bioluminesce. Sexual differences in intensity of light emission have been reported, suggesting a role in mating behaviour.

The primary mechanisms in mate location and recognition are probably through detection of chemicals such as pheromones released by the female, and also vibrations. It is thought that the male detects pheromones using sensory structures on the A1 called aesthetascs, supported by the fact that these mainly develop in Co6 and are much larger and more numerous in males than in females. Some copepod families, e.g. Centropagidae, have limited A2 sensory structures, but show strong sexual dimorphism, especially in the shape of the last metasome somite and the urosome (e.g. Centropages typicus; Fig. 38). Individual swimming styles, body shape and ornamentation in general may produce species specific swimming wakes that males can detect.

In mate capture the male generally uses the hinged geniculate A1 to capture the females by the furcae or urosome, but in Family Centropagidae the right P5 has a claw (e.g. Centropages typicus; Fig. 38F) that is used, at least by some species, for holding the female by the urosome. The A1 of male copepods may also bear complex thickening, hooks and other structures involved in accurate positioning of the female after capture. Little is known about mate capture in males without a geniculate A1, but in the Euchaetidae the male grasps the female's urosome with the right P5, while the Calanidae can use their maxillipeds to grasp the prosome of the female.

Once a spermatophore has been extruded from the male genital somite it is attached to the genital double-somite of the female using the male P5. Male P5 are of three main types: both legs present, each usually biramous, with functional swimming setae (e.g. Calanus helgolandicus; Fig. 25 E ), so can be used for spermatophore transfer and also swimming; both legs present, each uniramous or biramous, without functional swimming setae, sometimes highly modified into a grasping device (e.g. Paraeuchaeta hebes; Fig. 21D); only one functional leg present, without functional setae, both legs uniramous (e.g. Paracalanus parvus; Fig. 28E). The latter two types probably only function during mating. Some males have a specialised structure on the transferring leg that appears to be used for tactile inspection and cleaning of the female's genital area prior to spermatophore transfer.

What follows extrusion of the spermatophore has been observed in several groups. It is either temporarily attached to a tuft of fine setules close to the end of the left leg, gripped by distal spines or processes on the left leg, or grasped by some modified element or segments. The spermatophore may be held in the left leg ready for attachment, or retained internally until both sexes are in the correct mating position. Species without elaborate copulatory mechanisms have probably become more efficient in spermatophore transfer and mate recognition, keeping tactile inspection to a minimum. They may also have more highly evolved pheromone or hydromechanical sensitivity.

There are two types of calanoid spermatophores. The simplest are tube-shaped flasks with a narrow neck that adhere to the female by a cement-like secretion, but in some groups the spermatophore flask is connected to a coupling apparatus which fits over the female genital double-somite (e.g. Paracartia grani; Fig. 36C, D). The genital somite is usually ornamented with spines, processes and swellings that fit the profile of the coupler, reproductively isolating closely related species. Empty spermatophores are usually removed after they are discharged and this appears to be achieved in numerous calanoid families by the specialised P5 of the female. In species without a P5 the preceding legs seem to do this task, probably aided by serrations on segment edges.

## A few hints before starting to try and identify a copepod

First establish if the copepod is an adult, as most identification texts only give descriptions of the adult (C06) stages. However, some copepods with very characteristic morphology can be identified in pre-adult stages to species, or at least genus, e.g. Candacia armata (Fig. 37) Paraeuchaeta hebes (Fig. 21), especially if they are the only member of their genus found in the region.
Co6 females usually have a prominent, swollen genital somite, although some have only a slight swelling. However, a slight problem with some females, e.g. Acartia and Paracalanus spp., is that the genital somite is slightly swollen in $\mathrm{Co5}$, while the number of body somites is usually identical between Co5 and Co6. In Co5 the segments of the P5 and somites of the urosome are not as distinctly defined as in the adult stages, obvious when you examine them together. Additionally, the slightly swollen genital somite does not have any obvious external or internal structures until the typically paired genital apertures, genital opercula and seminal receptacles appear in the Co6, although some families e.g. Centropagidae (Figs. 38-41) do not have seminal receptacles.
Most calanoid C 06 males have five free somites in the urosome, four in Co5. The P5 are present in Co5, but are typically crude and poorly segmented. In males that develop a geniculate A1, the geniculation is poorly defined in Co5, but is sometimes observable even in Co4.

## Main morphological differences between the six copepod orders described

More details about each of the six copepod orders are given at the beginning of their respective sections, but the adults of the different orders described should be separable on the morphological features given in Figure 10 and in the key below.


Fig. 10. Examples of copepods (mainly females) of the six orders sampled off Plymouth. Arrows indicate the genital somites. (A after Sars, 1903; B, C after Sars, 1918; D after Giesbrecht, 1893; E from Sars, 1911; F after Sars, 1921a; G from Scott \& Scott, 1913; H from Sproston, 1942; I from Gotto, 1993).

## Key to the six copepod orders described

1. Major movable articulation (bending joint) of the body located posterior to the fifth pedigerous somite, so all the swimming legs are on the prosome; males with one geniculate A1 or none $\qquad$
Calanoida Fig. 10A

- Major articulation of the body located posterior to the fourth pedigerous somite (Fig. 10B-G, I), thus the first somite of the urosome bears the P5 (generally much reduced); males with both, or neither A1 geniculate $-2$

2. Body tubular; A1 short, pointing forwards, of no more than five segments; other anterior appendages missing; short oral tube opening on the anterior ventral body; adult females carry eggs on ovigerous spines Monstrilloida Fig. 10F - All anterior appendages usually present; A1 of at least six segments; adult females without ovigerous spines; eggs typically carried in sacs
3. Oral cone around mouth; mandible rod-shaped, passing into oral cone; body shape very variable Siphonostomatoida Fig. 10G-I

- Oral cone absent from around mouth

4. Urosome usually narrower than prosome; P5 reduced to setae, similar in both sexes, endopod usually absent; females with paired egg-sacs ------------------------------------Cyclopoida Fig 10B, C - Urosome obviously narrower than prosome; resembling a calanoid; P5 smaller than other legs, but not rudimentary; symmetrical in both sexes; A1 at least 16-segmented in both sexes; females have single egg-sac, with large eggs $\qquad$ Misophrioida Fig 10E - A1 short, at most nine segments in females, 14 in males; prosome and urosome usually merge with less of an obvious change in width than in other orders; both sexes with six pairs of swimming legs, P5 smaller than other legs, but not rudimentary, P6 usually rudimentary in females; females usually carry single egg sacs ventrally

Harpacticoida Fig. 10D

## Sub-class Copepoda: Infraclass Neocopepoda

## Superorder Gymnoplea:

The adult body articulates between the last pedigerous (leg-bearing) metasome somite (somite 11) and the genital somite (somite 12).

## Order Calanoida:

Calanoida is the most numerous and diverse pelagic copepod order. The A1 are usually long, apart from in some of the benthic species. Some males have one A1 geniculate (swollen/hinged/with strong spines, etc.), sometimes remarkably modified (e.g. Anomalocera patersoni; Fig. 44). If the male A1 is geniculate it is usually on the right, except in two of the genera described here, Paramisophria and Metridia spp., where it is on the left.
The prosome is much broader than the urosome. In many species the cephalosome is fused to the first pedigerous somite forming a cephalothorax and the last two metasome somites are sometimes also fused. In females, the posterior of the last metasome somite, and the urosome tend to be bilaterally symmetrical (both sides a mirror image) or only slightly asymmetrical, while in males they are often very asymmetrical (e.g. Anomalocera patersoni; Fig. 44). Females usually have five pairs of swimming legs, occasionally four pairs as in families Aetideidae (Fig. 14) and Euchaetidae (Fig. 21), or in some individual genera (e.g. Pseudocalanus elongatus; Fig. 18). The female P5, when present, are usually symmetrical, although often much reduced in size and complexity compared to P1-P4 (e.g. Paracalanus parvus; Fig. 28). Males always have five pairs of legs, the P5 usually greatly modified and asymmetrical (e.g. Candacia armata; Fig. 37). The P6 is reduced in both sexes to one or two tiny opercular plates that close the genital opening on the genital somite and are difficult to discern unless using high power microscope. Females usually have four free somites in the urosome (not counting the furcae) e.g. Calanus spp. (Figs. 25 \& 26), but occasionally three e.g. Acartia spp. (Figs. 30-35), or even two e.g. Calocalanus spp. (Fig. 29), due to fusion. Males of the species described here almost always have five free urosome somites, rarely only four as in Centropages spp. (Figs. 38-40). There are usually five setae on each furca in both sexes, but sometimes only three or four.
Females either spawn their eggs directly into the sea (e.g. Calanus, Temora and Acartia spp.), or they are held in a single egg sac or egg mass (e.g. Pseudocalanus elongatus; Fig. 18.), rarely paired egg sacs (e.g. Pseudodiaptomus marinus., a tropical/subtropical alien introduction appearing in some European coastal areas (de Olazabal \& Tirelli, 2011)). In at least Eurytemora affinis (Fig. 47) the eggs are held in a matrix that can remain for some time after all the eggs have hatched. Egg sacs are usually knocked off during sampling and preservation, but some females (e.g. Paraeuchaeta spp.) are frequently found bearing eggs.

## Key to Calanoida described

## Prosome, urosome and P5 usually bilaterally symmetrical; A1 never geniculate; urosome usually of

 four somites, sometimes three, rarely two; genital somite swollen ventrallyFemale

> Prosome and urosome often not bilaterally symmetrical; one or neither A1 geniculate; P5 asymmetrical; urosome of five somites, rarely four; genital somite no ventral swelling ---------- Male

## Females

1. Small rounded copepod; last metasome somite with slim, pointed extensions projecting backwards close to urosome, often difficult to see ---------------------------- Diaixis hibernica Fig. 19

- Small rounded copepod; last metasome somite with two strong, dorsal spines

Paramisophria spp. Figs. 11, 12

- Last metasome somite in dorsal view with sharp lateral points close to urosome (e.g. Fig. 20), or widely spaced (e.g. Fig. 40)$-2$
- Last metasome somite rounded (e.g. Fig.17), with blunt points close to the urosome (e.g. Fig. 42),or with tiny inconspicuous points (e.g. Fig. 13)7

2. Last metasome somite slightly asymmetrical; three somites in urosome ..... 3

- Last metasome somite symmetrical; three somites in urosome ..... 4
- Last metasome somite symmetrical; four somites in urosome ..... 8

3. Very long furcae; last metasome somite with lateral wings, broader than prosome, with curvinginner lobesEurytemora americana Fig. 49

- Strong spine on ventral genital somite, fine setae laterally Centropages hamatus Fig. 40
- Large, robust; in dorsal view anterior cephalosome square-ended with pronounced "shoulders";body often tinged with black pigmentCandacia armata Fig. 37

4. Sharp strong spines on A1 segments one, two and five; curved lobes interior to spines on last metasome somite ---------------------------------- Centropages typicus and C. chierchiae Figs. 38, 39- Last metasome somite extended into large triangular wings; genital somite with lateral extensions;one seta on each furca enlarged into robust spinesParacartia grani Fig. 36

- Sharp hooks laterally on anterior cephalosome and glassy lenses dorsally ..... 5
- Very long furcae ..... 6

5. One pair of dorsal lenses; dorsal swelling on genital somite Labidocera wollastoni Fig. 43

- Two pairs of dorsal lenses; dorsolateral spine on genital somite --Anomalocera patersoni Fig. 44

6. Lateral edges of last metasome somite spiny; brackish waters Eurytemora velox Fig. 48

- Lateral edges of last metasome somite smooth; brackish waters Eurytemora affinis Fig. 47
- P5 slender, three segments; cephalosome cloak-like Temora stylifera Fig. 46

7. Only four pairs of swimming legs ..... 9

- Five pairs of swimming legs; P5 tiny, vestigial, a single uniramous limb; A1 reach just beyond
furcae ..... Ctenocalanus vanus Fig. 16
- Five pairs of swimming legs, all similar size and structure ..... 10
- Five pairs of swimming legs, P5 small and quite simple ..... 11

8. P5 missing; anterior cephalothorax very rounded in lateral view Aetideus armatus Fig. 14 - P5 tiny, two segments Xanthocalanus minor Fig. 20
9. Large, wide-bodied copepod; urosome stubby, of three somites with bulbous genital somite; A1reaching just beyond furcae ---------------------------------------------------- Subeucalanus crassus Fig. 50- Cephalothorax pointed anteriorly; long setae on A1; in lateral view strong rostrum, with frontaleminence behind; maxilliped massive -------------------------------------------- Paraeuchaeta hebes Fig. 21- Tiny copepod ( $0.7-0.9 \mathrm{~mm}$ ); rounded body; short urosome ---------- Microcalanus pusillus Fig. 17- Medium-sized copepod ( $0.9-1.6 \mathrm{~mm}$ ); urosome approximately half the length of the prosome;genital somite longPseudocalanus elongatus Fig. 18
10. A1 reaches urosome; anterior cephalosome clearly rounded in lateral view; P5 basal segment distinctly concave internally -------------------------------------------------- Calanus helgolandicus Fig. 25 - A1 reaches urosome; anterior cephalosome slightly angular in lateral view; P5 basal segment straight or slightly convex internally ------------------------------------------ Calanus finmarchicus Fig. 26 - A1 reaches urosome; anterior cephalosome distinctly pointed in dorsal view, angular in lateral view; P5 basal segment slightly convex internally ----------------------- Calanoides carinatus Fig. 27 - Small copepod ( $\sim 0.8 \mathrm{~mm}$ ); A1 short, just reaching metasome ---- Pseudocyclops obtusatus Fig. 51
11. Prosome "coffin-shaped"; A1 with long fine setae; setae on furcae usually intact, forming a fan; P5 uniramous, terminating in spiny segment, with long seta on previous segment -- Acartia spp. 12

- Prosome rounded; P5 uniramous -----------------------------------------------------------------------------15
- Prosome rounded; P5 biramous, well developed with small endopod; swelling on left dorsal face of genital somite, two strong spines on ventral face Isias clavipes Fig. 41
- Prosome rounded; P5 biramous and simple with small endopod; urosome of three somites, pair of strong spines dorsoposteriorly on second somite --------------------- Parapontella brevicornis Fig. 42

12. Rostral filaments absent -------------------------------------------------------------------------------------------13

- Rostral filaments present -------------------------------------------------------------------------------------------------14

13. Furcae obviously flattened; no spines on last metasome somite or urosome somites; second urosome somite with dorsal, rounded, slight protuberance distally--------- Acartia discaudata Fig. 32 - Prominent spine on each side of posterior, last metasome somite -------- Acartia longiremis Fig. 33 - Small spines dorsally and laterally on posterior margin of last metasome somite and first and second urosome somites; length $1.04-1.08 \mathrm{~mm}$--------------------------------------- Acartia clausi Fig. 30 - Small spines dorsally and laterally on posterior margin of last metasome somite, none on urosome; length 0.79-0.91 mm - Acartia margalefi Fig. 31
14. P5 second segment with internal lobe, third with bulbous base --------------- Acartia tonsa Fig. 34 - P5 simple -------------------------------------------------------------------------------------------- Acartia bifilosa Fig. 35
15. P5 one segment, flattened, plate-like; urosome very narrow; anterior cephalothorax in lateral
 - P5 of four segments; urosome only two somites; genital somite globular; furcae usually divergent - Calocalanus pavo Fig. 29

- P5 of three segments -----------------------------------------------------------------------------------------------------16

16. Segments on anterior edge of A1 raised in jagged outline; genital somite rounded ventrally, usually with pair of large golden seminal vesicles; P5 with long distal spines; last metasome somite with tiny points, close to urosome Metridia lucens Fig. 13

- Anterior edge of A1 not jagged in outline

17. Prosome short and rounded in dorsal view; urosome of four somites; P5 of three segments, distal with external spine row, or pair of sub-distal spines ---------------- Stephos spp. Figs. 23, 24

- In dorsal view, prosome kite-shaped; furcae very long; urosome of three somites; P5 of three segments terminating in four spines --------------------------------------------- Temora longicornis Fig. 45
- In dorsal view, prosome parallel-sided for much of length; urosome of four somites ----------------18

18. Genital somite almost as long as the following two somites together; P5 simple, of three segments, robust, last segment notched at end ---------------------------- Clausocalanus jobei Fig. 15 - Genital somite shorter than following two somites together; P5 delicate, tiny, usually of two or three segments, slender distal spine and smaller spine externally -- Paracalanus parvus Fig. 28

## Males

1. Lateral hooks and one pair of large lenses on anterior cephalosome
Labidocera wollastoni Fig. 43

- Lateral hooks and two pairs of small lenses on anterior cephalosome; lateral pointed projection on
first urosome somite Anomalocera patersoni Fig. 44
- No anterior hooks or lenses ..... 2

2. Small round-bodied copepod; A1 short, geniculate on left; last metasome somite with two strong dorsal spines in at least one of the two species ------------------------ Paramisophria spp. Figs. 11, 12

- Last metasome somite in dorsal view with widely spaced, sharp, lateral points (e.g. Fig. 38) ..... 3
- Last metasome somite in dorsal view with no conspicuous points ..... 8

3. Furcae almost as long as urosome ..... Temora stylifera Fig. 46

- Furcae less than half the length of urosome; prominent spines on basal segments of A1 ..... 4
- Furcae less than half the length of urosome; no spines on basal segments of A1 ..... 5

4. Single spine on swollen geniculate section of A1 Centropages typicus Fig. 38

- Two spines on swollen geniculate section of A1 Centropages chierchiae Fig. 39

5. Spines on last metasome somite quite symmetrical; urosome symmetrical ..... 6

- Spines on last metasome somite very asymmetrical; urosome with one large or two small lateral projections ..... 7

6. P5 almost as long as urosome, right leg missing Aetideus armatus Fig. 14

- P5 around half length of urosome, strong claw on right leg ..... Centropages hamatus Fig. 40

7. First urosome somite with lateral projection; body/legs often tinged black
Candacia armata Fig. 37

- Third and fourth urosome somites with small lateral projections -- Parapontella brevicornis Fig. 42

8. P5 reaching to end of, or beyond urosome ..... 9

- P5 does not reach urosome ..... 13

9. Right A1 strongly geniculate; right P5 twice as long as left; Paracartia grani Fig. 36

- A1 not geniculate ..... 10

10. Large ( $\sim 2.75 \mathrm{~mm}$ ); rostrum extended into point with frontal eminence behindParaeuchaeta hebes Fig. 21

- Medium-sized ( $0.87-1.18 \mathrm{~mm}$ ); P5 slender, right leg a short stump ---- Clausocalanus jobei Fig. 15
- Medium-sized (0.97-1.46 mm); P5 legs of similar length, quite straight and simple ..... 11
- Small (0.74-1.1 mm); P5 complex and bulky ..... 12

11. Right P5 terminating in long blunt segment; rudimentary endopods presentScolecithricella minor Fig. 22

- Right P5 terminating in sharp stylet, no endopods Pseudocalanus elongatus Fig. 18

12. P5 slightly longer than urosome, right leg ending in sickle-shaped segment ..... Stephos spp. Figs. 23, 24

- P5 much longer than urosome, right leg terminating in a movable segment with two processes ---
Diaixis hibernica Fig. 19

13. A1 geniculate; furcae as long as previous two somites together- ..... 14
-A1 geniculate; furcae much shorter than previous two somites together ..... 16

- A1 not geniculate ..... 2114. Lateral projection on somite three of urosomeIsias clavipes Fig. 41
- Left P5 terminating in claw Temora longicornis Fig. ..... 45
- Left P5 terminating in long segment ..... 15

15. Left P5 terminating in three processes with hollow between ..... Eurytemora affinis Fig. 47

- Left P5 last segment terminating in two lobes, one ending in a spine Eurytemora velox Fig. 48
- Left P5 last segment terminating in blunt lobe Eurytemora americana Fig. 49

16. A1 about same length as cephalosome Pseudocyclops obtusatus Fig. 51

- A1 about same length as prosome, with characteristic fine long setae; prosome narrow ..... 17

17. Rostral filaments absent ..... 18

- Rostral filaments present ..... 20

18. Right P5 second segment not expanded at inner border, left P5 first segment with two rows ofspines, one large the other smallAcartia discaudata Fig. 32

- Right P5 second segment expanded at inner border, left P5 first segment with one large spine on
inner distal border Acartia longiremis Fig. 33
- Left P5 first segment with one or two rows of small setae, all the same size ..... 19

19. Distal segment of right P5 with no inner spine, maximum body length $\sim 1.32 \mathrm{~mm}$

$\qquad$

- Distal segment of right P5 with inner spine; maximum body length $\sim 0.90 \mathrm{~mm}$Acartia margalefi Fig. 31

20. Second segment of right P5 with two inner expansions, one bearing a spine
Acartia bifilosa Fig. 35

- Second segment of right P5 without obvious expansions or spine Acartia tonsa Fig. 34

21. P5 biramous, of quite similar structure and length as other legs ..... 22

- P5 uniramous, of quite different structure to other legs ..... 24

22. Endopod of left P5 reduced to a stump without setae Calanoides carinatus Fig. 27

- Endopods of both P5 well developed ..... 23

23. Last segment of right P5 exopod almost reaching end of second last segment of left exopod ..... ----
Calanus helgolandicus Fig. ..... 25

- Last segment of right P5 exopod reaching around middle of last segment of left exopod
Calanus finmarchicus Fig. 26

24. Right P5 missing or just a tiny stump, left leg reaches halfway down urosome ..... 25

- P5 legs of very unequal lengths, right leg very short ..... 26
- P5 legs of similar lengths ..... 28

25. Right P5 missing Subeucalanus crassus Fig. 50

- Right leg a tiny stump Ctenocalanus vanus Fig. 16

26. Urosome around half length of rounded prosome Microcalanus pusillus Fig. 17

- Urosome less than half length of elongated prosome ..... 27

27. Right P5 tiny, around a quarter length of left P5, two segments Paracalanus parvus Fig. 28

- Right P5 almost half length of left P5, four segments ..... Calocalanus pavo Fig. 29

28. P5 long, slender, straight, without internal projections Xanthocalanus minor Fig. 20- P5 flattened, bent, with internal spines around middle of both legs- Metridia lucens Fig. 13

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Arietellidae:

## Genus Paramisophria

Paramisophria cluthae T. Scott, 1897
Both sexes have a short urosome and medium-sized P5; fourth and fifth metasome somites fused. Female: A1 very short, hardly reaching beyond the cephalosome (Fig. 11A), slightly longer on the left; posteriodorsal border of last metasome somite bearing two small teeth, one around the centre of each side. P5 with basal segment and two further segments, internal projection on middle segment bearing a small spine and a longer seta, distal segment twice as long as the other two together, bearing four external and two distal spines (Fig. 11C).
Male: A1 unusual among male calanoids, being geniculate on the left (Fig. 11D, F); a pair of teeth dorsally on the last metasome somite, similar to the female (Fig. 11D). Second last segment of the P5 broad on both legs, with external spines; distal segment on right leg spine-like, with two smaller spines at base; distal segment on left leg broad, with three distal spines.
Bottom-living; would probably only be sampled in turbulent conditions.


