Identification of the copepodite developmental stages of twenty-six North Atlantic copepods

Fig. 7

David V.P. Conway



Fig.1A

Fig.4

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Fig. 5

Fig. 6

Identification of the copepodite developmental stages of twenty-six North Atlantic copepods

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Cover picture: Nauplii and copepodite developmental stages of Centropages hamatus (from Oberg, 1906).

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Preface

This identification guide to the copepodite developmental stages of twenty-six North Atlantic copepods was originally published in 2006, based on an unpublished manuscript by Conway & Minton (1975). It has been revised to correct some taxonomic and other errors, to include some new information and to give additional information on how to determine sex in the later copepodite stages of gymnoplean copepods.

Introduction

Most free-living copepods moult through five copepodite development stages (Co1-Co5), prior to becoming adult females or males in the final sixth stage (Co6). In zooplankton research there is often the requirement to be able to individually identify and count these stages for species being studied. At each stage, number of body somites (the term somite is used for major body divisions, while segment is used for divisions of appendages) and number and complexity of the various appendages changes, so the six stages can be individually separated. Most copepods show a basically similar configuration in number of somites and appendages at each stage. Separation of copepodite stages is made easier because of the crustacean characteristic of moulting of the exoskeleton and rapid growth between stages. Because of this there may be little or even no overlap in length between stages. Under a microscope it is thus often possible to initially, roughly sort the stages of an individual species on size alone. For many species it is also possible, in the later stages, to determine the sex before they become adults by using particular limb features (see below). Included in this guide are tables of information, where available, on number of somites and appendage found in each stage of 26 north Atlantic copepods. Various measurements of the stages are also tabulated. The majority of this information was compiled from literature sources, some from original observations.

Copepod classification:

Marine species of Sub-class Copepoda are currently divided into two Infraclasses:

Infraclass Progymnoplea, containing only Order Platycopioida.

Infraclass Neocopepoda, divided into two superorders containing seven orders.

Superorder Gymnoplea - Order Calanoida.

Superorder Podoplea - Orders Cyclopoida, Harpacticoida, Misophrioida, Monstrilloida, Siphonostomatoida and Mormonilloida.

An additional podoplean order, Poecilostomatoida, is still used in some classifications, but current evidence indicates that poecilostomatoids should be merged within Order Cyclopoida (Boxshall & Halsey, 2004) and this has been followed here. Only information for some pelagic species from the three largest orders, Calanoida, Cyclopoida and Harpacticoida is included here.

Copepod body divisions:

Before detailing how to identify copepodite stages it is useful to review copepod morphology and nomenclature, using gymnopleans as the main example. The current generally accepted copepod morphological terminology is given in Figures 1 and 2. Some of 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 copepod somites are fused together and the different function of some of the appendages. The adult (Co6) body (Fig. 1) is divided, from anterior to posterior, into cephalosome (Ce), metasome (Me) and urosome (Ur) regions. The cephalosome and metasome together are termed the prosome (Pr). Theoretically, the body of all adult copepods is composed of 16 somites, but all the individual somites are not visible externally (free), because some are fused together. 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, 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 termed the cephalothorax. Many gymnoplean species also have the last two pedigerous, metasome somites fused together.

The urosome in all copepod orders is defined as the series of somites posterior to the major body articulation (bending joint). The position of this articulation in adult copepods differs by one somite between Superorders Gymnoplea and Podoplea. The articulation in gymnopleans is located behind the fifth pedigerous somite, so all the swimming legs are in front of the articulation (Fig. 1). 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 gymnopleans and six in podopleans, but in females of both superorders, the two somites posterior to the P5 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, some species have only three free urosome somites, including several of the gymnopleans described here, occasionally two, due to additional somite fusion. All male gymnopleans described here have five free somites in the urosome, except for *Centropages* spp. (pages 19-20), which have four, unusual among gymnopleans. All cyclopoid and harpacticoid females described here have five free somites in the urosome and all males six, but a small number of other species in these orders have fewer. The first somite of the urosome in gymnopleans, the second in podopleans, is the genital somite (a double-somite in females) and is where the genital apertures in both sexes are located, usually dorsally, sometimes ventrally. 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. 1, 2). The anterior somite bears the antennules (A1), which are sensory and each is uniramous (single branch). The following five somites bear the feeding appendages comprising: antennae (A2), mandibles (Md), maxillules (Mx1), maxillae (Mx2) and maxillipeds (Mxp). Each of these is biramous (two branches), apart from the maxillae and maxillipeds that are typically uniramous. 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. 2E).