Fig. 11. Paramisophria cluthae. (A-E after Sars, 1903; F from Breemen, 1908).
Recorded: PMF. L4, not recorded. West Norway. Around British coast.
Total length: Female $1.2-1.4 \mathrm{~mm}$; male 1.1 mm .
Further information: Sars, 1903; Breemen, 1908; Rose, 1933.

Paramisophria spooneri Krishnaswamy, 1959
Female: A1 short with around 20 obvious segments (Fig. 12C); body slightly compressed laterally; dorsoposterior margin of last metasome somite bearing two small teeth, one on each side (Fig. 12A, B), similar to most other Paramisophria species. Urosome short; furcae wider than long, each bearing six setae, inner margins with tiny hairs. Second last segment of the P5 with an inner seta and an outer spine (Fig. 12D, E), extended on the inner side into a bifid process not found in $P$. cluthae; distal segment three times longer than wide, with an array of spines, obvious in lateral view.
Male: Resembles the female in general body shape. Apart from two cave-dwelling Paramisophria species, all other males and females have been described as having a pair of dorsoposterior teeth on the last metasome somite (Ohtsuka et al., 1993). This feature was not drawn or mentioned for the male of this species when described by Krishnaswamy (1959), but possibly might be present? A1 19-jointed, unusual among male calanoids in being geniculate on the left side (Fig. 12H); urosome of five somites (Fig. 12G). Third and fourth segments of left P5 each bear an outer plumose spine (Fig. 12F), the broad distal segment produced into three spiny processes; right P5 second segment carries a distinctive long blunt lobe that reaches to the end of the fourth segment (not present in the male of $P$. cluthae), third and fourth segments each with an outer plumose spine, distal segment forms a spiny process with two teeth at the base.
First described from Plymouth and named after Mr G.M. Spooner of the MBA Laboratory. Bottomliving; probably would only be sampled in turbulent conditions.


Fig. 12. Paramisophria spooneri (from Krishnaswamy, 1959).
Recorded: Plymouth. West Ireland.
Total length: Female 0.62 mm ; male 0.62 mm .
Further information: Krishnaswamy, 1959.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Metridinidae:

## Genus Metridia:

Metridia lucens Boeck, 1865
Both sexes quite similar in appearance; in lateral view the body is generally widest just behind the A1, presenting a very characteristic profile (Fig. 13B, H); long urosome over half the length of the prosome. Segment one of the endopod of the P2 in both sexes with upwardly pointing spines, characteristic of the family (Fig. 13E, J).
Female: A1 somites are heavily ridged on the anterior edge giving a serrated appearance (Fig. $13 \mathrm{~B}, \mathrm{C})$, many setae also present; small, inconspicuous, lateral points on the last metasome somite (Fig. 13B, F). P5 small, delicate and simple (Fig. 13D), of three segments, three distal and one lateral spine on last segment. Urosome of three somites (Fig. 13B); genital somite smooth ventrally, not very pronounced in lateral view, usually with an obvious pair of golden coloured seminal receptacles
Male: Similar in shape to female (Fig. 13G, H); A1 slightly geniculate on left, unusual for a male copepod; right P5 with long internal process on the third segment; left P5 with short spine on the fourth segment.


Fig.13. Metridia lucens (A-E, G-H, J from Bradford-Grieve, 1999a; F, I after Sars, 1903, from Rose, 1933).

Recorded: PMF. L4, usually in quite low numbers. Irish Sea. North Sea. Western Ireland.
Total length: Female $2.25-2.90 \mathrm{~mm}$; male $1.80-2.30 \mathrm{~mm}$.
Further information: Sars, 1903; Rose, 1933; Bradford-Grieve, 1999a; Gerber, 2000; Conway, 2012.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Aetideidae:

## Genus Aetideus:

Aetideus armatus (Boeck, 1872)
First pedigerous somite fused to cephalosome forming cephalothorax and fourth and fifth pedigerous somites fused.
Female: A1 reaches to end of furcae (Fig. 14A, B); anterior cephalothorax very rounded in lateral view, with a continuous curve to the tip of the rostrum; rostrum strong, thick with two, well separated points (Fig. 14C). Last metasome somite produced into two strong, backwardly pointing, sharp processes, reaching almost to end of the genital somite; in dorsal view genital somite swollen in middle; furcae longer than anal somite. No P5.
Male: Smaller and slenderer than the female (Fig. 14D, E); A1 shorter than in the female, not geniculate, reaching almost to the second urosome somite; no rostrum, anterior cephalothorax rounded in lateral profile. Sharp processes on last metasome somite, shorter than in the female; urosome very narrow, furcae often divergent. P5 almost as long as urosome (Fig. 14D-F); right P5 missing, five segments on left leg, the third the longest, the last small and bearing fine setae.

The copepod Bradyidius armatus (Vanhöffen, 1897), also in Family Aetideidae, is similar in appearance and size to Aetideus armatus. Previously called Undinopsis bradyi, it has a cosmopolitan distribution, but is only found inshore around Britain in some of the deep fjordic lochs in north-western Scotland, such as Loch Linnhe, and also along the Norwegian coast. The female differs from $A$. armatus in having a much less rounded anterior cephalosome in lateral view and the points on the last metasome somite are more widely spaced. The male P5 is biramous, the right limb only a quarter the length of the left.


Fig. 14. Aetideus armatus (from Sars, 1903).
Recorded: Not recorded off Plymouth. Irish Sea. West of Ireland. Western Norway.
Total length: Female $1.80-1.95 \mathrm{~mm}$; male 1.40-1.53 mm .
Further information: Sars, 1903; Rose, 1933.

## Family Clausocalanidae:

## Genus Clausocalanus:

Clausocalanus jobei Frost \& Fleminger, 1968
Clausocalanus spp. are small to medium sized copepods that may initially be confused with Paracalanus, Pseudocalanus or Ctenocalanus spp., but can be separated by the size and form of the male and female P5. First pedigerous somite fused to cephalosome forming cephalothorax (Fig. 15A, H) and fourth and fifth fused; exopods of P2-P4 of both sexes with long distal blades, finely serrated on the outer edge (Fig. 15G).
Female: A1 reaching beyond genital somite (Fig. 15A); rostrum in lateral view quite long and slender, curving downwards (Fig. 15C, D); genital somite in lateral view protruding anteriorly, narrowing from the region of the genital pore (Fig. 15E), almost as long as the two following somites together; weak separation of the dorsal and lateral lobes of the seminal receptacle in both lateral and ventral views. P5 tiny, three segments, simple but robust (Fig. 15F); last segment bifurcated distally.
Male: A1 extending only to around the second metasome somite (Fig. 15H); rostrum in lateral view knob-like and protrudes ventrally (Fig. 15J); second urosome somite as long as the following two somites together. P5 uniramous and asymmetrical (Fig. 15K-M), right leg a short stump, left leg robust, longer than urosome.


Fig. 15. Clausocalanus jobei (from Frost \& Fleminger, 1968).
Recorded: PMF, not recorded. L4, seasonally quite abundant. West of Ireland.
Total length: Female 1.01-1.56; male 0.87-1.18.
Further information: Frost \& Fleminger, 1968; Bradford-Grieve, 1994; Avancini et al., 2006; Vives \& Shmeleva, 2006.

## Genus Ctenocalanus:

Ctenocalanus vanus Giesbrecht, 1888
First pedigerous somite fused to cephalosome to form cephalothorax and fourth and fifth fused (Fig. 16A, G); superficially similar in appearance to Paracalanus, Pseudocalanus and Clausocalanus spp., but can be separated by the form and size of the female and male P5 and length of the A1; exopod of P2-P4 of both sexes with long distal blade, finely serrated on the outer edge (Fig. 16F).
Female: A1 reaches just beyond end of urosome, longer than in Pseudocalanus elongatus, but often broken off. Unusual in female copepods, the P5 comprises a tiny, single uniramous limb, variable in shape and extremely vestigial (Fig. 16C, D), so is unlikely to serve any useful purpose. It is often difficult to see, potentially leading to misidentification as a $P$. elongatus (which lacks a P5). Additionally, Marshall (1949) reported that in Loch Striven (western Scotland), a variable proportion ( $<1 \%$ ) of Co6 female P. elongatus can have an additional rudimentary P5, so it is possible that this type of intersex female (see Gusmão \& McKinnon, 2009) could initially be confused with $C$. vanus. Urosome $\sim 36 \%$ the length of prosome; exopod segment three of the P3 and P4 with two external spiny, comb-like structures (Fig.16E, F).
Male: A1 extends to around the end of the urosome (Fig. 16G, H); second urosome somite as long as the two following somites together; P5 reaching halfway down the urosome, to the end of the second urosome somite (Fig. 16G), small and slender (Fig. 16I), five segments on the left limb, only a stump on the right.
A) Female, lateral showing P4 and P5 only





Fig. 16. Ctenocalanus vanus (A, D, H, I from Razouls, 1972; B from Séret, 1979; C from Giesbrecht, 1893; E, F from Esterly, 1924, G from Björnberg, 1981).

Recorded: PMF, not recorded. L4, in low numbers. Western English Channel. West of Ireland.
Total length: Female 0.92-1.35 mm; male 1.20-1.46 mm.
Further information: Esterly, 1924; Rose, 1933; Ramirez, 1966; Heron \& Bowman, 1971; Razouls, 1972; Chen \& Zhang, 1974; Séret, 1979; Björnberg, 1981; Avancini et al., 2006.

## Genus Microcalanus:

Microcalanus pusillus G.O. Sars, 1903
Two species of Microcalanus have been described in European waters, M. pygmaeus (Sars 1900) and M. pusillus Sars, 1903. They have the same distribution and are morphologically quite similar, the greatest difference being that the A1 reaches the furcae in $M$. pygmaeus, while in $M$. pusillus it only reaches the genital somite. Additionally, in $M$. pygmaeus the P1-P4 are slender and the distal spines on the P2-P4 exopods have a finely serrated edge, while in $M$. pusillus the P1-P4 are comparatively short and broad, and the distal spines on the P2-P4 exopods have a coarsely serrated edge. The two species are listed in the World Register of Marine Species (WORMS) website as separate species. Razouls et al. (2005-2012) also list both species, but includes notes discussing whether they should be treated as a single species, considering the evidence from studies such as by Mazzocchi et al. (1995), who found specimens intermediate in morphology between the two species. If genetical studies indicate they are the same species, the name $M$. pygmaeus will take precedence. Specimens collected at Plymouth most closely resemble the description for $M$. pusillus, so this description has been included here.

Tiny copepod with characteristic rounded, short, deep body; first pedigerous somite fused to cephalosome to form cephalothorax and fourth and fifth fused (Fig. 17A, D), giving three somites in metasome; rostrum of two fine filaments; exopod of P2-P4 of both sexes with long distal blade, serrated on the outer edge (Fig. 17B, C).
Female: Prosome approximately three times the length of the urosome (Fig. 17A); last metasome somite not quite as rounded as Figure 17A suggests; A1 reaches genital somite; P1-P4 comparatively short and broad (Fig. 17B). No P5.
Male: A1 not geniculate (Fig. 17D); urosome longer than in female, around half the length of prosome; P5 asymmetrical, around half the length of the urosome, more than twice as long on the left as the right (Fig. 17E), sub-equal setae on distal left leg.
This is one of the smallest calanoid copepods and tends to be found in highest numbers towards the sea bottom (Østvedt, 1955). Even in the earliest stages the characteristic prosome shape is obvious.


Fig. 17. Microcalanus pusillus (after Sars, 1903, from Rose, 1933).
Recorded: PMF, not recorded. L4, rare. All around Britain and Ireland. North Sea. Norwegian coast.
Total length: Female $0.7-0.88 \mathrm{~mm}$; male $0.7-0.8 \mathrm{~mm}$.
Further information: Sars, 1900, 1903; Rose, 1933; Brodskii, 1950; Mazzocchi et al., 1995; Conway, 2012.

## Genus Pseudocalanus:

Superficially similar in appearance to Paracalanus, Ctenocalanus and Clausocalanus spp. Frost (1989) carried out a study on the distribution of this genus and found $P$. elongatus all around the European region. A second species, $P$. acuspes, was distributed around northern Scotland, the northern North Sea and in the Baltic region. The two species are not particularly easy to separate morphologically. P. acuspes is generally much larger (female 1.26-2.27 mm; male 1.19-1.74 mm), but the length ranges of the two species overlap. However, length ranges usually do not overlap where they co-exist.

Pseudocalanus elongatus (Boeck, 1865)
A1 of both sexes reaches half-way down the urosome (Fig. 18A, D); first pedigerous somite fused to cephalosome to form cephalothorax and fourth and fifth fused; exopods of P2-P4 with a distal blade, serrated on the outer edge (Fig. 18B).
Female: Urosome $\sim 44 \%$ of length of prosome (Fig. 18A); genital somite as long as the following two somites together, in lateral view quite produced anteriorly; P1 smaller than other legs. No P5. Marshall (1949) reported that in Loch Striven (western Scotland), a variable proportion ( $<1 \%$ ) of Co6 female $P$. elongatus can have an additional rudimentary P5, so it is possible that this type of intersex female (see Gusmão \& McKinnon, 2009) could initially be confused with Ctenocalanus vanus. Intersex $P$. elongatus sometimes occur in very low numbers at L4.
Male: Slenderer than the female; anal somite very short (Fig. 18C-E); P5 asymmetrical (Fig. 18F), large, robust and extending to around the end of the urosome (Fig. 18C, D), longer on left; five segments on left P5, four on right, distal segment on right in form of a sharp stylet.

Eggs appear to be carried as an egg mass without an enclosing membrane (Marshall, 1949) and can be easily detached. From measurements of preserved eggs from the Celtic Sea in April 1983, they have a diameter of $0.13-0.14 \mathrm{~mm}$ (unpublished) and from off Plymouth as $0.12-0.13 \mathrm{~mm}$ (Frost, 1989). Fresh eggs from off Plymouth were 0.10-0.12 mm (Conway et al., 1994).


Fig.18. Pseudocalanus elongatus (A-C, E, F after Sars, 1903, from Rose, 1933; D from Breemen, 1908).

Recorded: PMF. L4, common. All around Britain and Ireland. North Sea.
Total length: Female $0.93-1.77 \mathrm{~mm}$; male $0.97-1.37 \mathrm{~mm}$.
Further information: Sars, 1903; Breemen, 1908; Rose, 1933; Brodskii, 1950; Corkett, 1968; Corkett \& McLaren, 1969; Frost, 1989; Avancini et al., 2006; Conway, 2012.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Diaixidae:

## Genus Diaixis:

Diaixis hibernica (A. Scott, 1896)
Generally found close to the sea bottom in shallow waters. In both sexes rostrum simple, without filaments; first pedigerous somite fused to cephalosome to form cephalothorax (Fig. 19A, D).
Female: A1 reaching the end of the genital somite (Fig. 19A); last metasome somite with pointed extensions either side of urosome (Fig. 19B) that can be quite transparent and not particularly conspicuous; maxilla with a set of approximately five worm-like sensory appendages at the tip (Fig. 19C), similar to those found in Family Scolecitrichidae. No P5.
Male: A1 not geniculate; prosome shape resembling the female (Fig. 19D), but last metasome somite very small and rounded; urosome slender; P5 massive, asymmetrical and irregular (Fig. 19D, E), extending well beyond urosome; basal segment swollen, bearing a group of around five curved spines; right P5 distal segment movable, with two processes; last two segments of left P5 very short, distal segment with a slender seta and two short spines (Fig. 19F).


Fig. 19. Diaixis hibernica (A, B, D-F after Sars, 1903, from Rose, 1933; C from Sars, 1903).
Recorded: PMF, not recorded. L4, rare. Coastal regions of Britain, Ireland, and Norway Total length: Female 1.2 mm ; male 1.1 mm .
Further information: Sars, 1903; Rose, 1933; Avancini et al., 2006.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Phaennidae:

Genus Xanthocalanus:
Xanthocalanus minor Giesbrecht, 1893
Large scavengers, living close to the sea bottom. Both sexes with a pair of small anterior eyes; first pedigerous somite partially fused to cephalosome.
Female: Last metasome somite with sharp points distally (Fig. 20A, B, D) that curve slightly outwards when viewed dorsally (Fig. 20A); urosome of four somites, narrow; genital somite hardly swelling ventrally (Fig. 20D), with two dorsal, spherical seminal receptacles; anal somite short, hardly visible in dorsal view. P5 small, uniramous, symmetrical (Fig. 20C), of two segments, first segment with fine spines on inner border, second segment with fine spines on outer border that extend around onto posterior surface, P5 with three short, distal, thick spines of slightly different lengths.
Male: A1 not geniculate; body slender, particularly anteriorly, often more transparent than female; last metasome somite without points; urosome of five somites; anal somite very short and furcae often divergent; P5 very slender, reaching two-thirds down urosome, uniramous and similar length both sides (Fig. 20E); left leg five-segmented, fifth segment very small with short setae opposite an extension of the fourth segment; right leg six-segmented, distal segment sharply pointed.


Fig. 20. Xanthocalanus minor (A-C from Sars, 1921b; D from Bradford-Grieve, 2004; E from Aurevillius, 1898, as $X$. fragilis).

Recorded: Not recorded from Plymouth. Irish Sea. Norwegian coast.
Total length: Female $2.50-2.95 \mathrm{~mm}$; male 2.15 mm .
Further information: Giesbrecht, 1893; Aurevillius, 1898; Sars, 1921b; Matthews, 1964; BradfordGrieve, 2004.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Euchaetidae:

## Genus Paraeuchaeta:

Paraeuchaeta hebes (Giesbrecht, 1888)
First pedigerous somite partially fused to cephalosome; both sexes with long urosomes and also very large maxillipeds (Fig. 21A), associated in the females with their carnivorous diet. In the Euchaetidae, males do not feed and some parts of the mouthparts are atrophied. The retention of large maxillipeds in males may be associated with capture of females during mating. In both sexes the A1 have characteristic very long, fine setae (Fig. 21A) that seem to survive sampling and preservation well; anterior body pointed in dorsal view; in lateral view a single strong rostrum is obvious, with a frontal eminence just behind (Fig. 21B). Innermost (appendicular) seta on each furca very well developed and much longer than the other caudal setae (Fig. 21A).
Female: A1 reaches genital somite (Fig. 21A); genital somite very prominent when viewed laterally, with small notch on mid-dorsal surface (Fig. 21C); No P5. Often sampled bearing eggs.
Male: A1 not geniculate; P5 very large and characteristic (Fig. 21D), with rudimentary endopods internally on both legs; right leg with very elongated segment distally; left leg with a complex distal joint.

A larger Paraeuchaeta species, P. norvegica (Boeck, 1872), is found in more northern waters, although there are isolated populations in deep fjordic lochs on the Scottish north-west coast, such as Loch Etive. However, there is an isolated record from the Irish Sea (Nicholas \& Nash, 1999; as Euchaeta norvegica) when two females were sampled around the same time as a few $P$. hebes.


Fig. 21. Paraeuchaeta hebes (after Sars, 1925, from Rose, 1933; as Euchaeta hebes).
Recorded: PMF (as Euchaeta hebes). L4, in low numbers. Irish Sea. Western English Channel. West of Ireland.
Total length: Female $2.85-2.95 \mathrm{~mm}$; male 2.75 mm .
Further information: Sars, 1925; Rose, 1933; Mauchline, 1999 (all as Euchaeta hebes); Avancini et al., 2006; Vives \& Shmeleva, 2006.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Scolecitrichidae:

## Genus Scolecithricella:

Scolecithricella minor (Brady, 1883)
In both sexes cephalosome and first pedigerous somite fused to form cephalothorax; rostrum bifurcated.
Female: A1 reaches just beyond the prosome; anterior cephalothorax broadly and distinctively rounded in lateral view (Fig. 22C); last metasome somite rounded in dorsal view, slightly angular in lateral view (Fig. 22A, B). In common with other members of this family, the maxilla terminates in worm-like sensory appendages (Fig. 22F). Urosome short and conspicuously narrow; genital somite in lateral view not very pronounced; P5 very reduced (Fig. 22D), two-segmented, uniramous, second segment symmetrical, generally oval and flattened, twice as long as wide, with a short spine on the outer margin and apex, and a long spine on the inner margin. However, in other areas, P5 have been found that are not short and oval, but more elongated (Fig. 22E).
Male: A1 not geniculate; resembles the female in size and general form (Fig. 22G), but the urosome is more elongated; posterior metasome somite rounded in dorsal and lateral view; P5 asymmetrical, longer than urosome (Fig. 22G, H); right P5 biramous, but with only a vestigial endopod; left P5 biramous, also with vestigial endopod that extends to around the middle of the second segment of the exopod; distal segment of the exopod elongated and bayonet-like.


Fig. 22. Scolecithricella minor (A-D, F, H from Sars, 1903; E, H from Mori, 1937).
Recorded: PMF, not recorded. L4, only Scolecithricella sp., but probably this species, rare. West of Ireland. North Sea.
Total length: Female $1.08-1.46 \mathrm{~mm}$; male $1.20-1.46 \mathrm{~mm}$.
Further information: Sars, 1903; Rose, 1933; Mori, 1937; Park, 1980.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Stephidae:

Genus Stephos:
Stephos scotti G.O. Sars, 1903
A very small species, found close to the bottom. Cephalosome fused with first pedigerous somite to form cephalothorax.
Female: A1 reaching the second urosome somite (Fig. 23A); cephalothorax longer than metasome; last metasome somite symmetrical; genital somite v-shaped in lateral view, smooth without any prominences (Fig. 23B); P5 tiny (Fig. 23C), simple, uniramous, distal segment with around ten coarse, short teeth externally.
Male: A1 not geniculate (Fig. 23D); smaller than female and urosome slenderer; large asymmetrical P5 (Fig. 23D, E), the right leg longer and slenderer than the left, terminating in a sickle-shaped segment, base of penultimate segment produced into a sharp projection; left P5 penultimate segment very swollen, last segment with four short flattened spines externally and two thin plates distally.


Fig. 23. Stephos scotti (from Sars, 1903).
Recorded: PMF. L4, not recorded. Millbay Marina, Plymouth, May 2011. Coastal regions of Britain, Ireland, Norway and southern North Sea.
Total length: Female 0.95 mm ; male 0.85 mm .
Further information: Sars, 1903; Rose, 1933.

## Stephos minor Scott, 1892

A very small species, found close to the bottom. Cephalosome fused with first pedigerous somite to form cephalothorax.
Female: A1 as long as prosome (Fig. 24A); prosome robust, rounded anteriorly; cephalothorax longer than metasome; last metasome somite symmetrical and rounded; P5 uniramous with basal segment and two further segments (Fig. 24B), last segment terminating in three points, one external, one internal and one apical.
Male: A1 not geniculate, similar to female A1 (Fig. 24C); P5 massive, longer than urosome (Fig. $24 \mathrm{C}, \mathrm{D}$ ), right P5 terminating in a long curved hook, base of the penultimate segment with much blunter projection than in S. Scotti; Left P5 shorter than right, penultimate segment not as swollen as in S. scotti, coming to an obtuse point internally, last segment with four short flattened spines externally and two long thin plates distally.


Fig. 24. Stephos minor (after Sars 1921b, from Rose, 1933).
Recorded: Not recorded from Plymouth, but could occur. Southampton. Coast of Scotland.
Total length: Female $0.74-0.95 \mathrm{~mm}$; male $0.74-0.85 \mathrm{~mm}$.
Further information: Scott, 1892; Sars, 1921b; Rose, 1933; Muxagata \& Williams, 2004.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Calanidae:

## Genus Calanus

Calanus helgolandicus (Claus, 1863)
A1 longer than body by two segments (Fig. 25B, D), the distal penultimate and previous segments each bearing a long seta of similar length; rostrum of two fine filaments.
Female: Anterior cephalosome slightly angular in lateral view (Fig. 25B); urosome of four somites, approximately half the length of the metasome; P5 similar in size and appearance to the other swimming legs, inner margin of basal segment obviously concave, with toothed fringe (Fig. 25C), teeth tending to be larger than those in Calanus finmarchicus.
Male: A1 not geniculate, proximal two segments fused and thickened, making base much more robust than in the female (Fig. 25D); anterior cephalosome in lateral view slightly more pointed than in male C. finmarchicus. P5 large, differing from most male copepods by having both legs quite similar (Fig. 25E), basal segments slightly concave with row of large teeth; left leg much longer than the right, distal segment of right leg almost reaching the end of the second last segment of the left leg. The P5 is also slightly asymmetrical in the Co5, so sexes can be separated.
A) Female, dorsal
B) Female, lateral
D) Male, lateral


Fig. 25. Calanus helgolandicus (A, B, D, E after Sars, 1903, from Rose, 1933; C from Sir Alister Hardy Foundation for Ocean Science (SAHFOS) training notes).

Recorded: PMF. L4, common. All around Britain and Ireland. North Sea.
Total length: Female $2.60-3.28 \mathrm{~mm}$; male 2.79-3.27 mm.
Further information: Sars, 1903; Rose, 1933; Marshall \& Orr, 1955; Frost, 1974; Gerber, 2000; Avancini et al., 2006; Conway, 2012; Vives \& Shmeleva, 2006.

Calanus finmarchicus (Gunnerus, 1770)
A1 longer than body by two segments (Fig. 26B, F), the distal penultimate and previous segments each bearing a long seta of similar length; rostrum of two fine filaments.
Female: Urosome of four somites (Fig. 26A-C), approximately half length of metasome; anterior cephalosome distinctly rounded in lateral view (Fig. 26B); P5 similar to other swimming legs, basal segment inner margin straight or slightly convex (Fig. 26D), up to 40 fine teeth.
Male: A1 not geniculate (Fig. 26F), proximal two segments fused and thickened, making base much more robust than in female; P5 large, similar to the other swimming legs (Fig. 26G), slightly asymmetrical, distal segment of right leg reaching around middle of the last segment of the left leg, internal margin of basal segment concave, with large teeth. The P5 is also slightly asymmetrical in the Co5, so sexes can be separated.
C. finmarchicus is a more northern species, but is recorded in low numbers from the English Channel and Western Approaches (Continuous Plankton Recorder Survey Team, 2004). It occasionally occurs off Plymouth, but always as a tiny proportion of the Calanus population. When C. finmarchicus and C. helgolandicus were first established as separate species (Rees, 1949), Russell (1951) re-examined Calanus sample from L4 that had been used in published papers and found small numbers of $C$. finmarchicus. Very small numbers of $C$. finmarchicus were noted in samples from L4 in April 2007 and January and February 2008, so probably occur most years, but sporadically in low numbers, so may be missed among the high numbers of $C$. helgolandicus.


Fig. 26. Calanus finmarchicus (A-C, E-G after Sars, 1903, from Rose, 1933; D from SAHFOS training notes
Recorded: PMF. L4, occasionally in low numbers. Northern North Sea. Irish Sea. West of Britain.
Total length: Female 2.4-3.9 mm; male 2.3-3.6 mm.
Further information: Sars, 1903; Rose, 1933; Frost, 1974; Conway, 2012; Vives \& Shmeleva, 2006.

## Genus Calanoides:

Calanoides carinatus (Krøyer, 1849)
Female: A1 does not extend beyond the end of urosome (Fig. 27A); anterior cephalosome distinctly pointed (Fig. 27A-C); last metasome somite rounded; P5 of similar size and appearance to other swimming legs (Fig. 27D), inner margin of basal segments slightly convex and smooth.
Male: A1 not geniculate; anterior cephalosome not pointed as in female (Fig. 27E), but more so than in Calanus helgolandicus male; endopod of left P5 reduced to a simple segment without setae (Fig. 27F); inner margin of basal segment smooth.


Fig. 27. Calanoides carinatus (A-C, F after Giesbrecht, 1893, from Rose, 1933, both as Calanus brevicornis; D from Alvarez-Marques, 1984; E from Corral Estrada, 1970).

Recorded: PMF, not recorded. L4, rare. Southwest of Britain and Ireland.
Total length: Female $2.25-2.85 \mathrm{~mm}$; male 2.2-2.5 mm .
Further information: Giesbrecht, 1893; Rose, 1933; Corral Estrada, 1970; Alvarez-Marques, 1984; Ramirez \& Sabatini, 2000; Conway, 2012; Vives \& Shmeleva, 2006.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Paracalanidae:

## Genus Paracalanus:

Paracalanus parvus (Claus, 1863)
May initially be confused with Clausocalanus, Pseudocalanus or Ctenocalanus spp., but differs in the shape of the male and female P5. No serrations on the outer edge of the long distal blade of the exopods of P2-P4 (Fig. 28C). First pedigerous somite fused to cephalosome to form cephalothorax.
Female: A1 reaches to around the middle of the urosome (Fig. 28A); urosome $\sim 0.31 \%$ of length of the prosome, so is relatively shorter than in Pseudocalanus, Ctenocalanus or Clausocalanus spp.; genital and anal somites approximately the same length. Segment three of exopods of P3 and P4 with row of fine spines on outside margin (Fig. 28C); P5 tiny, delicate, uniramous (Fig. 25B), distal segment with long slender spine at tip and a much smaller spine outside this, normally symmetrical and two-, occasionally three-segmented. lanora et al. (1987) found females with the left P5 with up to five segments, in the most extreme case closely resembling the male P5. Sars (1903) drew the distal spine with an internal seta mid-way down (Fig. 28B), but this was not drawn by Razouls (1972) or other authors, and has not been seen in $L 4$ specimens (it may require a high magnification to see?).
Male: A1 not geniculate, quite robust (Fig, 28D); slight hump on the dorsal prosome; second urosome somites the longest; P5 reaches half-way down the urosome (Fig. 28C), slender, asymmetrical, uniramous (Fig. 28E); right leg short, two-segmented, resembling the female P5 limbs; left leg five-segmented; both legs terminating in two sub-equal spines.


Fig. 28. Paracalanus parvus (A-E after Sars, 1903, from Rose, 1933).
Recorded: PMF. L4, very common. All around Britain. North Sea. West of Ireland.
Total length: Female 0.70-1.20 mm; male 0.8-1.4 mm.
Further information: Sars, 1903; Rose, 1933; Brodskii, 1950; Razouls, 1972; Gardner \& Szabo, 1982; Gerber, 2000; Avancini et al., 2006; Conway, 2012; Vives \& Shmeleva, 2006.

## Genus Calocalanus:

Both Calocalanus sp. and Ischnocalanus sp. have been recorded on very rare occasions from L4, but were not identified to species. Ischnocalanus is now considered synonymous with Calocalanus (Bradford-Grieve, 1994). While the copepods that were sampled were not identified to species, Calocalanus pavo, a species that could occur in the region is given as an example of this genus.

## Calocalanus pavo (Dana, 1852)

Female: Usually quite transparent; prosome stout, three times as long as wide (Fig. 29A, B); cephalosome and first pedigerous somite fused to form cephalothorax. Only in well-preserved specimens do the plumose setae on the A1 and furcae (Fig. 29B) survive; urosome of two free somites, genital somite onion-shaped (Fig 29A, D), slightly protuberant in lateral view (Fig. 29D); furcae symmetrical, elongate and typically divergent. P5 uniramous, symmetrical (Fig. 29C), foursegmented, distal segment with four plumose setae and one small spine distally, a further seta internally, also bearing two rows of tiny spinules.
Male: A1 not geniculate (Fig. 29F); body shape differs from female, but can also have plumose A1 and furcae; cephalosome and first pedigerous partially fused; posterior metasome extending laterally into almost square corners (Fig. 29E-F, H); urosome of five somites; furcae longer than wide, less divergent than in female. P5 small and uniramous (Fig. 291), limbs of unequal lengths, both terminating in two sub-equal spines, right leg with fine sub-distal spinules internal to longer spine; shorter right leg not extending as far as distal border of the second segment of the left leg.






Fig. 29. Calocalanus pavo (A, C, D, G-I from Bradford-Grieve, 1994; B, F after Giesbrecht, 1893, from Rose, 1933; E from Corral Estrada, 1972).

Recorded: PMF, not recorded. L4, only as Calocalanus sp., rare. Southwest of Britain and Ireland. Total length: Female $0.85-1.40 \mathrm{~mm}$; male $1.04-1.18 \mathrm{~mm}$.
Further information: Giesbrecht, 1893; Rose, 1933; Corral Estrada, 1972; Bradford-Grieve, 1994; Avancini et al., 2006.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Acartiidae:

Acartiidae are common copepods, especially in coastal and estuarine brackish water environments. Many are known to produce diapause eggs that allow them to lie dormant in the sediment until conditions become favourable for hatching, or to be transported in ballast water to other parts of the world, making them a common alien introduced species. It is also recognized that morphological anomalies may be created in polluted environments (e.g. Brylinski, 1984).
Genus Acartia:
Characteristically, the many fine setae on the A1 and furcae, survive sampling and preservation better than in most other copepods. Their slim bodies tend to be quite transparent, even when preserved and they usually have an obvious dark eye. Females have three free urosome somites.

## Acartia clausi Giesbrecht, 1889

Rostral filaments (see Fig. 34B) absent in both sexes. Resembles A. margalefi, but A. margalefi is much smaller and lacks the array of small spines on the urosome.
Female: A1 slightly shorter than prosome (Fig. 30A, B); two to four small, strong spines on posterior dorsal metasome and some small stiff hairs ventrally (Fig. 30D, E); genital and following somite bordered posteriodorsally with conspicuous small spines (Fig. 30C); in lateral view genital swelling centrally situated on genital somite (Fig. 30D).
Male: Posterior dorsal prosome bordered by small spines, ventrally by tiny stiff hairs (Fig. 30H); urosome somites one to four bordered posteriodorsally by tiny spines, not drawn on the first somite by Alcaraz (1976; Fig 30I). First segment of left P5 with two rows of tiny spines (Fig. 30J), one row on inner edge ridge and other on posterior surface, distal segment with spine, lobe and fine setae (Fig. 30K); distal segment of right P5 with no inner spine (as found in A. margaleff), previous two segments each with internal lobes (Fig. 30J).


Fig. 30. Acartia clausi (A-F, H, J from Bradford-Grieve, 1999b; G after Giesbrecht, 1889, from Rose, 1933; I and K from Alcaraz, 1976).

Recorded: PMF. L4, common species. All around Britain and Ireland. North Sea.
Total length: Female 0.81-1.47 mm; male 0.71-1.32 mm.
Further information: Giesbrecht, 1889, 1892; Sars, 1903; Rose, 1933; Alcaraz, 1976; BradfordGrieve, 1999b; Avancini et al., 2006; Conway, 2012.

Acartia margalefi Alcaraz, 1976
Brackish water species, an alien introduction in northern Europe. Rostral filaments (see Fig. 34B) absent in both sexes. Similar to A. clausi, but much smaller and lacks spines on the urosome in both sexes.
Female: Posterior metasome with two to five tiny spines (Fig. 31A), difficult to see and not as obvious as in A. clausi; genital somite swelling is anteriorly situated (Fig. 31B); seta on P5 longer than the pointed distal segment (Fig. 31D).
Male: Posterior metasome with tiny spines dorsally (Fig. 31E, F) and hairs ventrally; genital somite may have hairs distally, other somites without spines or hairs. Left P5 second segment usually with two posterior rows of small spines (Fig. 31H), proximal row short, but sometimes absent; second segment with an inner border of hairs, distal segment with a spine a lobe and setae. Right P5 distal segment with an inner spine, absent in A. clausi, previous segment with a distally rounded lobe.
Acartia teclae Bradford, 1976 (Female $0.71-0.87 \mathrm{~mm}$; male $0.64-0.72 \mathrm{~mm}$ ), is another alien introduction in northern Europe that is very similar morphologically to A. margalefi. The females have an overlapping length range, but $A$. teclae has a much smaller mean length, obvious if the species are sampled together. It has been recorded from western Scotland, western Norway and the western North Sea (Bradford, 1976). Specimens believed to be of this species have also recently been recorded from the coastal eastern Irish Sea. A further alien introduction, A. omorii (Bradford, 1976) was recorded from Calais harbour, northern France (Seuront, 2005), but may not have become established in the area.
A) Female, dorsa

B) Female, urosome lateral

C) Female, urosome dorsal

F) Male, urosome

D) Female, P5

I) Male, left leg, distal segment


Fig. 31. Acartia margalefi (A, E, G, I from Alcaraz, 1976; B-D, F, H from Bradford-Grieve, 1999b).
Recorded: PMF and L4, not recorded. Southampton, Plymouth and many other localities in Europe where it is an alien introduction, probably from the Mediterranean region.
Total length: Female 0.79-0.91 mm; male 0.80-0.90 mm.
Further information: Alcaraz, 1976; Bradford, 1976; Castro-Longoria \& Williams, 1996; BradfordGrieve, 1999b; Avancini et al., 2006.

## Acartia discaudata (Giesbrecht, 1881)

Brackish water species. Rostral filaments (see Fig. 34B) absent in both sexes.
Female: Last metasome somite and urosome without spines (Fig. 32A, B); urosome robust, genital somite large, second somite with posteriodorsal rounded extension; furcae distinctively broad and oval; anal somite flattened and expanded; P5 (Fig. 32C) similar to those of A. clausi.
Male: Furcae not broad as in the female (Fig. 32D); P5 large (Fig. 32E), right leg very elongated, more than twice as long as the left, with pronounced lobes on the first and third segments, but none on the second as found in A. clausi; left P5 first segment with two rows of small spines, the distal row longer.


Fig. 32. Acartia discaudata (A, C, D after Sars, 1903, from Rose, 1933; B, E from Bradford-Grieve, 1999b).

Recorded: PMF. L4, not recorded. Millbay Marina, Plymouth. Coastal regions of much of Europe. Total length: Female 1-1.2 mm; male 0.9-1.1mm.
Further information: Sars, 1903; Rose, 1933; Bradford-Grieve, 1999b.

Acartia longiremis (Lilljeborg, 1853)
Rostral filaments (see Fig.34B) absent in both sexes.
Female: A1 extends to middle of genital somite (Fig. 33A); last metasome somite rounded, a prominent large spine and a few inconspicuous fine spines distally on each side (Fig. 33B); urosome somites with fine spinules on lateral and posterior borders. P5 with long slender distal spine, slightly longer than the seta on the previous segment (Fig. 33C).
Male: Last metasome somite also with prominent large spine on each side (Fig. 33D); right P5 with the second and third segments expanded internally into round lamellar projections (Fig. 33E), left P5 first segment bearing a large and a small spine internally.


Fig. 33. Acartia longiremis (A, C, D after Sars, 1903, from Rose, 1933; B, E from Bradford-Grieve, 1999b).

Recorded: PMF and L4, not recorded. English Channel (Rose, 1933). North Sea off Newcastle (Frid \& Huliselan, 1996). Northern North Sea. West of Ireland.
Total length: Female $0.98-1.25 \mathrm{~mm}$; male $0.9-1.05 \mathrm{~mm}$.
Further information: Sars, 1903; Rose, 1933; Bradford-Grieve, 1999b; Gerber, 2000.

## Acartia tonsa Dana, 1849

Brackish water species. Rostral filaments (Fig. 34B) present in both sexes. Arrangement of spines and setae on the urosome may be variable, so illustrations from two authors are shown.
Female: Small fine spines on dorsoposterior border of last metasome somite (Fig. 34C, D) and on posterior of first two somites of urosome (but need high magnification to see); fine spinules sometimes present on dorsal surface of urosome somites and furcae (Fig. 34C); urosome short, genital somite broadest in anterior part. P5 first segment with internal lobe and outer seta; (Fig. 34 E ), second segment longer than the external seta on previous segment, with bulbous base, coarsely denticulate distally.
Male: Fine spines on dorsal posterior border of last metasome somite and on rear dorsal edge of the first to fourth urosome somites (Fig. 34F, G); tiny spinules present on dorsal surface of urosome somites and furcae; left P5 with distal spine and sub-distal lobe with thickened base (Fig. $34 \mathrm{H}, \mathrm{I})$.


Fig. 34. Acartia tonsa (A, D, E, G, H from Rémy, 1927; B, C, F, I from Bradford-Grieve, 1999b).
Recorded: PMF, upper River Tamar estuary. L4, not recorded. Coastal regions of Europe.
Total length: Female $1.3-1.5 \mathrm{~mm}$; male $1.0-1.1 \mathrm{~mm}$.
Further information: Rémy, 1927; Rose, 1933; Belmonte et al., 1994; Bradford-Grieve, 1999b; Gerber, 2000; Avancini et al., 2006.

Acartia bifilosa (Giesbrecht, 1881)
Brackish water, sometimes coastal species, previously described in the literature under two varieties, intermedia and inermis (e.g. Rose, 1933; Bradford-Grieve, 1999b). However, individuals have been shown to vary considerably in morphology, even in the same population (Brylinski, 1984). Hirst \& Castro-Longoria (1998) re-examined specimens used in original descriptions and also fresh specimens, and showed that the varieties are not valid, resulting from a combination of variable morphology and inadequate original descriptions. Some extra diagrams have been included in Figure 35 to illustrate the morphological variability.
Rostral filaments (Fig. 35H) present in both sexes.
Female: A1 not extending beyond the posterior margin of the genital somite (Fig. 35B); last metasome somite rounded and may bear fine setules, but no spines; genital and following somite with variable number of fine setules on dorsal surface, but no spines. However, Crisafi \& Crescenti (1972) drew a single sharp spine on each side of the metasome (Fig. 35A) and also small spines on the dorsal distal edges of the genital and following somite? P5 distal spiny segment distinctly swollen at base and with fine spines either side at tip (Fig. 35D), this segment slightly longer than outer seta on previous segment, but appearance variable (Brylinski, 1984).
Male: Last metasome somite and some of the urosome somites may bear fine setules, but no strong spines. However, Crisafi \& Crescenti (1972) drew small spines on the distal borders of some of the urosome somites (Fig. 35G)? P5 similar to that of $A$. clausi, but second segment of right leg with two inner expansions, with a spine on proximal one (Fig. 35I, J), distal segment of left P5 with two spines and a broad appendage, but appearance variable (Brylinski, 1984).


Fig. 35. Acartia bifilosa (A, F, G from Crisafi \& Crescenti, 1972; B, I from Giesbrecht, 1893; C-E, H from Rose, 1929 as A. bifilosa var. inermis).

Recorded: PMF, mid River Tamar. L4, not recorded. All around coast of Europe.
Total length: Female $1.02-1.10 \mathrm{~mm}$; male $1.0-1.1 \mathrm{~mm}$.
Further information: Rose, 1929, 1933; Crisafi \& Crescenti, 1972; Brylinski, 1984; Hirst \& CastroLongoria, 1998; Bradford-Grieve, 1999b; Avancini et al., 2006.

## Genus Paracartia:

Paracartia grani G.O. Sars, 1904
Brackish water, sometimes coastal species. Rostral filaments (see Fig. 35H) present in both sexes. Female: A1 nearly as long as the prosome (Fig. 36A); posterior prosome corners extended in form of wings; urosome without spines, short with genital somite strongly enlarged (Fig. 36C); spermatophore, if present, narrow and bottle-shaped with curved plate on each side (Fig. 36C, D); furcae each with a very thick spine. P5 first segment with short seta, second segment curved with distal array of fine spinules (Fig. 36B)
Male: Right A1 very strongly geniculate (Fig. 36E), segment after hinge, armed with a long spine; posterior prosome rounded; urosome slender and naked. P5 basal segment with a central, pointed projection (Fig. 36F); right P5 almost three times as long as left.


Fig. 36. Paracartia grani (A-B, E-F after Sars, 1904, from Rose, 1933; C from Bradford-Grieve, 1999b; D from Breemen, 1908).

Recorded: PMF, rare. L4, not recorded. Norwegian coast. French coast.
Total length: Female 1.0 mm ; male 1.0 mm .
Further information: Sars, 1904; Breemen, 1908 (as Acartia grani); Rose, 1933 (as A. grani); Bradford-Grieve, 1999b; Avancini et al., 2006.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Candaciidae:

## Genus Candacia.

Candacia armata Boeck, 1872
Medium-sized, robust copepod, with obvious square front to the cephalosome in dorsal view (Fig. 37A, D) and pronounced "shoulders" behind. Even in young stages, there may be tinges of black pigment on the ends of the swimming legs or dorsally between the prosome somites. Prosome comprises cephalosome and four free somites, the fourth and fifth pedigerous somites fused; maxilla conspicuously large in both sexes, associated with their carnivorous diet, obvious even in Co1; maxilliped much reduced.
Female: Last metasome somite ends in widely spaced, sharp points, reaching beyond the middle of the genital somite (Fig. 37A); urosome asymmetrical, of three free somites, the last somite with irregular dorsal lappet that curves to the left side dorsally (Fig. 37A, C); furcae asymmetrical, the left slightly smaller than the right. P5 small, uniramous, symmetrical (Fig. 37B), the last segment longer than the other two combined, terminating in a simple point, outer edge with three small denticles, inner edge smooth.
Male: A1 strongly geniculate on right (Fig. 37D), the swollen section ending in a usually darkly coloured, strongly serrated segment (Fig. 37F); last metasome somite asymmetrical, produced into widely spaced sharp points; urosome genital somite with a prominent pointed process, directed to the right. P5 small and simple (Fig. 37E).