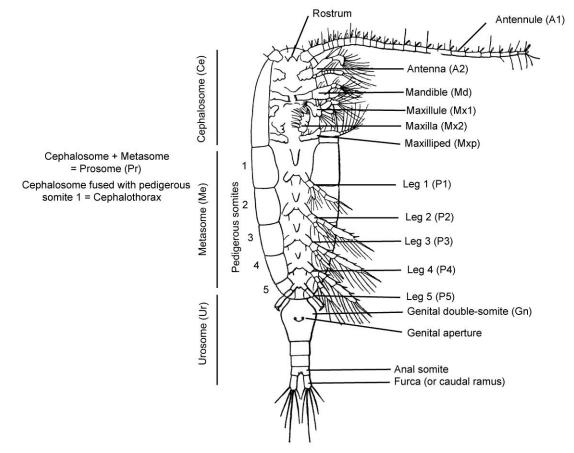


Fig. 1. The external morphology and appendages of an adult female gymnoplean copepod, ventral view. The example given shows the minimum possible fusion of somites. Abbreviations commonly used for parts are shown and the swimming legs (P1-P5) and pedigerous somites of the metasome are numbered (after 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. 1), commonly termed swimming legs, but in several gymnoplean genera the females lack the fifth pair (e.g. Pseudocalanus elongatus; page 15). In most copepods of all orders, only the first four pairs of swimming legs of both sexes could actually be used for swimming, as the fifth is usually too small or rudimentary, or in other ways structurally unsuitable for this purpose. In gymnopleans the P5 are usually involved in reproductive activities. Leg pairs are typically rigidly joined together at the base, so they beat simultaneously. In all copepods, at least P1-P4 are quite similar in structure and each individual limb is biramous, but the P5 is extremely variable in structure between species, making it one of the most useful features, at least in gymnopleans, for species identification. In most female copepods the P5 are reduced in size and complexity, in some cyclopoids to simple setae. Male gymnoplean 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 gymnopleans of both sexes, the P5 are often so reduced or modified from the basic leg pattern shown in Figure 2F, that it may not be immediately obvious which parts are exopods or endopods etc. The genital somite bears remnants of what are considered to be 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 gymnopleans have both A1 identical, these differing from, but generally resembling the female A1. In other gymnoplean 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 gymnopleans it is on the left (e.g. *Metridia lucens* page 24). Adult male podopleans in Order Harpacticoida and in Family Oithonidae of Order Cyclopoida have both A1 geniculate, while in other cyclopoid families (e.g. Oncaeidae) they lack any geniculation, although there is still sexual dimorphism in the structure of the A1.

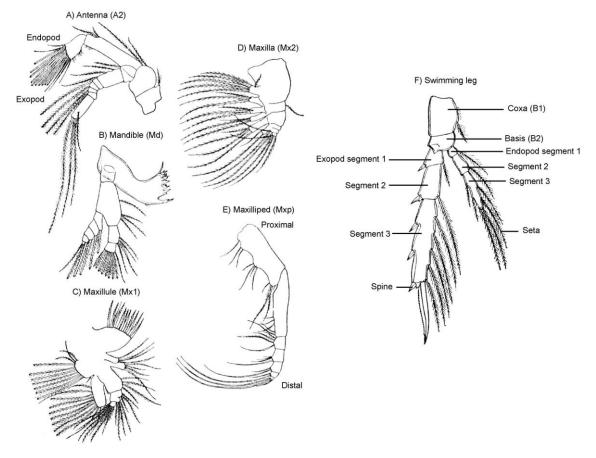


Fig. 2. Example of some gymnoplean prosome appendages (after Rose, 1933). Abbreviations used for parts are shown.