D) Male, dorsal

F) Male, geniculate A1 hinge area


Fig. 37. Candacia armata (after Sars, 1903, from Rose, 1933).
Recorded: PMF. L4, regularly in low numbers. North Sea. Irish Sea. West of Ireland.
Total length: Female 1.95-2.7 mm; male 1.7-2.7 mm.
Further information: Sars, 1903; Rose, 1933; Grice, 1963; Conway, 2012.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Centropagidae:

## Genus Centropages:

Centropages typicus Krøyer, 1849
In both sexes cephalosome narrows anteriorly, widening around a third of the way down; lateral corners of the posterior metasome somite ending in widely spaced sharp points, with a characteristic undulating edge on the section between the point and the urosome.
Female: A1 with strong spines on segments one, two and five (Fig. 38A, B); urosome asymmetrical, with three free somites; three spines on genital somite and slight bulge ventrolaterally on the right side of somite two (Fig. 38D); furcae widening distally, often slightly divergent. P5 with strong spine on the inner second segment of the exopod (Fig. 38C).
Male: A1 with strong spines on segments one, two and five, similar to female (Fig. 38E), geniculate on right, very thickened along part of its length, with a single spine on segment 16 of the thickened portion. Last metasome somite asymmetrical; urosome symmetrical and slender, with only four somites visible, unusual in male calanoids. P5 right exopod with a complex distal claw, typical of the genus (Fig. 38F).
Appearing in coastal areas of the Adriatic, as an alien introduction, is the tropical/subtropical species Pseudodiaptomus marinus (de Olazabal \& Tirelli, 2011). They could initially be confused with Centropages spp., but one obvious difference is that females have four somites in the urosome. They are now being reported from the southern North Sea (M. Wootton, L. Postel, pers. comm.).


Fig. 38. Centropages typicus (A-C, E-F after Sars, 1903, from Rose, 1933; D from SAHFOS training notes).

Recorded: PMF. L4, common. North Sea. Irish Sea. West of Ireland.
Total length: Female $1.6-2.0 \mathrm{~mm}$; male $1.4-1.9 \mathrm{~mm}$.
Further information: Sars, 1903; Rose, 1933; Gerber, 2000; Avancini et al., 2006; Conway, 2012; Vives \& Shmeleva, 2006.

## Centropages chierchiae Giesbrecht, 1889

Description the same as for C. typicus; the only differences are given below.
Female: Ventrolateral bulge on the right side of the second segment of urosome considerably more pronounced than in C. typicus (Fig. 39B, C).
Male: Thickened part of the geniculate A1 bears two spines (Fig. 39H), compared to one spine in C. typicus.


Fig. 39. Centropages chierchiae (A, B, E, G, H after Giesbrecht, 1889, from Rose, 1933; C from SAHFOS training notes; D, F from Lee, 1972).

Recorded: PMF, not recorded. L4, rare. Southwest of Britain and Ireland.
Total length: Female $1.8-1.9 \mathrm{~mm}$; male $1.65-1.75 \mathrm{~mm}$.
Further information: Giesbrecht, 1889; Rose, 1933; Lee, 1972; Vives \& Shmeleva, 2006.

## Centropages hamatus (Lilljeborg, 1853)

In both sexes, lateral corners of the posterior metasome somite end in a spine, with a characteristic undulating edge on the section between the spine and the urosome. No spines on the base of the A1 as found in Centropages typicus (Fig. 40A, D).
Female: Last metasome somite asymmetrical(Fig. 30A), but less expanded than in C. typicus; three free somites in the urosome; many fine setae on lateral edges of genital somite and strong spine on ventral surface, immediately in front of genital orifice (Fig. 40C); furcae almost three times as long as broad. P5 with strong spine on the inner second segment of the exopod (Fig. 40B), distal blade more coarsely serrated than in C. typicus.
Male: Slenderer than the female; A1 geniculate on right, very thickened along part of its length, without spines on the thickened section (Fig. 40D); last metasome somite slightly asymmetrical; urosome of only four somites; furcae comparatively longer than in female. Right P5 exopod with a complex claw, typical of the genus (Fig. 40E).


Fig. 40. Centropages hamatus (after Sars, 1903, from Rose, 1933).
Recorded: PMF. L4, less common than C. typicus. All around Britain and Ireland. North Sea. Total length: Female $1.27-1.62 \mathrm{~mm}$; male $1.27-1.47 \mathrm{~mm}$.
Further information: Sars, 1903; Rose, 1933; Gerber, 2000; Conway, 2012; Vives \& Shmeleva, 2006.

## Genus Isias:

Isias clavipes Boeck, 1865
Both sexes small with rounded prosome (Fig. 41); long urosome and furcae; large P5.
Female: A1 just reaches genital somite (Fig. 41B); P5 robust with strong spine on the hind face of the second segment, near the outer corner (Fig. 41C), endopod very small, second exopod segment with strong pointed projection on inner side; three free somites in urosome (Fig. 41A, B); swelling on left dorsal face of genital somite, sometimes difficult to see, two prominent hooks on ventral surface, one each side of the genital area (Fig. 41B, D); furcae four times as long as broad. Male: Slenderer than the female (Fig. 41E); right A1 moderately geniculate; urosome of five somites, longer and narrower than in the female, obvious lateral projection on somite three; furcae long, around four times as long as wide. Left P5 distal segment with four marginal spines (Fig. 41F), the inner edge with fine hairs, right P5 distal segment wide and oval, with pointed protuberance on the inside and one long and two short spines distally.


Fig. 41. Isias clavipes (B from Sars, 1903; A, C-F after Sars, 1903, from Rose, 1933).
Recorded: PMF. L4, rare. All around Britain and Ireland. Southern North Sea.
Total length: Female $1.25-1.3 \mathrm{~mm}$; male 1.25 mm .
Further information: Sars, 1903; Rose, 1933; Avancini et al., 2006.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Parapontellidae:

## Genus Parapontella:

Parapontella brevicornis (Lubbock, 1857)
Female: A1 short, reaching to the second somite of the metasome (Fig. 42A, B); three free somites in the urosome, second urosome somite with two dorsolateral spines on posterior margin; furcae around three times as long as broad. P5 exopod very narrow and slightly curved (Fig. 42C), ending in a slender spine with two smaller spines on outer edge; endopod half the length of exopod and ending in two short processes.
Male: Slenderer than the female (Fig. 42D); A1 strongly geniculate on the right (Fig. 42D, E); last metasome somite asymmetrical, ending in a point either side, longer on right; urosome somites three and four each with lateral projections pointing to the right. P5 asymmetrical (Fig. 42F), right leg longer than left, with broad first segment bearing a long spine internally; second segment of both legs with a short, sharp internal projection.


Fig. 42. Parapontella brevicornis (A,C, F, G after Sars, 1903, from Rose, 1933; B, D, E from Sars, 1903).

Recorded: PMF. L4, quite rare. Mainly coastal around most of Europe.
Total length: Female $1.37-1.60 \mathrm{~mm}$; male $1.25-1.55 \mathrm{~mm}$.
Further information: Sars, 1903; Rose, 1933

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Pontellidae

The two common pontellids sampled off southern Britain are described here. A third pontellid, Pontella lobiancoi (Canu, 1888), has been sampled on rare occasions off the northern French coast (Brylinski, 2009).
Genus Labidocera:
Labidocera wollastoni (Lubbock, 1857)
Both sexes with prominent lateral hooks on anterior cephalosome (Fig. 43A, F); two lenses on the dorsal cephalosome; deeply bifurcated rostrum
Female: Last metasome somite produced into two symmetrical broad points (Fig. 43A); urosome short and broad, of three somites, with large, bulbous swelling dorsally on the genital somite that overlaps the following somite (Fig. 43C); dorsal lenses small and widely spaced. P5 small, biramous, robust and simple (Fig. 43B), without any spines or setae.
Male: Slenderer than the female (Fig. 43D); A1 strongly geniculate (Fig. 43D, G, H); dorsal lenses very large and close together (Fig. 43F); lateral corners of last metasome somite shorter than in the female and obtusely rounded (Fig. 43D, E); P5 very asymmetrical, right leg terminating in a massive claw (Fig. 43I).


Fig. 43. Labidocera wollastoni (A-C, F-I after Sars, 1903, from Rose, 1933; D, E from Sars, 1903).
Recorded: PMF. L4, occasionally in small numbers. Southern North Sea.
Total length: Female 2.2-2.4 mm; male 2.2-2.3 mm.
Further information: Sars, 1903; Rose, 1933; Avancini et al., 2006.

## Genus Anomalocera:

Anomalocera patersoni Templeton, 1837
Surface-living species. Both sexes with prominent lateral hooks on the anterior cephalosome (Fig. 44A, D); posterior somite of metasome with large pointed processes; two pairs of lenses on the dorsal cephalosome and a ventral lens which extends anterioventrally between the deeply bifurcate rostrum (Fig. 44C). Typically tinged blue, especially when unpreserved.
Female: Urosome of three somites, with spine on right posterior margin of genital somite (Fig. 44A); P5 small, biramous with tiny endopods (Fig. 44B).
Male: A1 strongly geniculate on right (Fig. 44D); last metasome somite asymmetrical, left posterior corner similar to female, right corner longer and curving; first somite of the urosome produced into a lateral point. Both limbs of P5 of similar length, claw on right (Fig. 44E).


Fig. 44. Anomalocera patersoni (after Sars, 1903, from Rose, 1933).
Recorded: PMF. L4, regularly in low numbers. All around Britain and Ireland. North Sea. Total length: Female 3.2-4.1 mm; male 3.0-4.0 mm.
Further information: Sars, 1903; Rose, 1933; Avancini et al., 2006.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Temoridae:

## Genus Temora:

Temora longicornis (O.F Müller, 1785)
Cephalosome is widest part of prosome (Fig. 45A, D); prosome deepest half-way down (Fig. 45C); pedigerous somites four and five fused to give four somites in metasome. Furcae characteristically long in both sexes, obvious even in earliest stages.
Female: A1 reaches around end of anal somite (Fig. 45A); metasome narrows posteriorly, last somite rounded, urosome of three somites, middle somite shortest. P5 small, uniramous, threesegmented with two distal and two sub-distal spines (Fig. 45B).
Male: Prosome somites have less bulging profile than drawn in Figure 45D. A1 moderately geniculate on right (Fig. 45C, E); last metasome somite rounded (Fig. 45C, D). Left P5 larger than right, four-segmented (Fig. 45F), outer segments forming large claw; right P5 three-segmented, distal segment curving inwards.


Fig. 45. Temora longicornis (A-B, F after Sars, 1903, from Rose, 1933; C, E from Sars, 1903; D from Wilson, 1932).

Recorded: PMF. L4, very common. All around Europe.
Total length: Female $1.00-1.66 \mathrm{~mm}$; male $1.00-1.46 \mathrm{~mm}$.
Further information: Sars, 1903; Rose, 1933; Corkett, 1967; Gerber, 2000; Avancini et al., 2006;
Conway, 2012.

## Temora stylifera (Dana, 1849)

Similar to other Temora spp., furcae characteristically very long in both sexes (Fig. 46A, C, D). Pedigerous somites four and five fused to give four somites in metasome. Last metasome somite with pointed projections.
Female: Cephalosome wider than metasome (Fig. 46A), cloak-like, especially in pre-adults; three free somites in the urosome; P5 small, uniramous, three-segmented (Fig. 46B), ending in two distal and two sub-distal spines.
Male: A1 moderately geniculate on right (Fig. 46F); last metasome somite slightly asymmetrical (Fig. 46C, D). P5 very asymmetrical, left leg four-segmented, last segment broad and flattened (Fig. 46E), right leg three-segmented, curving around inner process on second segment of left leg (note reverse orientation of legs to show this feature).


Fig. 46. Temora stylifera (A-B, D-E after Giesbrecht, 1893, from Rose, 1933; C after Ramirez, 1966; F from Fleminger \& Hulseman, 1973).

Recorded: PMF, not recorded. L4, rare. Southwest Britain and Ireland. Atlantic coast of France.
Total length: Female $1.45-1.90 \mathrm{~mm}$; male $1.4-1.5 \mathrm{~mm}$.
Further information: Giesbrecht, 1893; Rose, 1933; Ramirez, 1966; Fleminger \& Hulseman, 1973; Cartotenuto, 1999; Avancini et al., 2006; Conway, 2012.

## Genus Eurytemora:

Eurytemora affinis (Poppe, 1880)
Brackish water species. Furcae very long in both sexes, up to seven times as long as wide (Fig. 47A, B, D); fifth pedigerous somite small.
Female: A1 reaching almost to end of metasome (Fig. 47A, B); prosome slender and parallelsided; slight dorsal hump at rear of last cephalosome somite; last metasome somite with divergent pointed processes, directed forwards in lateral view; urosome of three somites, genital somite swollen laterally, often with egg sac or remains, or festooned with spermatophores (Fig. 47B). P5 uniramous and robust, penultimate segment with two outer spines and a large inner spine (Fig. 47C).
Male: Slenderer than the female (Fig. 47D); A1 moderately geniculate on right; last metasome somite not extended in processes like female. P5 left distal segment with three projections at end and a hollow between (Fig. 47E, F), right distal segment long, slightly curved and tapering.


Fig. 47. Eurytemora affinis (A, C-F after Sars, 1903, from Rose, 1933; B from Sars, 1903; both as E. hirundoides).

Recorded: PMF, River Tamar, Plymouth, tidal reaches to Plymouth Sound. L4, not recorded. European brackish water regions.
Total length: Female $1.0-1.65 \mathrm{~mm}$; male $1.0-1.65 \mathrm{~mm}$.
Further information: Sars, 1903; Rose, 1933 (both as E. hirundoides); Dussart, 1967; Gerber, 2000.

Eurytemora velox (Lilljeborg, 1853)
Brackish water species. Furcae long in both sexes (Fig. 48A, B, D), but not as long as in Temora spp. or $E$. affinis.
Female: A1 reaches almost to end of metasome (fig. 48A, B); prosome more oval than in $E$. affinis; dorsal hump at rear of last cephalosome somite (Fig. 48B); last metasome somite with pointed processes, slightly outward curving when viewed dorsally, with spiny outer edges (Fig. 48A), points pointing forwards when viewed laterally (Fig. 48B); three free somites in the urosome; furcae slightly longer than anal somite. P5 uniramous and robust, with only one spine on the outer penultimate segment (Fig. 48C), compared to two in E. affinis.
Male: Much slenderer than the female (Fig. 48D); right A1 moderately geniculate; last metasome somite rounded; urosome narrow and elongate; furcae as long as the two previous somites. P5 slenderer than in $E$. affinis, left leg terminating in two lobes, the distal one pointed (Fig. 48E).


Fig. 48. Eurytemora velox (A, C-E after Sars, 1903, from Rose, 1933; B from Sars, 1903).
Recorded: PMF, in saline marshes bordering River Tamar tidal regions, Plymouth. L4, not recorded. European brackish water regions.
Total length: Female 1.3-2.0 mm; male 1.2-1.5 mm.
Further information: Sars, 1903; Rose, 1933; Dussart, 1967.

Eurytemora americana Williams, 1906
Brackish water species. This is considered to be an alien species, introduced from the USA. It was recorded in other parts of southern England around the same time that Gurney (1933b) recorded his single specimen in Plymouth Sound. It has not subsequently been recorded from Plymouth, which possibly may be because little brackish water plankton sampling is carried out locally. There also do not appear to be subsequent records from other areas of Britain, although it has been found on the northern French coast (Brylinski, 2009).

Female: A1 reaching genital somite; prosome slightly rounded laterally (Fig. 49A); generally no pronounced dorsal hump at rear of last cephalosome somite; last metasome somite with large, pointed lateral projections, the left side slightly larger, with rounded inner lobe (Fig. 49C); this somite of variable shape in different populations. Three free somites in the urosome (Fig. 49A, D); genital somite with distal lobe on ventral surface (Fig. 49C, D); anal somite and furcae covered dorsally in fine spinules (Fig. 49A); furcae around seven times as long as wide. P5 first exopod segment with long outer seta (Fig. 49B), penultimate segment with two external spines and strong inner spine; distal segment with two long apical spines of almost equal length. P5 structure variable between populations.
Male: A1 moderately geniculate (Fig. 49F), series of spines on segments 8 -12; small hump on dorsoposterior cephalosome; last metasome somite rounded (Fig. 49E); furcae from seven to nine times as long as wide (Fig. 49H). P5 right second segment expanded on inner edge and twice as long as broad (Fig. 49G), following segment long and slender and distal segment long and curved; left P5 distal segment expanded at end into two lobes.


F) Male, A1 and detail of segments 8-12

E) Male, dorsal

H) Male, urosome


Fig. 49. Eurytemora americana (A-D, F-H from Brylinski, 2009; E after Heron, 1964).
Recorded: PMF and L4 not recorded. Off Drake's Island, Plymouth Sound (Gurney, 1933b). Northern French coast.
Total length: Female $1.2-1.4 \mathrm{~mm}$; male $1.24-1.3 \mathrm{~mm}$.
Further information: Gurney, 1933b (appendix); Heron, 1964; Grice, 1971; Brylinski, 2009; Gerber, 2000.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Eucalanidae:

## Genus Subeucalanus.

Subeucalanus crassus (Giesbrecht, 1888)
First pedigerous somite fused with cephalosome and fourth and fifth pedigerous somites fused (Fig. 50A, C).
Female: A1 reaches to furcae (Fig. 50A); body robust; anterior cephalothorax wide and rounded anteriorly; urosome of three free somites, genital somite wider than long and markedly onionshaped (Fig. 50A, B); anal somite fused with furcae, furcae slightly asymmetrical. No P5.
Male: A1 not geniculate, reaching to around the end of the furcae (Fig. 50C); genital somite longer than wide, five somites in urosome. P5 right leg missing; left leg uniramous, four-segmented, with distal spine (Fig. 50D).

The large nauplii stages are sometimes sampled at Plymouth, in association with the adults, immediately recognisable by their large, boat-shaped bodies and long paddle-like A1 (Fig. 50E). The A1 in preserved specimens usually points diagonally forwards. Nauplii are usually colourfully tinged with orange pigment.


Fig. 50. Subeucalanus crassus (A, B from Bradford-Grieve, 1994; C, D from Fleminger, 1973; E from Björnberg, 1972).

Recorded: PMF not recorded. L4, regularly in low numbers. Southwest Britain and Ireland. Total length: Female: 2.46-3.70 mm; male: 2.40-3.10 mm.
Further information: Rose, 1933; Fleminger, 1973; Bradford-Grieve, 1994.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

## Family Pseudocyclopidae:

## Genus Pseudocyclops:

Pseudocyclops obtusatus Brady \& Robertson, 1873
This species probably lives close to the bottom.
Female: A1 very short, hardly reaching beyond cephalosome (Fig. 51A, B); prosome oval, rounded in lateral view; large eye may be visible; rostrum robust, sharply pointed (Fig. 51B, D). Last metasome somite very small; urosome of three somites, short; furcae around the same length as width. P5 endopod three-segmented (Fig. 51C); exopod distal segment with four internal setae and four distal spines.
Male: Slightly smaller than female (Fig. 51E); A1 very short, geniculate on right (Fig. 51E, F), about same length as cephalosome; urosome much slenderer than in female, with some of the somites slightly raised dorsally. P5 large, basal segments swollen (Fig 51G); left P5 terminating in a lobe and thin processes, right in two long curved projections.


Fig. 51. Pseudocyclops obtusatus (B-D, G after Sars, 1903, from Rose, 1933; A, E, F from Sars, 1903).

Recorded: PMF, inner Plymouth Sound, rare. L4, not recorded. Coasts of Britain, Ireland and Norway.
Total length: Female 0.8 mm ; male 0.7 mm .
Further information: Sars, 1903; Rose, 1933.

## Superorder Podoplea:

Cephalosome and first pedigerous somite free, partially fused, or fused to form cephalothorax, but additional fusion sometimes takes place, particularly in Order Siphonostomatoida and some of Order Cyclopoida; prosome and urosome articulate between pedigerous somites four and five rather than pedigerous somite five and the genital somite as in gymnopleans, so the first urosome somite bears the P5; urosome usually with five free somites in female, six in male, but some species have as few as two; males have either both A1 geniculate, or neither.

## Order Cyclopoida:

Copepods that were previously in Order Poecilostomatoida are now merged within Order Cyclopoida (Boxshall \& Halsey, 2004). This order includes many species that are parasites or associates of other animals. The prosome typically comprises cephalosome and four free pedigerous somites, and this is the case with all species described here, but there are members with fewer somites. The only common marine cyclopoid in which the males have geniculate A1 are in Family Oithonidae (page 101), where both are geniculate and structurally quite complex. A2 uniramous; sharp division between prosome and urosome; P1-4 well developed; urosome typically of five free somites in female, six in male, but some species have as few as three or even two (e.g. Corycaeidae; page 116); P5 much reduced, similar in both sexes. A few females carry single egg sacs (e.g. Monothula subtilis; page 109), but most have paired sacs attached laterally or dorsally, never to the ventral surface as in Harpacticoida.

## Key to families of Cyclopoida described

1. A1 of female with more than ten segments; male A1 geniculate on both sides $\qquad$ Oithonidae (page 101)

- A1 in both sexes at most of seven segments, never geniculate in males ---------------------2

2. Pair of elaborate cuticular lenses on anterior cephalothorax; prosome bilaterally compressed; caudal furcae cylindrical -------------------------------------- Corycaeidae (page 116)

- No lenses on anterior cephalosome

3
3. Prosome broad, dorsoventrally compressed; urosome broad ----------- Oncaeidae (page 106)

- Prosome and urosome elongated and slender ------------------------ Lubbockiidae (page 114)


## Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda: Superorder Podoplea: Order Cyclopoida:

## Family Oithonidae:

Oithona is the only Oithonidae genus recorded in the PMF. It is one of the commonest copepod genera sampled in all the worlds' oceans (Gallienne \& Robins, 2001). A1 quite long, geniculate both sides in male; generally small, slim, elongated bodies, tapering at opposing ends of the prosome; prosome comprising cephalosome and four free pedigerous somites; urosome of five free somites in female, six in male; P5 on the first urosome somite, in both sexes very simple, reduced in the species described here to two setae on each side, emerging from a papilla and a single exopod segment respectively. Females carry paired egg sacs laterally.
Only four species are found in northern European waters. The females of these are relatively simple to separate as they have easily observed morphological differences, but the males are more difficult to separate, requiring detailed examination of appendages. It should be taken into account that environmental condition can modify body length, and number and length of setae on the swimming and feeding appendages (Nishida et al., 1977). Some species, including some of those described here, have cosmopolitan distributions, but can show slight morphological variations in different parts of their range and it is possible that they represent more than one species.

## Key to Oithona species described

A1 long, not geniculate; five somites in urosome

## Females

1. Rostrum pointed in lateral view; A1 longer than prosome ---------------------------------------2

- No distinct rostrum in lateral view; A1 same length as prosome ------------ O. nana Fig. 52

2. Rostrum clearly visible dorsally ------------------------------------------------------------------------------3

- Rostrum not visible dorsally ------------------------------------------------------------- O. similis Fig. 55

3. Genital somite with characteristic tuft of hairs on ventral side ---------- O. plumifera Fig. 53

- Genital somite without tuft of hairs on ventral side ------------------------- O. atlantica Fig. 54


## Males

1. Outer edge of P1 exopod with one, one and three setae --------------------- O. nana Fig. 52

2. Outer edge of P1-P4 exopods with one, one and two setae O. similis Fig. 55

- Outer edge of P2-P3 exopods with one, one and three setae ---------- O. plumifera Fig. 53 or O. atlantica Fig. 54


## Genus Oithona:

Oithona nana Giesbrecht, 1893
Female: A1, around same length as prosome (Fig. 52A); prosome oval in dorsal view, no distinct rostrum (Fig. 52B). Outer edge of P1-P4 exopods with 1, 1, 3; 1, 1, 3; 1, 1, 3; 1, 1, 2 marginal spines on the segments (Fig. 52E-H); P5 on first urosome somite (Fig. 52A, D), comprising one seta attached to short dorsolateral process and one long ventrolateral free segment with one long seta; P6 on genital somite, with slightly curved tiny dorsal seta with minute setules, and thinner but longer ventral seta, both on a small protrusion. Genital somite approximately twice as long as wide, very swollen laterally in anterior quarter; anal somite as long as wide (Fig. 52A); furcae more than twice as long as wide.
Male: Prosome shorter than in female (Fig. 521); no distinct rostrum (Fig. 52J); outer edge of P1-P4 exopod with the same number of marginal spines on the segments as female (Fig. 52P-S); P5 as in female (Fig. 52N), P6 with two subequal setae that extend to posterior end of urosome somite three, attaching directly to small ventrolateral process on posterior margin of genital somite; genital somite slightly wider than following somite, slightly longer than wide, with two small oval seminal receptacles; anal somite as long as wide (Fig. 52O); furcae more than twice as long as wide.


D) Female, genital somite


Oithona plumifera Baird, 1843
This species is virtually identical to $O$. atlantica and there has been confusion among taxonomists when identifying them in the past, which is still not completely resolved, at least for males. Although O. plumifera is recorded in the PMF, any specimens should be examined carefully.
Female: A1 long, reaching anal somite Fig. 53B); anterior cephalosome narrows into pointed rostrum visible in dorsal view (Fig. 53A, B), in lateral view bent anterioventrally into sharp point (Fig. 53D). Outer edge of P1-P4 exopod with 1, 1, 2; 1, 0, 2; 1, 0, 1; 0, 0, 1 marginal spines on the segments (Fig. 53G-J); external marginal seta on the third segment of the P4 exopod smoothly curved inwards (less curved in O. atlantica); P3 and P4 exopod third segments with a small spinule externally; P5 with one long seta attached directly to lateral process of first urosome somite and one moderately long, free segment with a long seta (Fig. 53E); P6 on genital somite, with one tiny seta; genital somite twice as long as wide, swollen laterally in anterior third, with characteristic tuft of hairs on ventral proximal side and small protrusion beside. Furcae shorter than anal somite, three times longer than wide (Fig. 53F). Can have very plumose setae on the A1, P1-P4 and furcae (Fig. 53B), but this feature is variable.
Male: Anterior cephalosome shape very different to female (Fig. 53K); no distinct rostrum, in lateral view area comes to blunt point (Fig. 53L); outer edge of P1-P4 exopod with 1, 1, 2; 1, 1, 3; 1, 1, 3; 1, 1, 2 marginal spines on the segments (Fig. 53G-J). Genital somite, almost as wide as long (Fig. 53 K ), with two small oval seminal receptacles; anal somite similar length to two preceding somites. Wilson (1932) said that O. plumifera had a semicircular protrusion on the penultimate A1 segment, but the source of this information is unknown and possibly wrong. O. atlantica in the northwest Atlantic, has this protrusion (Gerber, 2000), which may distinguish males of the two species





Fig. 53. Oithona plumifera (A, C-J from Nishida, 1985; B, K from Rose, 1933 after Giesbrecht, 1893; L, M-P from Nishida et al., 1977).

Recorded: PMF. L4, not recorded. Southwest Britain. Northern North Sea. West of Ireland. Total length: Female $1.10-1.50 \mathrm{~mm}$; male $0.64-1.00 \mathrm{~mm}$.
Further information: Rose, 1933; Nishida et al., 1977; Nishida, 1985; Avancini et al., 2006.

Oithona atlantica Farran, 1908
This species is virtually identical to O. plumifera. It is not known if they occur off southern Britain, so any specimens thought to be $O$. plumifera should be examined with this species in mind.
Female: Same description as for 0 . plumifera, but in lateral view, proximal end of ventral side of genital somite does not have tuft of hairs (Fig. 54D), but has same small ventral protrusion. External marginal seta on the third segment of the P4 exopod less curved inwards than in 0 . plumifera (Fig. 54H).
Male: Same description as for O. plumifera. Gerber (2000) illustrated males with a semicircular protrusion on the penultimate segment of the A1 (Fig. 54I, K), similar to that found in O. similis (Fig. 55P). These were sampled in association with females that fitted the description for the species and in water masses that O. plumifera would be unlikely to be found in (R. Gerber, pers. comm.). They were larger than $O$. similis males present in the same sample and showed different spination on P1-P5. This antennular protrusion feature was not drawn by Sars (1918), and it may not be present on individuals in other parts of its range.


Fig. 54. Oithona atlantica (A, B, D, I-K from Gerber, 2000; C, E-H from Nishida, 1985.
Recorded: PMF, not recorded. L4, not recorded. West of Britain and Ireland?
Total length: Female $1.14-1.43 \mathrm{~mm}$; male $0.65-0.82 \mathrm{~mm}$.
Further information: Sars, 1918 (as O. spinirostris); Nishida et al., 1977; Nishida, 1985; Gerber, 2000.

Oithona similis Claus, 1866
Female: A1 slender, not quite reaching genital somite (Fig. 55A, B, D), bearing fine, long setae. Cephalosome narrowed anteriorly, but not to a point; rostrum present, but not visible dorsally, in lateral view directed forwards, pointed and slightly curving (Fig. 55C). Outer edge of P1-P4 exopod with $1,1,2 ; 1,0,1 ; 1,0,1 ; 0,0,1$ marginal spines on the segments (Fig. 55F-I); minute notch on middle external edge of third exopod segment of P2-3. Urosome approximately same length as prosome (Fig. 55A, B); genital somite more than twice as long as wide (Fig. 55J, K), anterior third swollen laterally; anal somite slightly longer than wide (Fig. 55E); furcae shorter than anal somite, more than twice as long as wide, divergent; second furcal seta when intact, longer than urosome (Fig. 55B); ovisacs usually with single row of very large eggs.
Male: Prosome broader than in female (Fig. 55L, M); A1 short double-geniculate, with semicircular protrusion on penultimate segment (Fig. 55P); no distinct rostrum, in lateral view comes to slight point (Fig. 55N). Outer edge of P1-P4 exopod with 1, 1, 2; 1, 1, 2; 1, 1, 2; 1, 1, 2 marginal spines on the segments (Fig. 55F-I). Genital somite rounded, with two oval seminal receptacles, slightly wider than following somite; furcae as long as wide, similar length to anal somite (Fig. 55R).


Fig. 55. Oithona similis (A, C-K, from Nishida, 1985; B, Q from Rose, 1933 after Sars, 1918 as 0. helgolandica; L, N from Nisheda et al., 1977; M, O from Wilson, 1932; P, R from Gerber, 2000).

Recorded: PMF (as O. helgolandica). L4, common. All around Britain and Ireland. North Sea
Total length: Female $0.68-0.96 \mathrm{~mm}$; male $0.50-0.70 \mathrm{~mm}$.
Further information: Wilson, 1932; Rose, 1933 (as O. helgolandica); Nishida et al., 1977; Nishida, 1985; Gerber, 2000; Avancini et al., 2006; Conway, 2012.

## Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda: Superorder Podoplea: Order Cyclopoida:

## Family Oncaeidae:

Most oncaeids are quite small, with half of the known species being $<0.6 \mathrm{~mm}$ in length. Some species can show morphological variations and many are very similar, so identification requires careful dissection and examination. These factors, in association with a lack of adequate descriptions and reliable identification keys for some areas, have lead to erroneous identifications and distribution records (Böttger-Schnack, 2001; Böttger-Schnack \& Schnack, 2009).
The number of species described for Family Oncaeidae keeps increasing and the family structure has been revised by Huys \& Böttger-Schnack (1997) and Böttger-Schnack (1999). Some species, previously included in the genus Oncaea have been reclassified to become the genera Triconia and Monothula, including species that have been recorded from the Plymouth area. Because of advances in oncaeid identification, the list of species included here will probably not represent all those occurring off southern Britain, as newly described sister or sibling species previously may have been recorded under one common name. Because of the taxonomic difficulties associated with the Oncaeidae, I gratefully acknowledge the help given by Dr Ruth Böttger-Schnack in checking this section of the guide.

A1 six-segmented in females, four-segmented and non-geniculate in males; A2 three-segmented. Maxillipeds four-segmented in females, three-segmented in males, ending in a hook or claw. Prosome comprises cephalosome and four free pedigerous somites; distinct boundary between prosome and urosome; urosome with five free somites in females, six in males. Paired genital apertures on the genital double-somite, situated dorsally in females, ventrally in males. Females carry paired egg sacs, except in Monothula, which has a single egg sac. The sacs are carried in a dorsal position, corresponding to the position of the genital apertures.

Key to Oncaeidae species described



## Females

1. P2-P4 endopod distal segment with outer sub-distal spine ------------------------------------------2

- P2-P4 endopod distal segment without outer sub-distal spine ---------------------------------------3

2. P4 endopod distal segment with conical projection between distal and sub-distal spine $\qquad$ Triconia minuta (Fig. 56)

- P4 endopod distal segment without conical projection between distal and sub-distal spine

3. A2 distal segment shorter than previous segment; first and second post-genital somites short, shorter than anal somite; paired dorsal egg sacs Oncaea ornata (Fig. 61)

- A2 distal segment longer than previous segment; first and second post-genital somites long, longer than anal somite; single dorsal egg sac

Monothula subtilis (Fig. 57)
4. Maxilliped basis segment with distal seta $\sim 0.25$ length of segment

Oncaea mediterranea (Fig. 58)

- Maxilliped basis segment with distal seta $\sim 0.5$ length of segment 5

5. P4 endopod distal spine $\sim 0.5$ the length of distal segment Oncaea venusta (Fig. 59)

- P4 endopod distal spine $\sim 0.6-0.7$ the length of distal segment - Oncaea waldemari (Fig. 60)


## Males

1. P2-P4 endopod distal segment with outer sub-distal spine

- P2-P4 endopod distal segment without outer sub-distal spine

2. P4 endopod distal segment with conical projection between distal and sub-distal spines $\qquad$ Triconia minuta (Fig. 56)

- P4 endopod distal segment without conical projection between distal and outer sub-distal spines

3. A2 distal segment shorter than previous segment

Oncaea ornata (Fig. 61)

- A2 distal segment longer than previous segment Monothula subtilis (Fig. 57)

4. Genital flaps relatively large, visible dorsally $\qquad$ Oncaea mediterranea (Fig. 58)

- Genital flaps relatively small, not as prominent dorsally

5. Furcae approximately 1.7 times longer than wide Oncaea waldemari (Fig. 60)

- Furcae approximately 3.5 times longer than wide Oncaea venusta (Fig. 59)

Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda: Superorder Podoplea: Order Cyclopoida: Family Oncaeidae:

## Genus Triconia:

Triconia minuta (Giesbrecht, 1893)
Female: Very small copepod with slender body; prosome 2.4 times length of urosome excluding furcae (Fig. 56A, B); second pedigerous somite does not project dorsally (Fig. 6B); genital somite 1.8 times as long as maximum width (Fig. 56C), oval-shaped, widest anteriorly, gradually tapering posteriorly; anal somite around same length as furcae. A1 six-segmented (Fig. 56E); A2 threesegmented, distal segment with a comb-like strong seta and three curved setae proximally and five curved and two slender setae distally (Fig. 56F). Maxilliped basis segment broad and elongated (Fig. 56G), ornamented with tiny spinules and setae and two large setae of similar lengths on inner margin, distal segment (claw) with fine setae along two-thirds of curved inner margin. Distal endopod segment of P2-P4 with distal conical projection (Fig. 56H) and thin outer sub-distal spine; P5 with plumose seta representing the outer basal seta of the P5, emerging directly from lateral surface of first urosome somite (Fig. 56I), and a small free segment representing the exopod, with two setae, the larger stout and curved; P6 represented by operculae closing off the genital apertures (Fig. 56C), each armed with a large and small spinule.
Male: Slimmer than female (Fig. 56J); A1 four-segmented (Fig. 56M); basis segment of maxilliped with two slender setae on inner margin, shorter than in female (Fig. 56N), distal curved hook without ornamentation. Furcae shorter than in female, 1.4 times longer than wide (Fig. 56K); P1-P4 with armature as in female; P5 similar to female (Fig. 56K, L), but exopod without segmentation where it emerges from the first urosome somite; P6 represented by posterolateral genital flaps, closing off genital apertures, covered with spinules; spermatophore oval (Fig. 56L).


Fig. 56. Triconia minuta (from Böttger-Schnack, 1999).
Recorded: PMF (as Oncaea minuta). L4, not recorded. Southern UK. Norwegian and Irish coasts. Total length: Female $0.45-0.58 \mathrm{~mm}$; male $0.39-0.41 \mathrm{~mm}$.
Further information: Giesbrecht, 1893; Wilson, 1932; Rose, 1933; Razouls, 1974a; (all as O. minuta); Böttger-Schnack, 1999.

Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda: Superorder Podoplea: Order Cyclopoida: Family Oncaeidae:

## Genus Monothula:

Monothula subtilis (Giesbrecht, 1893)
Female: Prosome elongate, around twice the length of urosome excluding furcae (Fig. 57A, B); A2 distinctly curved backwards (Fig. 57C), distal segment longer than previous segment; basis segment of maxilliped with two long setae of equal length on inner margin (Fig. 57D), in addition to rows of spinules, distal claw segment with tiny spinules along four-fifths of curved inner margin; P2-P4 endopod distal segment without outer sub-distal spine, P4 distal spine as long as distal segment (Fig. 57E); P2 and P3 distal endopod segment with conical projection, P4 without; P5 comprising long seta emerging from first urosome segment, representing outer basal seta and a small segment fused to the urosome somite representing the exopod, bearing a stout and a slender seta (Fig. 57F). Genital double-somite 1.5 times as long as maximum width, lateral margins rounded, with largest width measured at anterior half, posterior part tapering gradually; P6 represented by an operculum armed with one long spine and a spinule. Anal somite slightly longer than wide and just longer than caudal furcae, which are slightly more than twice as long as wide (Fig. 57A). Single dorsal egg sac.
Male: Furcae around same length as anal somite, 1.8 times longer than wide (Fig. 57G, H); A2 distal segment longer than previous segment, similar to female; maxilliped basis segment with two setae on inner margin (Fig. 57K), the proximal longest, distal claw without spinules on inner edge. P1-P4 armature similar to female; outer sub-distal endopod spine on P2 and P3 almost as long as conical projection. P6 represented by posterolateral genital flaps closing off genital aperture, corners protruding laterally (Fig. 571), surface ornamented with tiny spinules.


Fig. 57. Monothula subtilis. (A-H from Heron \& Frost, 2000; I-K from Gallo, 1976).
Recorded: PMF. L4 (both as Oncaea subtilis). Southern North Sea. Coastal Ireland and Norway. Total length: Female $0.44-0.69 \mathrm{~mm}$; male $0.34-0.62 \mathrm{~mm}$.
Further information: Giesbrecht, 1893; Rose, 1933; Gallo, 1976; Heron \& Frost, 2000 (all as 0. subtilis); Böttger-Schnack \& Huys, 2001; Conway, 2012).

Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda: Superorder Podoplea: Order Cyclopoida: Family Oncaeidae:

## Genus Oncaea:

Oncaea mediterranea (Claus, 1863)
This oncaeid has one of the most widely recorded distributions (Böttger-Schnack \& Huys, 1997), but has often been misidentified, so some distributional records need verification.
Female: Prosome 1.9 times urosome length excluding furcae (Fig. 58A, B); third metasome somite with conspicuous raised lateral pore each side (Fig. 58A), last metasome somite obviously pointed in dorsal view, tips directed slightly outwards; genital somite elongate, nearly twice as long as maximum width (Fig. 58C, D), more than twice the length of posterior somites; anal somite 1.3 times wider than long, around two-thirds length of furcae; furcae around three times as long as wide. A2 three-segmented, distinctly bent backwards (Fig. 58F), proximal segment elongated and distal segment short; maxilliped basis segment inner margin with two strong setae of similar length, approximately quarter the length of the segment (Fig. 58G), spinules only on proximal half of inner margin of distal claw. P2 and P3 endopods with conical projection between distal and sub-distal spines (Fig. 58H), P4 without; distal endopod segment of P2-P4 with outer sub-distal spine (Fig. 581); P6 represented by operculum bearing a spine and two small spinous processes (Fig. 58C, D). Male: Smaller than female; last prosome somite conspicuously pointed laterally (Fig. 58K); maxilliped basis segment with two longer setae internally (Fig. 58O), but much smaller than in female, distal claw without ornamentation internally; P1-4 with armature as in female; furcae 1.8 times longer than wide (Fig. 58L), much shorter than in female; genital somite broad, nearly three times as long as posterior urosome somites; genital flaps at distal corners of genital somite, with prominent backward directed projections in both dorsal and ventral view (Fig, 58K-M).


Fig. 58. Oncaea mediterranea (from Böttger-Schnack \& Huys, 1997, © Natural History Museum, reproduced with permission).

Recorded: PMF. L4, not recorded. Exact distribution in northern Europe still to be established.
Total length: Female $1.00-1.30 \mathrm{~mm}$; male: $0.70-1.05 \mathrm{~mm}$.
Further information: Giesbrecht, 1893; Rose, 1933; Razouls, 1974a; Malt, 1983a, b; Heron \& Bradford-Grieve, 1995; Böttger-Schnack \& Huys, 1997; Böttger-Schnack, 2001.

Oncaea venusta Philippi, 1843 forma typica Farran, 1929, forma venella Farran, 1929
Two types of this species are described, forma typica and venella (e.g. Böttger-Schnack, 2001), which differ in size and also minor morphological features. Forma typica is described here.
Female: Prosome 2.1 times length of urosome, excluding furcae (Fig. 59A, B), third metasome somite with tiny but conspicuous lateral raised pore each side (as in O. mediterranea; Fig. 58A), last somite with rounded posterolateral corners; genital double-somite 1.5 times as long as wide, longer than remaining urosome somites (Fig. 59C, D); anal somite 1.6 times wider than long, about half the length of furcae; furcae about 3.5 times longer than wide; A2 distinctly curved backwards (Fig. 59F), middle segment almost triangular, distal segment short; basis segment of maxilliped with two long setae internally (Fig. 59G), distal one half length of segment. P2-P4 distal endopod segment with outer sub-distal spine (Fig. 59H), P2-P3 with distal conical projection, P4 without; P4 endopod distal spine about half the length of distal segment; P6 armature represented by a spine and two small spiny processes (Fig. 591), only one of which really visible under light microscope. Egg sacs paired.
Male: Body narrower than female (Fig. 59J); prosome 2.0 times length of urosome, excluding furcae; genital somite more than three times longer than remaining urosome somites (Fig. 59K, L), posterolateral genital flaps with small lateral points, hardly visible dorsally; furcae around 2.5 times longer than wide. Maxilliped with two longer setae on internal basis segment (Fig. 590), much smaller than in female; P1-P4 with armature as in female; conical projection on distal endopod segment of P2-P3 as in female, but longer (Fig. 59P), around half the length of sub-distal spine.


Fig. 59. Oncaea venusta. (from Böttger-Schnack, 2001, © Natural History Museum, reproduced with permission).

Recorded: PMF. L4. Distribution in northern European area uncertain.
Total length: Forma typica female $1.00-1.23 \mathrm{~mm}$; male $0.88-0.95 \mathrm{~mm}$. Forma venella female $0.70-0.92 \mathrm{~mm}$; male $0.57-0.73 \mathrm{~mm}$
Further information: Rose, 1933; Boxshall, 1977; Malt, 1983a, b; Heron \& Bradford-Grieve 1995; Böttger-Schnack, 2001; Avancini et al., 2006.

Oncaea waldemari Bersano \& Boxshall, 1996 ["1994"]
Female: Prosome 1.7 times length of urosome, excluding furcae (Fig. 60A, B); A2 second segment 1.4 times longer than distal segment (Fig. 60E), distal segment short, less than 2.5 times longer than wide; basis segment of maxilliped with two long setae internally (Fig. 60F), distal spine longer than proximal, distal claw with row of fine spinules along most of curved inner margin; distal endopod segment of P2-P4 with outer sub-distal spine (Fig. 60G, H), only P2 and P3 with conical projection on distal endopod; P4 endopod distal spine approximately two thirds the length of distal segment; genital somite 1.4 times as long as maximum width (Fig. 60C); anal somite short, two thirds as long as furcae, about 2.6 times longer than wide; furcae 2.6 times longer than wide, very variable in length.
Male: Similar body form to female; genital somite almost twice as long as wide, with evenly rounded convex lateral sides (Fig. 601); third to fifth urosome somites very short; anal somite around twice as wide as long; furcae about 1.2 times length of anal somite, 1.7 times longer than greatest width, shorter than in female; maxilliped basis segment more robust than in female (Fig. 60 K ), armed with two longer setae internally, shorter than in female, distal claw almost as long as basis, without spinules on internal curved edge; P1-P4 armature similar to female; P6 represented by posterolateral flaps with sharp lateral corners (Fig. 60I), visible dorsally.