Copepod moulting and development:

An example of the typical sequential development of somites in a gymnoplean copepod (*Calanus* sp.) from Co1-Co6 is given in Figure 3. Between moults a somite is added, always immediately in front of the anal somite. In the example in Figure 3, the shaded somite in Co1 was added between the sixth nauplius stage (N6) and Co1. At the moult into Co2 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 Co2 to Co3, the stage at which the final metasome somite complement is reached. After Co3, further somites added are incorporated into the urosome, until the final urosome somite complement is reached in Co6. In this gymnoplean example it is five somites in the 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, but fewer in females of some species due to additional somite fusion. In species that have sharp points on the posterior metasome in Co6 (e.g. *Centropages typicus*; page 20), these may first appear in Co4, the stage after the last metasome somite appears, but in other species may not appear until the Co6 (e.g. Undinula vulgaris; page 14). In Temora stylifera (page 23) evidence of points are present from Co1. Because fusion of both prosome and urosome somites sometimes takes place during development (e.g. Pseudocalanus elongatus; page 15 and Acartia clausi; page 18), there can be interspecific differences in number of free somites, differences that can be useful in separation of species and stages.

The Co1 of most copepods usually have two urosome somites, but sometimes only one according to a table in Mauchline (1998). Certainly Co1 *Oncaea waldemari* (page 30) was noted as having one somite in the urosome by Malt (1982; as *Oncaea media*). In Co1 there are typically two pairs of swimming legs, but some species sometimes have one or even two additional rudimentary pairs that do not develop properly until subsequent moults (e.g. *Calanus* spp.; pages 10-11 and *Oncaea waldemari*; page 30). Following each moult an additional pair of reasonably developed swimming 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 do 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.

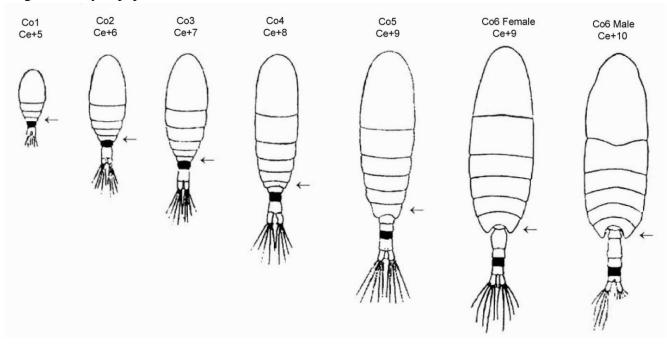


Fig. 3. Sequence of body somite increase between copepodites Co1-Co6 of a gymnoplean copepod, *Calanus* sp. Arrows indicate the last metasome somite. The shaded somite is the one added at the previous moult. Number of free somites, in addition to the cephalosome (Ce), is noted as e.g. Ce+5 (after Mauchline, 1998).

Sex determination in late gymnoplean copepodite stages:

As already mentioned, in gymnopleans there is considerable difference in the morphology of the P5 between the sexes. The P5 appear at Co4, apart from females that do not develop a P5. They are not fully developed to the adult structure in Co4, but are initially quite rudimentary, becoming more complex in Co5 and fully formed after the moult to Co6. Both sides of the P5 of female gymnopleans are usually symmetrical from Co4, while most male P5 are usually at least slightly 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 podopleans the P5 are similar and symmetrical in both sexes, so the same method of separation of the sexes is not possible. In gymnopleans 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 adults, females usually predominating, it is thought that ultimate sex, in at least some copepod species, may be determined by environmental factors, such as 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.

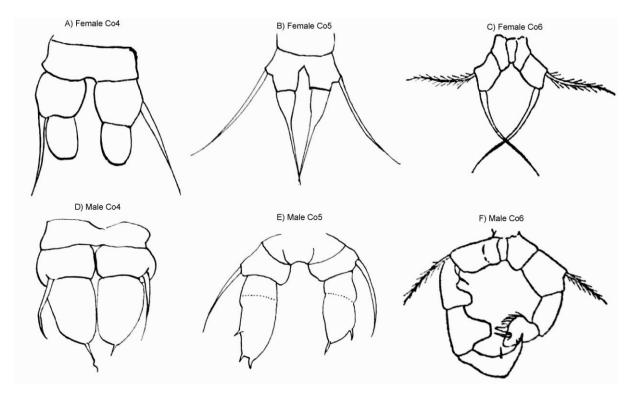


Fig. 4. P5 of female and male copepodite stages Co4-Co6 of *Acartia* spp. (A-B, D-E from Björnberg, 1972; C, F from Rose, 1933, after Sars, 1903).

SUPERORDER GYMNOPLEA: ORDER CALANOIDA

In adult gymnoplean copepods the major movable articulation (bending joint) of the body is located between the fifth pedigerous and genital somites, between the eleventh and twelfth body somites, so all the pedigerous somites are on the prosome. Number of prosome somites on its own is not the most useful character to separate stages, as individual somites are often difficult to distinguish. Additionally, in some species fusion of prosome somites takes place during development, so numbers increase and then decrease e.g. *Pseudocalanus elongatus* (page 15), or numbers may be variable at particular stages e.g. *Paracalanus parvus* (page 17).

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	4	5	6	6	6	6
No. of free urosome							♀ 4
somites	1	2	2	2	3	4	₫5
No. of pairs of							
swimming legs	1	2+1	3+1	4+1	5	5	5
Mean total length							₽2.70
(mm)	2	0.77	1.06	1.37	1.81	2.44	∂2.66
Range of total length							♀2.44-3.08
(mm)	2	0.73-0.84	1.01-1.15	1.29-1.46	1.66-1.94	2.25-2.61	∂ ^{2.50-2.85}
Mean total length							₽3.41
(mm)	3	0.88	1.23	1.66	2.16	2.89	∂3.41
Range of total length							♀3.00-3.92
(mm)	3	0.81-0.95	1.10-1.32	1.46-1.79	1.98-2.38	2.56-3.44	∂3.22 - 3.59
Mean prosome length							₽2.11
(mm)	2	0.60	0.83	1.09	1.44	1.90	∂2.07
Range of prosome							♀ 1.86-2.44
length (mm)	2	0.56-0.67	0.73-0.90	1.01-1.18	1.29-1.55	1.74-2.03	∂1.97-2.15
Range of mean							♀2.23-2.82
prosome length (mm)	4*	0.63-0.76	0.90-1.09	1.23-1.51	1.58-1.98	2.00-2.51	<i>∛</i> 2.34-2.67
Mean prosome width							♀0.64
(mm)	2	0.21	0.25	0.31	0.41	0.54	∂0.61
Range of greatest							♀0.58-0.76
prosome width (mm)	2	0.20-0.23	0.23-0.28	0.28-0.34	0.37-0.45	0.46-0.58	<u>്</u> 0.58-0.64

Calanus finmarchicus (Gunnerus, 1770)

*Values are the range of mean sizes of groups of copepods sampled on different dates.

Notes:

1). From Marshall & Orr (1955).

2). From measurements of copepods sampled in the northern North Sea in April 1974.

3). From measurements of copepods sampled in the Irminger Sea in August 2002 (samples from S.J. Hay, FRS Aberdeen).

4). From measurements of copepods sampled in the Firth of Clyde, western Scotland, January to October 1933 (Marshall *et al.*, 1934).

In Co1-Co3 of *Calanus* spp., an additional pair of small but obvious rudimentary legs may be present, which are noted separately in the table (e.g. 2+1). If present, these additional legs only become developed close to their final structure after the next moult. Sex cannot easily be determined in Co4-Co5 of *Calanus* sp. using morphology of the P5, as can be done for many other gymnopleans, because in Co6 $Q \Im$ the P5 are not strongly sexually dimorphic, but of similar size and appearance, so the P5 of earlier stages also appear similar.

Eriksson (1973), working on the west coast of Sweden, gave the female prosome length range as 2.00-3.12 mm.

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	4	5	6	6	6	6
No. of free urosome							♀ 4
somites	1	2	2	2	3	4	්5
No. of pairs of							
swimming legs	1	2+1	3+1	4+1	5	5	5
Mean total length							Q2.91
(mm)	1					2.69	്3.01
Range of total length							Q2.60-3.28
(mm)	1					2.31-3.16	∂2.79-3.27
Mean total length							Q2.9
(mm)	2				1.9	2.4	∂2.7
Range of total length							♀2.7-3.2
(mm)	2				1.8-2.0	2.1-2.7	∂2.7
Mean total length							\$3.53
(mm)	3	0.93	1.23	1.64	2.34	2.98	്3.39
Range of total length							♀3.09-3.94
(mm)	3	0.86-1.00	1.15-1.34	1.53-1.79	2.27-2.46	2.79-3.20	∂3.01-3.72
Mean prosome length							Q2.79
(mm)	3	0.74	0.97	1.30	1.75	2.38	්2.64
Range of prosome							Q2.46-3.12
length (mm)	3	0.71-0.78	0.89-1.04	1.19-1.41	1.79-1.97	2.27-2.60	∂2.34-2.90

Calanus helgolandicus (Claus 1863)

Notes:

1). From copepods sampled in the Celtic Sea in January 1982.