Fig. 60. Oncaea waldemari. (from Bersano \& Boxshall, 1996 ("1994")).
Recorded: PMF and L4, not recorded. Plymouth Sound (Malt, 1982; as O. media forma minor Sewell, 1947). Southwest UK.
Total length: Female $0.62-0.69 \mathrm{~mm}$; male $0.50-0.52 \mathrm{~mm}$. Lengths from Plymouth area (Malt, 1982) but highly variable in different regions of the world (Böttger-Schnack, 2001).

Further information: Malt, 1982 (as O. media); Bersano \& Boxshall, 1996 ("1994"); BöttgerSchnack, 2001; Conway, 2012).

Oncaea ornata Giesbrecht, 1891
Of the two forms of Oncaea ornata sensu Boxshall (1977), form one is the genuine O. ornata while form two is another species, O. englishi (Heron, 1977). See Heron \& Frost (2000).
Female: Prosome rounded, urosome narrow (Fig. 61A, B); A2 distal segment shorter than previous segment (Fig. 61E); basis segment of maxilliped with many fine spinules and two setae on inner margin (Fig. 61F), the distal one long and denticulate, the proximal much shorter, distal claw with fine spinules on concave margin; only P2 and P3 with conical projection on distal endopod (Fig. 61L), not clear in figures 611 and 61J; P5 small and fused (not visible in figure 61G) to first urosome somite, with one single seta on exopod and outer basal seta emerging directly from somite (Fig. 61G); spinules sometimes present on dorsal surface of first urosome somite beside P5; genital somite tapering posteriorly, distinctively long with ratio of 2.15:1 to rest of urosome (Fig. 61A, C); furcae equal in length to anal somite, around two times as long as wide.
Male: Basis segment of maxilliped with two very small setae on denticulate inner margin (Fig. 61M), distal claw smooth; P2 and P3 with conical projection on distal endopod (Fig. 61P); genital somite oval in outline, long, with ratio of $2.8: 1$ to rest of urosome (Fig. 61N, O), genital lappets extending posteriorly, rounded; caudal furcae only slightly longer than anal somite.


Fig. 61. Oncaea ornata (A, B, D-K, M, N, P from Malt, 1983b; C, L, O from Heron \& Frost, 2000).
Recorded: PMF. L4, not recorded. Southwest UK. Western Ireland.
Total length: Female 0.75-1.07 mm; male 0.52-0.93 mm.
Further information: Giesbrecht, 1892; Rose, 1933; Boxshall, 1977 (form 1); Malt, 1983a, b; Heron \& Frost, 2000.

Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda: Superorder Podoplea: Order Cyclopoida:

## Family Lubbockiidae:

Body elongated, prosome comprising cephalosome and four free pedigerous somites; A1 four to seven segments, non-geniculate in males; A2 three segments; maxilliped large with claw-like distal segment; urosome of five somites in female, six in male; P5 a single long segment with two apical setae, relatively larger and more complex than in the other cyclopoids described here. Only Genus Lubbockia recorded in the PMF.

## Genus Lubbockia:

Lubbockia aculeata Giesbrecht, 1891
Female: Elongated body (Fig. 62A); prosome longer than urosome; corners of last metasome somite pointed; A1 short, of six segments (Fig. 62B); A2 simple (Fig. 62C), first segment without spines, second segment with one spine on inner edge, third segment elongate bearing six distal setae, some curved, two setae on inner margin and two patches of fine setules near outer edge; mandible, maxillule and maxilla very short and simple; maxilliped proximal segment with one inner denticle (Fig. 62D), second segment with five denticles on inner surface, third segment without spines, distal segment claw-like with small distal denticle. P5 elongate, single segment, terminating in an outer spiny process and two setae (Fig. 62E), the inner seta longer, almost reaching end of genital somite; P6 a flat opercular plate with a single seta; posterior margins of genital and following two somites with toothed edge.
Male: Corners of last metasome somite pointed as in female (Fig. 62F); A1 very short, of three segments (Fig. 62G); A2 similar to female (Fig. 62H), with same number of distal setae, but arranged and shaped slightly differently; maxilliped second segment (Fig. 62I) with irregular row of spinules, rounded prominence on inner margin, third segment without any spines, distal segment claw-like, very curved, with tiny spinule proximally; other appendages similar to female.


Fig. 62. Lubbockia aculeata. (from Boxshall, 1977, © Natural History Museum, reproduced with permission).

Recorded: PMF. L4, not recorded. West of UK.
Total length: Female $2.06-2.35 \mathrm{~mm}$; male $2.35-2.74 \mathrm{~mm}$.
Further information: Giesbrecht, 1893; Rose, 1933; Boxshall, 1977; Avancini et al., 2006.

## Lubbockia squillimana Claus, 1863

Female: Body elongated (Fig. 63A), prosome longer than urosome; corners of last metasome somite rounded compared to Lubbockia aculeata. A1 five-segmented (Fig. 63C); A2 as in L. aculeata; maxilliped proximal segment without any spines (Fig. 63D), second segment with five large denticles on inner surface; third segment without spines, distal segment claw-like with smooth concave edge and tiny proximal spinule; P5 similar to $L$. aculeata, but with the large inner seta reaching just beyond the genital somite (Fig. 63E). All other appendages as in L. aculeata. Furcae slightly longer than anal somite and around five times longer than broad.
Male: Prosome longer than urosome (Fig. 63F); corners of last metasome somite rounded as in female; anal somite with obvious constriction in middle (Fig. 63F, I); A2 similar to that in male L. aculeata, but according to Boxshall (1977) having only one small spine on inner margin of distal segment (Fig. 63G), while two spines were drawn by Giesbrecht (1892). Maxilliped without spines on proximal segment (Fig. 63H), second segment with a row of fine spinules and distal prominence on the inner margin, third segment without spines, distal claw with tiny proximal spinule.


Fig. 63. Lubbockia squillimana. (B, F after Giesbrecht, 1893, from Rose, 1933; A, C-E, G-I from Boxshall, 1977, © Natural History Museum, reproduced with permission).

Recorded: PMF. L4, not recorded. Southern Ireland.
Total length: Female 1.45-1.60 mm; male 1.8-2.1 mm
Further information: Giesbrecht, 1893; Rose, 1933; Boxshall, 1977; Avancini et al., 2006.

## Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda: Superorder Podoplea: Order Cyclopoida:

## Family Corycaeidae:

A1 short, six-segmented, setose, non-geniculate in males; A2 four-segmented, claw-like distally, larger in males. Prosome comprises cephalosome fused with first pedigerous somite to form cephalothorax, sometimes with suture marking the point of fusion and three free pedigerous somites; third pedigerous somite typically produced into backwardly directed, pointed plates, fourth pedigerous somite narrower, these somites often fused. Immediately recognisable to family by large pair of cuticular lenses on anterior cephalothorax, an elaborate naupliar eye. Urosome of three somites in females and males of species described here, but females of some species of this family have only two somites; first somite of urosome is fifth pedigerous somite, imperfectly developed and tiny (this region seldom drawn in illustrations), bearing the P5 which are reduced to two setae on surface of somite; P6 represented by pair of genital operculae bearing a long seta and sometimes an additional small spine in the male, situated dorsolaterally in females, ventrally in males, corresponding to position of genital apertures; furcae narrow and elongate; P1-P3 biramous with both rami three-segmented; P4 exopod three-segmented, endopod reduced to small knob bearing one or two setae. Females carry paired egg sacs dorsally. Only genus Corycaeus recorded in the PMF and only two species.

## Genus Corycaeus:

Corycaeus anglicus Lubbock, 1857
Female: Cephalosome fused to first pedigerous somite, but a dorsal suture remains indicating plane of fusion (Fig. 64A, B); A1 short, six-segmented (Fig. 64D); A2 with two spines around joint between first and second segment (Fig. 64C), distal segment armed at the base with two claw-like spines and a much stronger curved claw; third pedigerous somite produced laterally into pointed lappets extending to around middle of genital somite (Fig.64B), fourth pedigerous somite much narrower, also pointed laterally; urosome of three somites (Fig. 64E), first somite small and imperfectly developed, bearing the simple P5; genital somite with pointed projection on ventral, median anterior face (Fig. 64A); furcae longer than genital somite, typically divergent (Fig. 64E). P4 endopod reduced to small knob, bearing two setae, with small projection anterior to knob (Fig. 64F); P5 two simple setae (Fig. 64E); P6 a single dorsolateral seta on the genital operculae.
Male: Around same size as female, but body more club-shaped (Fig. 64G); appendages similar to female; lateral lappets of third pedigerous somite less pronounced than in female; A2 stronger than in female (Fig. 64J); genital somite with distinct dorsolateral swellings (Fig. 64H), pointed projection on ventral, median anterior face (Fig. 64I); anal somite smaller than in female; furcae two-thirds length of genital somite, scarcely divergent; P6 represented by genital operculae bearing a long seta and a short spine (Fig. 64H).


Fig. 64. Corycaeus anglicus. A-C, F, G, I after Sars, 1918, from Rose, 1933; D from Sars, 1918; E, H from Razouls, 1974b).

Recorded: PMF. L4, common. All European region.
Total length: Female 0.9-1.1 mm; male 0.9-1.1 mm
Further information: Sars, 1918; Dahl, 1912; Rose, 1933; Cervigon, 1964; Razouls, 1974b.

Corycaeus giesbrechti Dahl, 1894
The species recorded in the PMF as Corycaeus venustus Dana is believed to be this species, a complexity of synonyms causing some uncertainty ( $C$. crassiusculus being the other possibility).
Female: Cephalosome incorporates first pedigerous somite, but a dorsal suture may remain indicating the plane of fusion (Fig. 65A); A2 similar to C. anglicus (Fig. 65F); third pedigerous somite produced laterally into pointed lappets extend to around middle of genital somite (Fig. 65A, B), fourth pedigerous somite much narrower, also pointed laterally, sometimes difficult to see segmentation between this and third somite; urosome of three somites (Fig. 65E), first somite, the fifth pedigerous somite, imperfectly developed and small, bearing the simple P5, reduced to two setae; the genital somite (Fig. 65D) has not been described or illustrated as having a pointed projection on the ventral, median anterior face as found in the male (Fig. 65H) and in both sexes of C. anglicus, so this feature appears to be absent; furcae less than two-thirds length of genital somite, typically divergent (Fig. 65E). P4 endopod (Fig. 65G) reduced to small knob, bearing only one seta and without small projection anterior to endopod as found in C. anglicus; P6 a single dorsolateral seta on the genital operculae (Fig. 65E).
Male: About same size as female (Fig 65H, I), body more club-shaped; appendages similar to female; lateral lappets of third pedigerous somite similar to female, but not quite reaching middle of genital somite; A2 stronger than in female (Fig. 65J); genital somite with less distinct dorsolateral swellings compared to male C. anglicus, pointed projection on ventral, median anterior face (Fig. 65 H ); anal somite similar length to female; furcae scarcely divergent; P6 represented by a pair of genital operculae, each bearing a long seta (Fig. 65I).


Fig. 65. Corycaeus giesbrechti (A-D, F, G, I, J from Campaner, 1985; E from Razouls, 1974b; H from Dahl, 1912).

Recorded: PMF (as Corycaeus venustus), very rare. L4, not recorded. Southwest of UK.
Total length: Female $0.80-1.12 \mathrm{~mm}$; male $0.70-0.87 \mathrm{~mm}$.
Further information: Dahl, 1912; Rose, 1933; Cervigon, 1964 (as Onchycorycaeus giesbrechti); Corral Estrada, 1970; Chen \& Zhang, 1974; Razouls, 1974b; Campaner, 1985.

## Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda; Superorder Podoplea:

## Order Harpacticoida:

Although a large order with approximately 3372 species, there are only 17 species that can be considered truly pelagic (Boxshall, 1979), most being either benthic or epibenthic. In the European area, away from shallow coastal areas, they are usually one of the least commonly sampled of the copepod orders. Families with pelagic species found around southern Britain are Ectinosomatidae, Peltidiidae (Subfamily Clytemnestrinae) and Euterpinidae. The large number of non-pelagic species requires specialist identification, so while they are occasionally taken in samples, only a few examples of some particularly characteristic species are included here, from families Porcellidiidae, Peltidiidae (Subfamily Peltidiinae) and Harpacticidae. An online key to the identification of marine harpacticoid copepods, based on Wells (1976), with updated information, is given by Garlitska (see references).

The prosome typically comprises cephalosome fused to first pedigerous somite to form a cephalothorax and three free pedigerous somites; A1 short, double-geniculate in males. Usually not such a sharp demarcation between prosome and urosome as in orders Calanoida and Cyclopoida. Urosome typically of five free somites in female, six in male, but one species included here (Porcellidium fimbriatum) has only three free somites in both sexes (fifth pedigerous, genital and anal). Both sexes with six pairs of swimming legs, but P6 usually rudimentary in females. Females, with few exceptions, carry single egg sacs ventrally on the genital somite.

## Key to Harpacticoida families and species described

1. Whole body obviously dorsoventrally compressed, broad, ovoid, shield-shaped ------------- 2

2. Lateral plates of third free metasome somite rudimentary in female; P5 located laterally, surrounding the whole urosome ------------- Porcellidiidae, Porcellidium fimbriatum (Fig. 73)

- Lateral plates of third free metasome somite well developed in both sexes; P5 located ventrally, or when laterally located not surrounding urosome

3. P1 endopod distal segment tiny, with single claw-like spine; obvious separation between prosome and urosomeHarpacticidae, Zaus spinatus (Fig. 74)

- P1 endopod distal segment quite long, with several distal spines, not claw-like

4. Dorsal ridge of projections; P1 endopod 2-segmented --------- Peltidium purpureum (Fig. 72)

- No dorsal projections; P1 endopod 3-segmented; first segment of maxilliped short $\qquad$
Alteutha interrupta (Fig. 70)
- No dorsal projections; P1 endopod 3-segmented; first segment of maxilliped long

Alteutha depressa (Fig. 71)
5. Body spindle-shaped, laterally compressed; clear prosome/urosome boundary; anterior cephalothorax comes to gradual point in dorsal view

Euterpinidae, Euterpina acutifrons (Fig. 75)

- Body spindle-shaped, laterally compressed; no clear prosome/urosome boundary; anterior cephalothorax rounded in dorsal view -------------------------------------------- Ectinosomatidae 6
- Body dorsoventrally compressed; clear prosome/urosome boundary; prosome pedigerous somites with obvious lateral angular projections; rostrum forms a broad point on anterior cephalothorax in dorsal view --------------------------- Peltidiidae, Subfamily Clytemnestrinae 7

6. Longest furcal setae around same length as body ----------- Microsetella norvegica (Fig. 66)

- Longest furcal setae around twice length of body ----------------- Microsetella rosea (Fig. 67)

7. P5 exopod distal segment with five setae ------------------------- Goniopsyllus clausi (Fig. 68)

- P5 exopod distal segment with at least six setae -------------- Clytemnestra gracilis (Fig. 69)

Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda; Superorder Podoplea: Order Harpacticoida:

## Family Ectinosomatidae:

## Genus Microsetella:

Microsetella norvegica (Boeck, 1865)
Body slender, laterally compressed, without obvious prosome/urosome boundary (Fig. 66A, B, E); prosome of four free somites with first pedigerous somite fused to cephalosome forming cephalothorax; urosome of five somites in female, six in male; rostrum short, directed downwards (Fig. 66A, F); A1 of six segments (Fig. 66C; although some authors suggest five), slender, short; furcae short, two of the furcal setae longer, the longest usually around same length as body, varying from $20 \%$ less to $44 \%$ more, the shorter about a third of the length of the longer.
Female: Furcae about as long as wide (Fig. 66B), sometimes divergent; P5 symmetrical (Fig. 66D), consisting of a basoendopod with an outer seta and two inner setae of very different lengths, one twice as long as the other, and a one-segmented exopod with one ventral surface seta and three around the margin, the distal pair longest, of similar length and fringed with spinules.
Male: Smaller than female, but body similar in shape (Fig. 66E); A1 double-geniculate (Fig. 66F); P5 smaller than in female, symmetrical (Fig. 66G), consisting of a basoendopod and a onesegmented exopod with one ventral surface seta and two marginal setae of different lengths, the lateral one not fringed with spinules; furcae slightly wider than long.


Fig. 66. Microsetella norvegica (A-D, G from Boxshall, 1979, © Natural History Museum, reproduced with permission; E from de Guerne, 1938 (as Ectinosoma atlanticum); F from Hirakawa, 1974).

Recorded: PMF. L4. Southampton. Most of the European region.
Total length: Female $0.35-0.57 \mathrm{~mm}$; male $0.33-0.42 \mathrm{~mm}$.
Further information: Giesbrecht, 1893; Sars, 1911; Rose, 1933; de Guerne, 1938 (as Ectinosoma atlanticum); Hirakawa, 1974; Boxshall, 1979; Diaz \& Evans, 1983; Gerber, 2000; Avancini et al., 2006; Conway, 2012.

Microsetella rosea (Dana, 1848)
Body sometimes has a rosy or reddish tinge, hence the name. General description same as for Microsetella norvegica, but almost twice the length; two longer setae on furcae, the longest around twice as long as body (Fig. 67A, C), the shorter around 10-15\% of length of the longer. Female: The two inner setae on the P5 basoendopod of similar length (Fig. 67B).
Male: Both setae on distal margin of P5 exopod bearing spinules (Fig. 67D).


Fig. 67. Microsetella rosea (from Boxshall, 1979, © Natural History Museum, reproduced with permission).

Recorded: PMF, not recorded. L4, not recorded. Western Ireland. English Channel. Total length: Female $0.64-0.85 \mathrm{~mm}$; male $0.60-0.70 \mathrm{~mm}$.
Further information: Rose, 1933; Johnson, 1942; Boxshall, 1979; Avancini et al., 2006.

Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda; Superorder Podoplea: Order Harpacticoida:

## Family Peltidiidae:

## Subfamily Clytemnestrinae:

First pedigerous somite fused with cephalosome, forming bell-shaped cephalothorax; three free pedigerous somites; A1 slender, six or seven-segmented in female, in male seven-segmented and double-geniculate between last two segments; rostrum large; body distinctly tapering posteriorly; prosome dorsoventrally flattened; prominent angular projections at posterior corners of all prosome somites. Mandibles, maxillules and maxillae reduced; urosome cylindrical, of five somites in female, six in male; anal somite as long as penultimate somite; furcae short and wide. P5 rudimentary, two-segmented, segments narrow and elongate, similar and quite symmetrical in both sexes. Females carry single, median egg sacs.

Since 1891 it was considered that there was only one genus in Subfamily Clytemnestrinae and two cosmopolitan species, Clytemnestra scutellata and C. rostrata, both of which were recorded from the European region. However, re-examination of specimens by Huys \& Conroy-Dalton (2000) from the major expedition collections has shown this perception to be false and there are at least five species in two genera. The only species recorded in the PMF was noted as C. rostrata (Brady 1883), but the species now recognised under this name probably does not occur in the European region. Material has been re-examined from L4 and what was previously called C. rostrata has now been confirmed as being Goniopsyllus clausi. A description of the other species believed to be found in the European region, Clytemnestra gracilis, is also included.

## Genus Goniopsyllus:

Goniopsyllus clausi Huys \& Conroy-Dalton, 2000
General description as for family. A1 slender, distinctly six-segmented in female (Fig. 68D), indistinctly seven-segmented in male (Fig. 68I). P5 distal segment with five setae (Fig. 68E, J).
Female: Rostrum triangular (Fig. 68A); segment six of A1 very long (Fig. 68D), plumose setae on segments one to four; P1 held below body, usually not visible dorsally; P5 almost reaching distal margin of genital somite (Fig. 68C); five somites in urosome; furcae short, convergent, conical (Fig. 68F).
Male: Body shape similar to female (Fig. 68G), but rostrum more pointed; P5 very similar to female, with identical proportions and setation (Fig. 68J), but lateral setae of exopod slightly shorter; P6 asymmetrical, represented by two flaps covering the single large genital aperture (Fig. 68 H ), with a small naked seta at the outer distal corner of each flap lobe; furcae short, slightly slenderer than in female.


Fig. 68. Goniopsyllus clausi (from Huys \& Conroy-Dalton, 2000, © Natural History Museum, reproduced with permission).

Recorded: PMF. L4 (both as Clytemnestra rostrata). Portuguese coast.
Total length: Female $0.90-1.97 \mathrm{~mm}$; male 1.02 mm .
Further information: Huys \& Conroy-Dalton, 2000.

## Genus Clytemnestra:

Clytemnestra gracilis (Claus, 1891)
General description as for family. A1 slender, distinctly seven-segmented in both sexes (Fig. 79A). P5 exopod distal segment with six setae in female (Fig. 69B), seven in male (Fig. 69D).
Female: Rostrum triangular with rounded anterior margin (Fig. 69A); P1 held below body, usually not visible dorsally; P5 elongate, extending clearly beyond posterior margin of genital somite (Fig. 69B), exopod about two and a half times as long as basal segment. Urosome of five somites, without dorsal ornamentation, penultimate and anal somites with multiple rows or patches of spinules around ventral hind margin and lateroventral patches on second abdominal somite; furcae about twice as long as wide, tapering slightly posteriorly.
Male: Body similar to female; urosome slenderer than female, of six somites (Fig. 69D); P5 similar shape to female; P6 weakly asymmetrical, forming membranous flap covering single, large median genital aperture, each limb produced into cylindrical process with one apical and two lateral naked setae; urosome somites four, five and anal somite with spinules around ventral hind margin; furcae longer and slenderer than in female (Fig. 69E).


Fig. 69. Clytemnestra gracilis (from Huys \& Conroy-Dalton, 2000, © Natural History Museum, reproduced with permission).

Recorded: PMF and L4, not recorded. Norwegian coast. Portuguese coast.
Total length: Female 1.24-1.56 mm; male 1.42-1.53 mm.
Further information: Huys \& Conroy-Dalton, 2000.

## Subfamily Peltidiinae:

There are three species of this family recorded in the PMF, Alteutha interrupta, A. depressa and Peltidium purpureum. While these distinctive species generally have an association with inshore algae, some are occasionally caught in plankton nets and even in Continuous Plankton Recorder tows, which start sampling well away from the coast at a constant depth of $\sim 6.5 \mathrm{~m}$ (Beaugrand, 2004; Continuous Plankton Recorder Survey Team, 2004).

## Genus Alteutha:

P1 endopod three-segmented (Fig. 70C); exopod three-segmented, distal small segment with four claw-like setae and usually one moveable seta; first pedigerous somite fused to cephalosome forming cephalothorax (Fig. 70A).