2). From copepods sampled off north-western Iberia in July 2005.

3). From copepods sampled in the Celtic Sea in May 1980

In Co1-Co3 an additional pair of small but obvious rudimentary legs may be present, which are noted separately in the table (e.g. 2+1). If present, these additional legs only become developed close to their final structure after the next moult. Sex cannot easily be determined in Co4-Co5 of *Calanus* sp. using morphology of the P5, as can be done for many other gymnopleans, because in Co6 $Q \circ$ the P5 are not strongly sexually dimorphic, but of similar size and appearance, so the P5 of earlier stages also appear similar.

Alvarez-Marques (1984) sampled throughout the year off northern Spain and measured *Calanus* helgolandicus Co6 \bigcirc as 2.26-3.57 mm total length (mean 2.81 mm) and Co6 \bigcirc as 1.98-3.08 mm (mean 2.76 mm). Eriksson (1973), working on the west coast of Sweden, gave the female prosome length range as 1.88-3.08 mm.

Neocalanus gracilis (Dana 1849)

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							♀ 5
somites	1	3	4	5	5	5	ð6
No. of free urosome							♀ 4
somites	1	2	2	2	3	4	₫5
No. of pairs of							
swimming legs	1	2	3	4	5	5	5
Range of total length							Q2.43-4.00
(mm)	2						∂2.30-3.10
Mean prosome length							
(mm)	1	0.78	1.01	1.30	1.55	2.10	

Notes:

1). From copepods sampled in the Gulf of Marseilles (Gaudy, 1962).

2). From Rose (1933).

There is one less somite in the prosome in Co1-Co5 of *Neocalanus gracilis* than in e.g. *Calanus helgolandicus*, as the prosome and first pedigerous somite fuse to form a cephalothorax. In the Co6 \bigcirc this fusion persists, but not in the Co6 \bigcirc . It may be possible, but has not been checked, to determine sex in Co4-Co5 of *N. gracilis* using morphology of the P5, as can be done for many other gymnopleans, because in Co6 \bigcirc \bigcirc the P5 are more strongly sexually dimorphic than in most other Family Calanidae. Because of this the P5 of Co4-Co5 may also differ between sexes.

Gaudy (1962) did not provide measurements of adult prosomes. From sampling throughout the year off northern Spain, Alvarez-Marques (1984) measured *N. gracilis* Co5 \bigcirc as 2.14-2.38 mm total length, but provided no measurements of males.

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	3	4	5	5	5	5
No. of free urosome							♀ 4
somites	1	2	2	2	3 [§]	4	ి5
No. of pairs of							
swimming legs	1	2	3	4	5	5	5
Range of total length							♀1.70-2.30
(mm)	2						∂1.20-2.01
Mean prosome length							
(mm)	1	0.48	0.60	0.72	0.92	1.20	

Nannocalanus minor (Claus, 1863)

[§]Gaudy (1962) noted four somites in the urosome, but drew three in his figure.

Notes:

1). From copepods sampled in the Gulf of Marseilles (Gaudy, 1962).

2). From Bradford-Grieve (1994).

There is one less somite in the prosome of Co1-Co6 than in e.g. *Calanus helgolandicus*, as the prosome and first pedigerous somite fuse to form a cephalothorax. Sex probably cannot be determined in Co4-Co5 of *Nannocalanus minor* using morphology of the P5, as can be done for many other gymnopleans, because in Co6 $Q \Im$ the P5 are not strongly sexually dimorphic, but of similar size and appearance, so the P5 of earlier stages may also appear similar.

Gaudy (1962) did not provide measurements of adult prosomes. From sampling throughout the year off northern Spain, Alvarez-Marques (1984) measured *Nannocalanus minor* Co6 \bigcirc as total length 1.81-2.20 mm (mean 2.05 mm) and Co6 \bigcirc as 1.78-1.95 mm (mean 1.86 mm).

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1				6	6	6
No. of free urosome							♀4 ♂5
somites	1				3	4	්5
No. of pairs of							
swimming legs	1				5	5	5
Mean total length							Q2.5
(mm)	1				1.7	2.2	්2.3
Range of total length							Q2.4-2.6
(mm)	1				1.5-1.8	2.0-2.3	∂2.2-2.5
Mean prosome length							₽2.0
(mm)	1				1.4	1.8	∂1.8
Range of prosome							♀1.9-2.1
length (mm)	1				1.2-1.5	1.7-1.9	∂1.7-1.9
Mean prosome width							♀0.6
(mm)	1				0.4	0.5	്0.5
Range of greatest							♀0.5-0.6
prosome width (mm)	1				0.3-0.4	0.5	∂0.5-0.6

Calanoides carinatus (Kröyer, 1849)

Notes:

1). From off north-western Iberia in July 2005 (Samples from D. Bonnet, University of Montpellier).

Stage information for *Calanoides carinatus* is only available for Co4-Co6, as Co1-Co3 could not be distinguished with any certainty from Co1-Co3 stages of *Calanus helgolandicus* occurring in the same samples. Number of free somites in Co4-Co6 is the same as in *C. helgolandicus*, so are probably the same in all stages. Co4-Co6 *C. carinatus* can easily be distinguished from other common Calanidae that occur in the region (*C. helgolandicus, Neocalanus gracilis, Mesocalanus tenuicornis* and *Nannocalanus minor*) as the anterior cephalosome comes to a point when viewed dorsally. The Co6 does not show this feature, but the anterior cephalosome is certainly more pointed than in Co6 *C. helgolandicus.* Co4-Co5 probably have a pointed cephalosome, as all Co4-Co5 of *C. carinatus* using morphology of the P5, as can be done for many other gymnopleans, because in Co6 does of this the P5 of earlier stages may also differ.

Alvarez-Marques (1984) sampled throughout the year off northern Spain and measured *Calanoides* carinatus Co6 \bigcirc as 2.00-3.09 mm total length (mean 2.36 mm) and Co6 \bigcirc as 1.98-2.69 mm (mean 2.29 mm).

Undinula vulgaris (Dana, 1849)

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome somites	1	2/3	4	5	5	5	5
No. of free urosome somites	1	2	2	3	3	4	♀4 ♂5
No. of pairs of swimming legs	1	2	3	4	5	5	5
Total length range (mm)	1	0.65-0.70	0.81-1.19				
Mean total length (mm)	2		0.86	1.20	♀1.68 ♂1.56	2.24 2.14	2.89 2.51
Range of total length (mm)	2		0.84-0.86	1.12-1.30	♀1.56-1.86 ♂1.42-1.74	2.10-2.48 1.84-2.38	2.68-3.14 2.42-2.72
Mean total length (mm)	3			1.05	♀1.32 ♂1.27	1.63 1.65	2.07 1.96
Range of total length (mm)	3			1.04-1.10	♀1.25-1.42 ♂1.22-1.34	1.56-1.89 1.56-1.74	1.89-2.62 1.88-2.08

Notes:

1). From copepods sampled in the Caribbean off Curaçao (Björnberg, 1966).

2). From copepods sampled in the Indian Ocean at Station 555 (Sewell, 1929).

3). From copepods sampled in the Indian Ocean at Station 614 (Sewell, 1929).

There is one less somite in the prosome in Co1-Co6 than in e.g. *Calanus helgolandicus*, as the prosome and first pedigerous somite fuse to form a cephalothorax. In most members of Family Calanidae the P5 in both sexes are usually quite similar, but in *Undinula vulgaris* they are remarkably different and this difference can be seen from when the P5 first appear in Co4. Sewell (1929) described the differences. In the Co4 $^{\circ}$ the exopod of the left P5 is longer and broader than the corresponding appendage on the right side, while the distal spine is shorter, a feature even more pronounced in Co5 $^{\circ}$. The P5 is symmetrical in the Co4 $^{\circ}$. The Co5 $^{\circ}$ has prominent spines on the posterior metasome somite, absent in the Co6 $^{\circ}$. The Co5 $^{\circ}$ does not have these spines. This differs from some other species that develop metasomal spines, such as *Candacia* and *Centropages*, where they are present from Co4.