## Alteutha interrupta Goodsir, 1845

Female: Body compact, quite deep, greatest width anterior to middle, gradually tapering towards rear (Fig. 70A), capable of rolling into a ball; cephalothorax half the length of prosome, posterolateral corners rounded; rostrum short, rounded. Urosome flattened, genital somite broad and bulging dorsally; furcae slightly longer than broad, obliquely cut off at the tip (Fig. 70E). A1 slender, eight segments, second segment longest (Fig. 70B); maxilliped first segment short (long in A. depressa), same length as width (Fig. 70F), third segment elongated, more than twice as long as broad, distal claw long. P1 very slender, last joint of exopod very small (Fig. 70C), armed with five claws, gradually increasing in length inwards, endopod much shorter than exopod; P5 proximal segment very short, distal segment oblong, flattened, with three strong spines at tip and two smaller ones on outer edge (Fig. 70D). Live specimens usually coloured chocolate brown.
Male: Body similar to female; A1 robust, both geniculate (Fig. 70G); urosome of six somites (Fig. 701), the first bearing the flattened P5 (Fig. 70H), the genital somite largest bearing the simple P6 laterally; other limbs similar to female.


Fig. 70. Alteutha interrupta (A-C, E, G-I from Lang, 1948 after Sars, 1911; D, F from Huys et al., 1996).

Recorded: PMF. L4, not recorded. Around most European coasts
Total length: Female 1.2 mm ; male length unknown.
Further information: Sars, 1911; Lang, 1948; Huys et al., 1996.

Alteutha depressa (Baird, 1837)
Female: Body oval-shaped, flattened (Fig. 71A, B); cephalothorax posterolateral corners acutely angled; rostrum large, broad and prominent; three metasome somites with posterolateral corners acutely angled; first urosome somite with posterolateral corners evenly rounded and narrower than metasome somites, remainder of urosome short and broad, similar to A. interrupta. A1 shorter and stouter than in A. interrupta and with nine distinct segments; maxilliped first segment long (Fig. 71C), length at least twice width (short in A. interrupta), third segment oval, approximately 1.5 times longer than broad, distal claw long; P1 more robust than in A. interrupta (Fig. 71D), with less difference in length between endopod and exopod; P5 large and robust, distal segment with three thick distal spines (Fig. 71E). Colour when alive usually yellowish olive green, with a dark purplish transverse band across the metasome somites.
Male: Similar to female, but little information available; P5 as in Figure 71F.


Fig. 71. Alteutha depressa (from Huys et al., 1996)
Recorded: PMF. L4, not recorded. Around most of British, Norwegian and French coasts.
Total length: Female: 1.3 mm ; male length unknown.
Further information: Sars, 1911; Lang, 1948; Huys et al., 1996.

## Genus Peltidium:

Body strengthened with conspicuous chitinous strips (Fig. 72A); first pedigerous somite fused to cephalosome; P1 endopod two-segmented (Fig. 72D), exopod three-segmented, third segment with one or two stout claws and usually a more slender moveable claw.

Peltidium purpureum Philippi, 1839
Female: Body oval, dorsoventrally flattened (Fig. 72A, B), posterolateral corners of somites acutely produced; cephalothorax and following four somites with prominent triangular, dorsal projections (Fig. 72B); rostrum large and prominent, square at the tip; A1 less than half the length of cephalothorax, of seven segments and very setose; genital somite with long dorsolateral projections extending almost to end of furcae (Fig. 72C), smaller acute projection on following somite; furcae widely separated, the second innermost seta coarser than others and longer than urosome; P1 exopod distal segment small and armed with three strong claws and a curved seta (Fig. 72D), endopod slightly shorter than exopod; P5 distal segment evenly curved, armed with six strong ciliated spines, three of the spines on the outer edge (Fig. 72E).
Male: Smaller than female, but of similar appearance; A1 robust, both geniculate (Fig. 72F); P5 large, reaching almost to end of furcae (Fig. 72G); other limbs similar to female.


Fig. 72. Peltidium purpureum (A, C, E-G from Lang, 1948, after Sars, 1911; B, D from Huys et al., 1996).

Recorded: PMF. L4, not recorded. British, Irish and Norwegian coasts.
Total length: Female: 0.8-1.05 mm; male length unknown.
Further information: Sars, 1911; Lang, 1948; Huys et al., 1996.

Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda; Superorder Podoplea: Order Harpacticoida:

## Family Porcellidiidae:

## Genus Porcellidium:

Two species of this genera are recorded in the PMF, $P$. fimbriatum and $P$. viride (Philippe, 1840), but only the former is described here. The British records of $P$. viride are probably P. sarsi (Huys et al., 1996). Currently there appears to be some uncertainty about the taxonomy of this group and descriptions and illustrations are limited, so it may be best to identify them only to Porcellidium spp. Males are generally insufficiently described for easy separation, but females can be separated mainly on features of the furcae.

## Porcellidium fimbriatum Claus, 1863

Female: Body shield-shaped, dorsoventrally flattened (Fig. 73A); prosome of four somites, cephalothorax and three free pedigerous somites; lateral plates of last metasome somite (fourth pedigerous somite) rudimentary; cephalothorax and pedigerous somites with a clear membrane around the edges; urosome of only three somites (fifth pedigerous, genital and anal somites); P5 flattened (Fig. 73C), located laterally, the limbs and expanded genital somite surrounding the anal somite and long flattened furcae (Fig. 73A, B); genital apertures ventral, asymmetrical, forming a naked membranous flap on one side only.
Male: Body shape similar to female, but lateral plates of fourth pedigerous somite well developed (Fig. 73D); urosome also of three somites (Fig. 73E); genital flap and furcae as in female; P6 asymmetrical, represented in male by a naked plate on one side only (Fig. 73D).


Fig. 73. Porcellidium fimbriatum (A, C, E from Boxshall \& Halsey, 2004; B, D from Bocquet, 1948).
Recorded: PMF. L4, not recorded. English Channel.
Total length: Female: 1.69 mm ; male 1.47 mm .
Further information: Bocquet, 1948; Huys et al., 1996; Boxshall \& Halsey, 2004.

Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda; Superorder Podoplea: Order Harpacticoida:

## Family Harpacticidae:

Body variable in shape; usually with distinct boundary between prosome and urosome.
Genus Zaus:
Two species of Zaus are recorded in the PMF, Z. spinatus and Z. goodsiri Brady, 1910, but Huys et al. (1996) considered the latter was distinctly different and should be in another genus. $Z$. abbreviatus, not recorded in the PMF, but a common species around the UK and Ireland, has a shield-shaped body, similar to Porcellidium and Alteutha spp.

## Zaus spinatus Goodsir, 1845

Female: Cephalothorax narrowly rounded anteriorly (Fig. 74A); rostrum slightly prominent, blunt at tip; fifth pedigerous somite (first somite of urosome) very short and much narrower than previous somites; urosome around half the length of the prosome, genital somite broad, expanded laterally with fine seta at edges; last three somites of urosome rapidly reducing in size; furcae as long as broad, blunt at tip, the second innermost setae elongated to around half the length of body (not drawn). A1 slender (Fig. 74B), almost as long as cephalothorax; A2 distal endopod with three large spines (Fig. 74C), fringed on outside with dense brush of fine setae, the distal spine longer than the distal clump of setae; sub-distal segment of maxilliped almost rectangular (Fig. 74D); P1 endopod over half length of exopod (Fig. 74E), last segment small with single apical claw, of the same appearance as those on the exopod; P5 two segments, exopod short and oval (Fig. 74F).
Male: Considerably smaller than female with urosome narrower and distinctly of six somites (Fig. 74G); A1 robust, six segments, third large and gradually widening distally, last claw-like (Fig. 74H); P5 first segment much smaller and not expanded compared to female (Fig. 74I), second segment same as female; other limbs similar to female.


Fig. 74. Zaus spinatus (A, C, D, F from Huys et al., 1996; B from Lang, 1948 after Sars, 1911; E, G-I from Sars, 1911).

Recorded: PMF. L4, not recorded. All coastal regions of northern Europe.
Total length: Female 0.56 mm ; male 0.44 mm
Further information: Sars, 1911; Lang, 1948; Huys et al., 1996; Boxshall \& Halsey, 2004.

Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda; Superorder Podoplea: Order Harpacticoida:

## Family Euterpinidae:

Prosome comprises cephalothorax and three free pedigerous somites; urosome of five somites in females, six in males. A1 of males double-geniculate. There is only one species, Euterpina acutifrons.

Genus Euterpina:
Euterpina acutifrons (Dana, 1847)
Female: In dorsal view, prosome widest at posterior cephalothorax, then narrows posteriorly (Fig 75A), in lateral view has typically bent shape (Fig. 75B); A1 seven-segmented (Fig. 75C), half as long as the cephalothorax (Fig. 75A, B); rostrum well developed, pointing forwards, acute at tip. P5 a flattened plate (Fig. 75D), symmetrical, one-segmented with four distal spines and a fine seta and a short spine on the outer margin, the spine has a fine setule emerging from the base; furcae slightly longer than wide (Fig. 75A).
Male: Body shape similar to female (Fig. 75E), with same lateral bent shape; A1 strongly geniculate and indistinctly five-segmented (Fig. 75F), fourth segment thickened; urosome of six somites (Fig. 75G); P5 simple and symmetrical (Fig. 75H), fused into single plate with a median notch in the distal margin, each side bearing two distal spines, and on the outer margin a fine seta and short spine with a fine setule emerging from the base; P6 a single plate divided into two lobes each bearing two serrated spines distally (Fig. 75G, I).


Fig. 75. Euterpina acutifrons (A, B from Sars 1921b; C, E, G-I from Boxshall, 1979, © Natural History Museum, reproduced with permission D, F from Rose, 1933, after Giesbrecht, 1893).

Recorded: PMF. L4, regularly in medium numbers. All European region.
Total length: Female $0.50-0.75 \mathrm{~mm}$; male $0.50-0.56 \mathrm{~mm}$.
Further information: Sars, 1921b; Rose, 1933; Haq, 1965; Wells, 1976; Boxshall, 1979; Avancini et al., 2006; Conway, 2012.

## Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda: Superorder Podoplea:

## Order Misophrioida:

This order shares some features of the Calanoida, Cyclopoida and Harpacticoida and was at one time placed in the latter order. Articulation of prosome and urosome between the fourth and fifth pedigerous somite, so P5 on first somite of urosome. All known males appear to have the A1 geniculate on both sides. Only one species is recorded in the PMF and lives in shallow waters, close to, or in the sea bottom.

## Genus Misophria:

Misophria pallida Boeck, 1865
Prosome comprises cephalosome and four free pedigerous somites, but anterior edge of first pedigerous somite hidden behind extension of cephalic shield (Fig. 76A, B, F), giving appearance of a cephalothorax; A1 moderately long in both sexes; A2 and mouthparts resemble those of calanoids; body narrows abruptly at the metasome/urosome boundary.
Female: Body deep, evenly rounded in lateral view (Fig. 76A, B); A1 of 16 segments, extending to around the posterior edge of first pedigerous somite; rostrum robust, pointed, directed downwards; last metasome somite small; urosome of five indistinct somites (Fig. 76C); genital somite as long as the following somites combined. Furcae broader than long; apical setae long, plumose. P5 with first segment produced internally, bearing long spine (Fig. 76D, E). Female carries single, ventral ovisac containing small numbers of large, globular eggs (Fig. 76A, B).
Male: Body symmetrical, shape similar to female (Fig. 76F), but smaller; A1 of 13 segments (Fig. 76 G ), double-geniculate; urosome of six somites; genital somite swollen, often carrying large oval spermatophore on each side (Fig. 76F). P5 symmetrical (Fig. 76H), very similar to those of female.


Fig. 76. Misophria pallida (from Sars, 1911).

Recorded: PMF. L4, not recorded. North Sea. Norwegian coast.
Total length: Female 0.70 mm ; male 0.55 mm .
Further information: Sars 1911.

Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda: Superorder Podoplea:

## Order Monstrilloida:

There is only one family in Order Monstrilloida, Family Monstrillidae, so order and family description are the same. Boxshall \& Halsey (2004) noted that "the taxonomic history of this order and family is complex and confused", which will become obvious to anyone using a selection of literature to identify specimens. Isaac $(1974,1975)$ made revisions to the naming of genera, but most of the changes have not been adopted. A complete revision of the order is currently underway, some details of which are given in an excellent (open access) review of all aspects of Order Monstrilloida by Suárez-Morales (2011). The WORMS classification lists six genera, but Suárez-Morales (2011) considers there are only four, Monstrilla, Cymbasoma, Monstrillopsis and Maemonstrilloida, all of which except the latter have species recorded in the PMF. Since the publication of the last PMF in 1957 six new species of Monstrillidae (not included here) have been recorded from the Irish Sea and Bristol Channel (Isaac, 1974, 1975), indicating how poorly this group have been studied, even in the European area. A dedicated survey would probably increase the Plymouth species list, as was shown when the previously unrecorded Monstrilla grandis was collected inside Plymouth Sound in 2011.

## Morphology

Monstrilloids are mainly found close inshore. Adults can easily be distinguished from other copepod orders by their elongate cylindrical shape, lack of A2, mouth-parts and gut (so cannot feed). They have no rostrum and there is a short oral tube or oral papilla, opening on the anterior ventral body (Fig. 77B). The distance the oral tube is situated from the anterior is a useful character for separation of the genera. The A1 are held parallel, pointing forwards in line with the body. The first pedigerous somite is fused with the cephalosome to form a cephalothorax and there are a further three free pedigerous somites on the metasome. As in other podopleans, the body articulates between the fourth and fifth pedigerous somites, the theoretical tenth and eleventh body somites. The P5 are thus on the first urosome somite. Depending on the genus, the caudal furcae bear different numbers of setae. A pair of eyes or ocelli, of variable structure, is often present and sometimes with large mirror surfaces.
Females have four indistinct segments in the A1. The P5 are one-segmented and generally bilobed, with up to three setae on the outer lobe (Fig. 77D) and zero to two setae on the inner lobe. However, the inner lobe can be much reduced or completely missing. The urosome has three to five free somites, so there are from one to three somites posterior to the genital somite. There are no egg sacs, instead there are a pair of slender, trailing, ovigerous spines (Fig. 77B, C), emerging from the ventral genital somite, their length differing between species. Clusters of eggs are attached to these spines (Figs. 77B) by means of a mucous secretion.
Males are smaller than females, often considerably so. Their A1 are of five segments and doublegeniculate, with a hinge between the two distal segments (Fig. 77F). The P5 are either completely missing, or have one or two setae on a small lobe (Fig. 77l). There are four to five somites in the urosome. The genital somite bears a ventral copulatory organ (Fig. 77J), one of the most useful characters for distinguishing between males of different species. This organ is typically a shaft of variable shape, usually with a pair of divergent distal lobes called genital lappets or flaps. These lappets can be simple lobes, or terminated in thin projections or spine-like processes. The lobes are absent in some species, the spines emerging directly from the sides of the copulatory organ (Fig. 80 G ). The copulatory organ is connected to internal sperm ducts that open at its distal end and spermatophores are thought to be carried on the genital lappets, prior to attachment to the female.

## Life cycle

The pre-adults, adults and first nauplius are free-swimming, while all other stages are parasitic in polychaetes or gastropods. Eggs hatch into a lecithotrophic, non-feeding nauplius that finds a host and burrows into its tissues, enters the blood system and transforms into a sac-like body, bearing root-like processes. When development is complete it leaves its host as a copepodite and rapidly moults once into an adult. Because only a short period of their life is free-living, the free-living stages tend to be rare in plankton samples. The adults tend to be caught more often at night (Suárez-Morales, 2011).

## Key to Family Monstrillidae described

With a pair of long ovigerous spines, that may be covered in eggs, emerging from the ventral
 Without ovigerous spines; a copulatory appendage situated ventrally on the genital somite; A1 double-geniculate, with hinged articulation between the two distal segments

## Females

1) Urosome of four somites; oral tube usually less than a third of the way back along the ventral cephalothorax ------------------------------------------ Monstrillopsis filogranarum Fig. 85

- Urosome of three somites; oral tube usually less than a third of the way back along the ventral

- Urosome of four or five somites; oral tube usually closer to the middle of the ventral Cephalothorax Monstrilla 3

2) Ovigerous spines as long as cephalothorax; last urosome somite without notch $\qquad$ Cymbasoma longispinosum Fig. 82

- Ovigerous spines a third cephalothorax length; last urosome somite without notch $\qquad$
- Ovigerous spines half cephalothorax length; last urosome somite with notch

Cymbasoma rigidum Fig. 84
3) P5 with five setae; furcae with six setae; urosome five somites - Monstrilla grandis Fig. 81


4) Furcae with six setae, one reduced ------------------------------ Monstrilla helgolandica Fig. 79

- Furcae with five setae, one reduced --------------------------------------Monstrilla leucopis Fig. 80

5) Furcae with five setae ---------------------------------------------------- Monstrilla longicornis Fig. 77

- Furcae with five setae, one reduced ----------------------------------- Monstrilla longiremis Fig. 78


## Males

1) Urosome of five somites; oral tube less than a third of the way back along the ventral cephalothorax - Monstrillopsis filogranarum Fig. 85

- Urosome of four somites; oral tube generally less than a third of the way back along the ventral cephalothorax
- Urosome of five somites; oral tube generally closer to the middle of the ventral cephalothorax

Monstrilla 3
2) Furcae with three setae; last urosome somite no notch ----- Cymbasoma thompsonii Fig. 83

- Furcae with three setae; last urosome somite with notch -------- Cymbasoma rigidum Fig. 84
- Furcae with four setae; last urosome somite no notch -- Cymbasoma longispinosum Fig. 82

3) No genital lappets, copulatory organ with long divergent spines - Monstrilla leucopis Fig. 80

- Genital lappets short, without spines ----------------------------- Monstrilla helgolandica Fig. 79
- Genital lappets long, without spines, with small projections -------- Monstrilla grandis Fig. 81
- Genital lappets short with spines

4) P5 with one seta ---------------------------------------------------------------Monstrilla longiremis Fig. 78

- P5 with two setae ----------------------------------------------------------- Monstrilla longicornis Fig. 77


## Family Monstrillidae:

## Genus Monstrilla:

Monstrilla longicornis Thompson, 1890
Female: With coarse granular exoskeleton; cephalothorax in dorsal view of quite similar width throughout; oral tube slightly behind the cephalothorax mid-point (Fig. 77B); eye not well developed, lacking any refractive elements; urosome of four somites; genital somite as long as following two somites together; ovigerous spines reach slightly beyond furcal setae; each furcae with five setae of similar length (Fig. 77C). Two small spines on inner, second basal segment of P1-P4 (Fig. 77E; M. clavata Sars, 1921 is considered a synonym, but Sars (1921a) only drew a single spine in his illustrations of it), distal exopod segment outer edge indented, with clumps of fine setae; P5 with external lobe bearing three setae, the inner seta smaller (Fig. 77D), single seta on inner angle of P5.
Male: Much smaller than female; A1 more robust than in female; cephalothorax in dorsal view of quite similar width throughout; urosome of five somites of similar lengths (Fig. 77F, H); genital somite with copulatory organ composed of two short, divergent lappets, each terminating in small spine (Fig. 77J); furcae each with four setae (Fig. 77F). Two small spines on inner second segment of P1 to P4, as in female; P5 tiny, two lobes merged at base, with two, sometimes one distal seta (Fig. 771).


Fig. 77. Monstrilla longicornis (after Sars, 1921a, from Rose 1933).
Recorded: PMF. L4, not recorded. West Ireland. Bristol Channel. West Norway.
Total length: Female $3.0-4.5 \mathrm{~mm}$; male $1.8-2.3 \mathrm{~mm}$.
Further information: Sars, 1921a; Rose, 1933; Isaac, 1975; Boxshall \& Halsey, 2004; SuárezMorales, 2011.

Monstrilla longiremis Giesbrecht, 1893
Female: Body slender, cephalothorax longer than remaining body, slightly narrowing anteriorly (Fig. 78A, B); urosome similar to M. longicornis, but ovigerous spines as long as metasome and urosome combined; caudal furcae narrow, very divergent, bearing five setae with the second innermost shorter than the others (Fig. 78C); A1 very slender and elongated, longer than cephalothorax; oral tube small, situated around the middle of the cephalothorax; P1 to P4 with only one small spine on inner second basal segment (Fig. 78D), distal exopod segment outer edge without indentations, but may bear bunches of fine setae; P5 similar to $M$. longicornis, but narrower and with inner expansion less prominent and evenly rounded (Fig. 78E). If carrying eggs, very numerous, forming long oval mass (Fig. 78A, B).
Male: Smaller than female, but with similar slender shape (Fig. 78F, G); cephalothorax almost cylindrical, longer than remaining body; A1 second segment very long; urosome of similar structure to M. Iongicornis, with distinct somites (Fig. 78H); copulatory organ also similar; furcae with four setae, obviously divergent as in female. P1-P4 as in female; P5 very small, knob-like, tipped with only a single slender seta (Fig. 781).


Fig. 78. Monstrilla longiremis (after Sars, 1921a, from Rose, 1933).
Recorded: PMF and L4, not recorded. Southern Irish Sea. West Norway.
Total length: Female $3.0-3.7 \mathrm{~mm}$; male $1.6-2.0 \mathrm{~mm}$.
Further information: Giesbrecht, 1893; Sars, 1921a; Rose, 1933; Isaac, 1975; Boxshall \& Halsey, 2004; Suárez-Morales, 2010.

Monstrilla helgolandica Claus, 1863
Female: Small, with short stout body (Fig. 79A, B); cephalothorax in dorsal view widest anteriorly; oral tube around mid-point of the cephalothorax; eye quite well developed; urosome of four somites; genital somite narrows posteriorly; ovigerous spines of moderate length, not reaching ends of furcal setae (Fig. 79C); furcae divergent, with six setae, third innermost one very small (Fig. 79D); P5 elongate and slim, angularly bent in middle (Fig. 79E), no inner lobe, terminating in two setae of slightly different lengths.
Male: Body also short and stout; cephalothorax of similar width throughout (Fig. 79F); oral tube indistinct (Fig. 79g); eyes inconspicuous; A1 distal joint with five small spines near tip (Fig. 791); urosome of five somites; genital lappets on copulatory organ short lobes (Fig. 79J). Furcae rounded, short, divergent with five setae (Fig. 79K); no P5.


Fig. 79. Monstrilla helgolandica (after Sars, 1921a, from Rose, 1933; male as M. serricornis).
Recorded: PMF. L4, not recorded. Southampton. West Ireland. West Norway. North Sea. Irish Sea. Bristol Channel.
Total length: Female $1.4-2.31 \mathrm{~mm}$; male 1.75 mm or less.
Further information: Sars, 1921a (male as M. serricornis); Rose, 1933 (male as M. serricornis); Isaac, 1975; Boxshall \& Halsey, 2004; Muxagata \& Williams, 2004; Suárez-Morales, 2011.

## Monstrilla leucopis Sars, 1921

This species was considered synonymous with Monstrilla conjunctiva Giesbrecht, 1902, but some of the original copepods described by Sars (1921a) were re-examined by Suárez-Morales (2010) and as a result $M$. leucopis has been reinstated as a valid taxon.
Female: Body very slender and elongated (Fig. 80A); cephalothorax in dorsal view of quite similar width throughout, considerably longer than rest of body; A1 slender, shorter than cephalothorax; oral tube small, situated just in front of the mid-cephalothorax (Fig. 80C), eye inconspicuous and replaced by an opaque whitish substance. Ovigerous spines not extending beyond furcal setae (Fig. 80B); furcae longer than last two somites combined, only slightly divergent, inner edge straight, outer edge bulging proximally; furcae each with five setae, three emerging distally and two (one of which smaller) from the proximal bulge. P5 narrows distally, bearing two setae, inner lobe very small (Fig. 80D).
Male: Much smaller than female, but with similar, slender body; cephalothorax in dorsal view of quite similar width throughout; copulatory organ pear-shaped, without lobes, but with rod-like, divergent spines emerging sub-distally (Fig. 80E, F, G); furcae same shape as in female, with one seta reduced, but with one fewer apical setae. P5 reduced to two tiny knob-like appendages, each tipped with a single slender seta (Fig. 80E).


Fig. 80. Monstrilla leucopis (after Sars, 1921a, from Rose, 1933)
Recorded: PMF and L4, not recorded. Southampton (as M. conjunctiva). North Sea. Bristol Channel. Western Scotland. Western Norway.
Total length: Female $3.3-3.85 \mathrm{~mm}$; male $1.50-1.60 \mathrm{~mm}$.
Further information: Sars, 1921a; Rose, 1933; Isaac, 1975 (as M. conjunctiva); Boxshall \& Halsey, 2004; Muxagata \& Williams, 2004 (as M. conjunctiva); Suárez-Morales, 2010, 2011.

Monstrilla grandis Giesbrecht, 1891
Female: Oral tube around the middle of the ventral cephalothorax (Fig. 81B); urosome of five somites; oviferous spines long, about same length as the cephalothorax; furcae with six setae. P5 with two lobes (Fig. 81C), three setae on outer lobe and two on inner lobe, outer lobe with a knoblike process internally, not drawn in Giesbrecht's original illustrations. Giesbrecht also drew the setae on the inner lobe as being of quite different lengths. In a specimen from Plymouth the setae were of different lengths, but not greatly different.
Male: Oral tube just in front of the middle of the ventral cephalothorax (Fig. 81E); P5 usually with one long seta each side (Fig. 81F, G), almost reaching the end of the furcae, but ones with three setae have been found (Isaac, 1974). Genital lappets quite long, terminating in short projections directed dorsally, not always visible in ventral view (Fig. 81G-H); usually six furcal setae (Fig. 81F, but sometimes only five;


Fig. 81. Monstrilla grandis (A, D-G from Suárez-Morales, 2000; B, H after Giesbrecht, 1893, from Rose, 1933; C from Isaac, 1974).

Recorded: PMF and L4, not recorded. Barn Pool, inner Plymouth Sound September 2011. North Sea. Bristol Channel. English Channel.
Total length: Female $1.80-3.75 \mathrm{~mm}$; male $0.65-1.90 \mathrm{~mm}$.
Further information: Sars, 1921a; Rose, 1933; Isaac, 1974; Isaac, 1975 (as Strilloma grandis); Suárez-Morales, 2000; Boxshall \& Halsey, 2004.

## Genus Cymbasoma:

All females described here have three free somites in the urosome, but some species, still classified by WORMS as being Cymbasoma, have four somites.
Cymbasoma longispinosum (Bourne, 1890)
Female: A1 short stout, around quarter length of cephalothorax, of four segments, the last as long as the three others combined (Fig. 82A, B); cephalothorax much longer than remainder of body, in dorsal view narrows anteriorly; oral tube situated very far forward; eyes quite well developed; genital somite square when viewed dorsally, projecting considerably ventrally; ovigerous spines exceedingly long, almost same length as whole body, joined at base over quite a distance (Fig. 82 C ); urosome of three somites, one somite after genital somite; furcae very small bearing three setae of equal length. P5 with three setae on outer lobe, the two outer the same length and longer than the inner (Fig. 82D), inner lobe with no setae, protruding at right angles to axis of leg.
Male: A1 of five segments, the middle three swollen and armed with spinules, distal segment tiny (Fig. 82E); cephalothorax relatively shorter than in female, also narrowing slightly anteriorly; eyes not as well developed as female. Urosome of only four somites (Fig. 82F); genital lappets on copulatory organ short, the two lobes divergent, without spines; furcae with four equal setae. No P5.


Fig. 82. Cymbasoma longispinosum (after Sars, 1921a, from Rose, 1933).
Recorded: PMF. L4, not recorded. Southampton. North Scotland. West Norway. Bristol Channel. North Sea.
Total length: Female 2.3-3.2 mm; male 1.8-2.3 mm .
Further information: Sars, 1921a; Rose, 1933; Isaac, 1975 (as Thaumaleus longispinosus); Boxshall \& Halsey, 2004; Muxagata \& Williams, 2004 (as C. Iongispinosus); Suárez-Morales, 2011.

Cymbasoma thompsonii (Giesbrecht, 1893)
Female: A1 short, around a third length of cephalothorax (Fig. 83A, B); cephalothorax much longer than rest of body, in dorsal view broadest anteriorly; eyes quite well developed; oral tube very far forward. Urosome very short, only three somites (Fig. 83C); genital somite rounded in dorsal view (Fig. 83A); furcae small with three setae (Fig. 83C); ovigerous spines extending beyond furcal setae; P5 with three setae on outer lobe (Fig. 83D), the innermost tiny, no setae on inner rounded lobe.
Male: A1 very robust, last segment thickened, with two distal spines (Fig. 83E, F); cephalothorax much shorter than in female, narrowing anteriorly; urosome of four somites; genital lappets on copulatory organ with pointed lobes, without spines (Fig. 83G); furcae with three setae. No P5.


Fig. 83. Cymbasoma thompsonii (after Sars, 1921a, from Rose, 1933; as C. thompsoni)
Recorded: PMF. L4, not recorded. Southampton. North Scotland. West Norway. Irish Sea. Bristol Channel.
Total length: Female 0.8-1.2 mm; male 0.65-0.8 mm.
Further information: Sars, 1921a; Rose, 1933 (both as Cymbasoma thompsoni); Isaac, 1975 (as Thaumaleus thompsoni); Boxshall \& Halsey, 2004; Muxagata \& Williams, 2004 (as C. thompsoni); Suárez-Morales, 2011.

Cymbasoma rigidum Thompson, 1888
Female: A1 short, around one third length of cephalothorax (Fig. 84A); body moderately slender; cephalothorax as long as the remainder of body, in dorsal view narrows anteriorly; eye well developed; oral tube small, around quarter way down the cephalothorax (Fig. 84B). Three somites in urosome (Fig. 84C); genital somite evenly narrowed behind; anal somite widening behind, with slight notch in front of middle (Fig. 84D); ovigerous spines long, extending well beyond furcal setae (Fig. 84A, B), but not as long as in C. longispinosum; furcae slightly longer than broad (Fig. 84D), not very divergent, each with three setae, one emerging from a prominent angle on outer furcal edge, a fine bristle usually also present. P5 with three distal setae, the innermost much smaller (Fig. 84E), inner lobe produced parallel to outer lobe.
Male: Shorter and more robust than female (Fig. 84F, G); A1 longer than in female, terminating in slender, slightly curved spine (Fig. 84I); cephalothorax in dorsal view quite parallel sided; urosome narrow, of four somites, the anal somite with a notch similar to the female (Fig. 84H); genital lappets on copulatory organ large diverging lobes, appear to have a short, distal spine, not mentioned by Sars (1921a); furcae with four setae on square end. No P5.


Fig. 84. Cymbasoma rigidum (after Sars, 1921a, from Rose, 1933).
Recorded: PMF. L4, not recorded. Southampton. West Norway. North Sea. Irish Sea. Bristol Channel.
Total length: Female $2.20-3.00 \mathrm{~mm}$; male, up to 1.75 mm .
Further information: Sars, 1921a; Rose, 1933; Isaac, 1975 (as Thaumaleus rigidus); Boxshall \& Halsey, 2004; Muxagata \& Williams, 2004 (as Cymbasoma rigidus); Suárez-Morales, 2011.

Genus Monstrillopsis:
Monstrillopsis filogranarum (Malaquin, 1896)
WORMS still gives this as an existing species, but there is virtually no description available for it and Isaac (1975) put a question mark against it.
Female: Urosome of four somites (Fig. 85); genital somite as long as the previous somite, not quite as long as the following two somites together; ovigerous spines not joined at base, extending beyond furcal setae; furcae with four setae of similar lengths. P5 with three setae of slightly different lengths on outer lobe, small inner lobe with no setae.
Male: Unknown.


Fig. 85. Monstrillopsis filogranarum (from Malaquin, 1901, as Haemocera filogranarum).
Recorded: PMF (as Cymbasoma filogranarum). L4, not recorded. English Channel.
Total length: Female: ?
Further information: Rose, 1933 (as Cymbasoma filogranarum); Isaac, 1975 (as Monstrilla filogranarum); Boxshall \& Halsey, 2004; Suárez-Morales, 2011.

## Class Maxillopoda: Sub-class Copepoda: Infraclass Neocopepoda: Superorder Podoplea:

## Order Siphonostomatoida:

Siphonostomatoida comprises $\sim 44$ families of parasitic and commensal species that are mainly associated with fish, but also with a variety of marine invertebrates. Developmental stages are only occasionally sampled, mainly at shallower inshore positions. Because of their adaptation to specialised lives, there is great variation in body morphology between genera. The free-swimming, or accidentally detached stages of the siphonostomatoid fish parasites are quite characteristic in appearance, but some associated with invertebrates closely resemble copepods of other orders. Some adults are just sacs with no visible somites. However, all siphonostomatoids can be recognised by the presence of a feeding apparatus called an oral cone at some stage in their life (Fig. 87B), the defining characteristic of the order. The oral cone varies in structure and development, but is typically formed by partial or complete fusion of the labrum and labium (Kabata, 1979), forming a cone around and above the oesophageal opening. The lateral margins of the lips remain separate from each other for a short distance at the base, creating a small opening through which the mandibles enter the cone. In some species fusion is also incomplete near the tips, which are often armed with setae or other structures. Males either have both A1 geniculate or neither. Fusion among prosome and urosome somites is very variable and more extensive than in other orders.

## Siphonostomatoida parasitic on fish hosts

Adaptation to a parasitic way of life on fish has resulted in substantial morphological modifications, particularly to enable attachment to the host and to increase reproductive potential. There are around 100 British species (Kabata, 2003) and $\sim 74$ are recorded in the PMF, mainly found during examination of fish and not from plankton sampling. Two fish parasite species that are sometimes taken in plankton samples have been included here as examples. They are commonly known as "sea lice", and are largely ectoparasitic, feeding on mucous, epidermal tissue and body fluids.
The nauplii larvae are free-living, heavily invested with lipid from the egg and non-feeding. They may go through from zero to six free stages, typically two, before moulting into the Co1. The Co1 is free-swimming and the infective stage, initially attaching to the host using an A2 modified into strong, grasping claws or hooks, and sometimes also other grasping limbs. They subsequently attach more permanently by a chitinous frontal filament that penetrates the host tissues. This frontal filament is sometimes described as being used to channel nutrition from the host, but is almost certainly only a tether, to secure the copepod while it grazes on the surrounding tissues. Once attached to their host and moulted they are called a chalimus stage. There are typically four chalimus stages before moulting into the adult. The adult males are free-swimming and their sole purpose is to fertilise the female, after which they die. The adult female may remain attached to their first host and metamorphose, or become free-swimming until it finds and attaches intimately or superficially to their second host, after which it may metamorphose further. Some females change their morphology so drastically in the process of metamorphosis that they are totally unrecognisable as the adult form of their own free-swimming stages.

## Family Caligidae:

The body is characteristically flattened in the adult stages (Fig. 86D-F) and has a membrane around the edges forming a simple sucker, allowing the copepod to adhere closely to the surface of the host (Boxshall \& Halsey, 2004). Neither of the male A1 are geniculate. The cephalothorax is fused down to the third pedigerous somite and the body articulates between the fourth and fifth pedigerous somites (Fig. 86F). The fifth pedigerous and genital somite are fused and may be fused to further somites, resulting in one to three free somites behind the genital somite.

## Genus Caligus:

Caligus elongatus von Nordmann, 1832
This is a parasite of a very wide range of fish species, particularly gadoids, and is one of the commonest fish parasites found around the British Isles (Kabata, 1979). It has in the past often been wrongly recorded (Parker, 1969) under the synonym Caligus rapax and the C. rapax recorded in the PMF is assumed to be this species.


Fig. 86. Caligus elongatus (A-F from Piasecki, 1996 © Canadian Science Publishing or its licensors; G, H from Schram, 2004).

The N1 hatches from the egg and moults into the N2 (Fig. 86G, H); both naupliar stages are nonfeeding, depending on yolk reserves for energy. They are elongated with two oar-shaped
appendages posteriorly, that protrude laterally. The posterior margin of the carapace has a central protrusion, more obvious in the N2. In living nauplii there are crimson pigmented areas in the body. The N2 moults into the Co1 stage (Fig. 86A, B), the infectious stage. This attaches to a suitable host, initially by the hook-like A2 and then by a frontal filament that penetrates the host tissue. It then moults to the chalimus one stage. There are a further three chalimus stages each separated by a moult. The Co1 and chalimus stages have a developed gastrointestinal tract and feed on host mucus and tissues within the range of their frontal filament allows. The fourth chalimus stage (Fig. 86C) moults to an adult. Males (Fig. 86D) are smaller than females, with slimmer posterior body regions. They reach maturity at the same time as females, but become mobile sooner, moving vigorously over the surface of the host, possibly in search of females. While the young adult females are still tethered by their frontal filament the males copulate with them, then the females detach. Both sexes may retain remnants of their frontal filaments all of their remaining lives. Both sexes are flattened dorsoventrally, an adaption to exposed living on the surface of their host.
Young adult females (Fig. 86E) grow only slightly more in length, but differ in shape from mature ovigerous females (Fig. 86F) whose genital somite expands greatly to accommodate the maturing eggs. Male numbers decrease rapidly after mating and it is believed they die (Piasecki \& MacKinnon, 1995). The free-swimming females attach superficially on the surface of their fish host, on the skin or mouth, using their hooked A2 and sometimes also other limbs. In some cases they can move between host fish. The eggs sacs they produce are rigid and tubular (Fig. 10G), and the eggs in their early stages are disc-shaped.

Recorded: PMF as Caligus rapax. L4, not recorded. Millbay Marina, Plymouth, caligoid nauplii frequently found in small numbers. Around most of Europe.
Total length: N1 $\sim 0.45 \mathrm{~mm}$; N2 $\sim 0.49 \mathrm{~mm}$; Co1 0.58-0.81 mm; young female 4.21-5.39 mm; adult female 4.97-5.71 mm; adult male 3.63-4.85 mm.
Further information: Parker, 1969; Kabata, 1974, 1979; Boxshall, 1979; Piasecki \& MacKinnon, 1995; Piasecki, 1996; Boxshall \& Halsey, 2004; Muxagata \& Williams, 2004; Schram, 2004.

Family Pennellidae:
Genus Lernaeocera:
Lernaeocera branchialis (Linnaeus, 1767)


Fig. 87. Lernaeocera branchialis developmental stages (A-E, G from Sproston, 1942; F from Kabata, 1979).

Lernaeocera branchialis is a common gill parasite, particularly of flounders (Pleuronectes flesus) and gadoids (Sproston \& Hartley, 1941; Kabata, 2003), but can occur on other fish species. There may be two naupliar stages (Wilson, 1917), but only one stage was observed by Sproston (1942). The N1 (Fig. 87G) is oval with two posterior oar-shaped appendages that protrude laterally. It moults into the free-swimming Co1 stage (Fig 87A). In aquaria the Co1 stages tended to gravitate towards the bottom where their usual flatfish host, the flounder, would normally be found. The A1 of the Co1 are indistinctly five-segmented and covered in fine setae. The A2 have strong claws, used to anchor the copepod to the gill filaments of their first host. Two pairs of biramous swimming legs with long setae are present, the P1 on the last cephalothorax somite and the P2 on the first metasome somite. The second free metasome somite bears two backwardly pointing lateral spines representing the P3. There are five long setae on each furca. When the Co1 moults into the first chalimus stage, a chitinous frontal filament is produced from the mid-frontal region and penetrates the gill, forming a more permanent connection to the host and keeping the copepod mouthparts in close proximity to the gills for feeding. While attached, the chalimus moults through three further stages, gaining further limbs etc. At least the swimming limbs are simplified structures, as they are non-functional. There are morphological changes following the moult between the fourth chalimus stage (Fig. 87B) and the free-swimming adult stages (Fig. 87C, D). Because adults are freeswimming, functional limbs appear. Neither of the male A1 are geniculate. The oral cone, typical of
siphonostomatoid copepods, is similar in both sexes. In the female the gonads are not yet mature, but copulation may take place before she has barely finished moulting, even while still attached to the gill of the flounder. Both adults have attained the same degree of structural development, but the female is a different shape to the male, with an elongated genital somite with a crenulated outline (Fig. 87D). Following copulation, the female genital somite elongates very rapidly until it is slightly longer than the rest of the body. By this time the female has detached from the flounder and swims actively in the hope of encountering a suitable gadoid host. It initially attaches to the host gills by the claw-like A2, loses the A1 and begins metamorphosis (Figs. 87E, F), during which time the body is highly transformed. Branching structures called "antlers" (Fig. 87F) develop that penetrate the gill and locate a major blood vessel for feeding. The final female adult appearance is more like a worm than a copepod. Eggs are produced in long coiled strings and are initially flattened and disc-like.

Recorded: PMF. L4, not recorded. Around most of Europe.
Total length: Nauplii $\sim 0.34-0.45 \mathrm{~mm}$; Co1 $0.39-0.63 \mathrm{~mm}$; free-swimming adult female $\sim 1.25-1.91$ mm ; metamorphosed female $\sim 40 \mathrm{~mm}$; adult male $\sim 1.00-1.50 \mathrm{~mm}$.
Further information: Sproston \& Hartley, 1941; Sproston, 1942; Heegaard, 1947; Boxshall, 1979;
Kabata, 1979, 2003; Boxshall \& Halsey, 2004.

## Siphonostomatoida parasitic or commensal on invertebrate hosts

While a few siphonostomatoid copepods that are parasitic or commensal on invertebrate hosts have adopted a parasitic relationship and life-cycle reminiscent of the fish parasites, in most cases the association may be no more than occupying part of the host body structure for shelter, sharing food, feeding on faeces, or for grazing on the host integument, all causing little harm. Some species may be closely associated at all stages of development with the host, while others may only have contact as adults. Where the association is less intimate, the life-cycle and developmental sequence may be quite similar to free-living copepods, but extremely little information on individual species is available. Some species certainly have six nauplius and six copepodite stages, but in others, several of the nauplius stages may be passed within the egg, and number of copepodite stages may be reduced. In many species the oral cone is stylet-like, suggesting that it is used to pierce the host.
This group are found in association with a wide variety of marine invertebrate phyla, but in contrast to some fish parasites their economic importance is probably quite limited. They only tend to be collected when sampling around marinas, or close inshore. There are $\sim 19$ species of siphonostomatoid copepods associated with marine invertebrates recorded In the PMF, none at L4, but exhaustive surveys have not been carried out locally. Four species that have been recorded at Plymouth are illustrated to show the morphological diversity.

D) Male, Cancerilla tubulata

E) Female. Asterocheres latus
F) Female, Asterocheres latus anterior head ventral


Fig. 88. Examples of four siphonostomatoid associates of invertebrates recorded in the PMF (From Gotto, 1993).

Bradypontius magniceps (Brady, 1880). Metasome somites widely separated laterally (Fig. 88A); oral cone very narrow, stylet-like, extending to the base of the P2 (Fig. 88B); furcae almost three times as long as wide. Male in this family have the A1 non-geniculate. Possibly have association with sponges. Female length: 1.2-1.8 mm; male unknown.

Cancerilla tubulata Dalyell, 1851. There are six nauplius and six copepodite stages. Prosome very inflated, particularly in female (Fig. 88C); male with numerous long setae on non-geniculate A1 (Fig. 88D). Associates from the Co 2 with brittle stars, but not permanently attached. Female length $0.9-1.1 \mathrm{~mm}$; male $0.9-1.0 \mathrm{~mm}$.

Asterocheres latus (Brady, 1872). Body cyclopoid-like (Fig. 88E); males in family have A1 geniculate on both sides; oral cone stylet-like, robust, reaching base of P1 (Fig. 88F); furcae less than three times as long as broad. Associates with sponges, sea urchins and algae. (Recorded in the PMF as Ascomyzon latum). Female length 0.8 mm ; male unknown.

Micropontius ovoides Gooding, 1957. Body of both sexes shield-shaped (Fig. 88G, H), the male more of an ellipse than the female; male A1 geniculate on both sides; oral cone rudimentary. Associates with sea urchins, probably living on body surface. Female length 0.39 mm ; male 0.35 mm .

Further information: Gooding, 1957; Carton, 1968; Gotto, 1979, 1993; Boxshall \& Halsey, 2004 (part 2); Muxagata \& Williams, 2004.

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## Some useful copepod websites

## www.nmnh.si.edu/iz/copepod

The world of copepods, Smithsonian National Museum of Natural History. Bibliography, taxonomy, techniques, researchers etc. Extremely useful for finding references if you only have a name and date etc.

## http://copepodes.obs-banyuls.fr.

Razouls C., de Bovée F., Kouwenberg J. \& Desreumaux N., 2005-Present. Diversity and geographic distribution of marine planktonic copepods. An amazing resource for checking which species of different genera occur in your work area, synonyms and most recent classification. Includes distribution maps, taxonomic illustrations, bibliography etc.

## http://www.marinespecies.org

World Register of Marine Species (WORMS) site. Classification, bibliography, synonyms, images, distribution etc. of marine species
http://www.faunedefrance.org/BibliothequeVirtuelleNumerique
Editions of Faune de France can be downloaded free, including Rose, M. 1933. Copépodes pélagiques, No 26.

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[^0]:    +1 in the swimming leg row indicates that tiny rudimentary leg-buds may be present that will not fully develop until the next moult.