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	4	5	6	5	5	4
No. of free urosome					₽3	♀ 4	♀ 4
somites	1	2	2	2	്3	්4	ී5
No. of pairs of					₽ 4	4	4
swimming legs	1	2+1	3+1	4	ె 5	5	5
Mean total length					♀0.80	1.05	1.54
(mm)	1			0.71	്0.86	1.00	1.12
Mean total length					♀0.96	1.20	1.21
(mm)	2	0.49	0.64	0.82	്0.96	1.11	1.05
Range of total length					♀0.85-1.01	♀1.10-1.32	♀0.93-1.55
(mm)	2	0.39-0.54	0.62-0.67	0.76-0.87	∂0.87-1.07	∂0.99-1.21	∂0.98-1.13
Mean prosome length					♀0.73	0.88	0.86
(mm)	2	0.39	0.50	0.65	്0.74	0.83	0.77
Range of prosome					♀0.65-0.79	0.79-0.93	0.65-1.15
length (mm)	2	0.31-0.45	0.48-0.53	0.59-0.70	∂0.67-0.84	0.73-0.90	0.73-0.84
Range of mean					♀0.61-0.75	0.68-0.91	0.75-1.06
prosome length (mm)	3*	0.35-0.43	0.43-0.54	0.52-0.64	∂0.60-0.73	0.68-0.85	0.65-0.84
Mean prosome width					Q0.28	0.35	0.34
(mm)	2	0.16	0.20	0.25	്0.28	0.32	0.33
Range of greatest					Q0.25-0.31	0.31-0.37	0.25-0.48
prosome width (mm)	2	0.14-0.18	0.17-0.23	0.23-0.28	∂0.25-0.34	0.28-0.37	0.31-0.37

Pseudocalanus elongatus (Boeck 1865)

*Values are the range of mean sizes of groups of copepods sampled on different dates.

Notes:

1). From Kraefft (1910).

2). From measurements of copepods sampled in the Firth of Clyde, western Scotland, in March 1974.

3). From copepods sampled off Plymouth throughout 1947 (Digby, 1950).

Pseudocalanus elongatus has a rather complex sequence of somite fusion. Between Co3 and Co4, the cephalosome and first pedigerous somites fuse to form a cephalothorax, and then between Co5 and Co6 the last two metasome somites fuse, so number of prosome somites increases and then decreases during development. In Co4 and Co5 the last metasome somite is small and not easily distinguished. In Co1-Co2 an additional pair of small rudimentary legs may be present, which are noted separately in the table (e.g. 2+1). If present, these additional legs only become developed close to their final structure after the next moult. Because *Pseudocalanus* females do not normally develop a P5 (see below), sex can be distinguished from Co4. The distal spine on the exopod of all swimming legs, except the P1, is serrated externally.

Marshall (1949) reported that in Loch Striven, a small proportion (<1%) of Co6 \bigcirc , which should only have four pairs of legs, had an additional rudimentary pair. This has also been observed off Plymouth and is thought to relate to the belief that, in at least some copepod species, sex may be determined by environmental factors at a late stage of development (Gusmão & McKinnon, 2009), males becoming females. In a small proportion of individuals, development may not be completely successful, resulting in a proportion of intersex females with intermediate types of legs. This will also be found in Co4 and Co5 females, but the legs will differ in appearance from those of Co4 and Co5 males.

Eriksson (1973), working on the west coast of Sweden, gave the female prosome length range as 0.62-1.30 mm.

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1						4
No. of free urosome							♀ 4
somites	1	2	2	2	3	4	ී5
No. of pairs of					₽ 4	4	4
swimming legs	1	2	3	4	₫5	5	5
Mean total length					♀0.48	0.57	0.66
(mm)	1	0.25	0.35	0.41	്0.53	0.62	0.70
Range of total length					♀0.45-0.51	0.51-0.59	0.62-0.70
(mm)	1	0.25	0.31-0.42	0.39-0.42	്0.48-0.65	0.56-0.68	0.67-0.73
Mean prosome length					♀0.38	0.47	0.52
(mm)	1	0.20	0.28	0.33	്0.40	0.48	0.49
Range of prosome					♀0.37-0.39	0.42-0.51	0.48-0.56
length (mm)	1	0.20	0.23-0.34	0.31-0.34	്0.34-0.51	0.45-0.51	0.48-0.51
Mean prosome width					Q0.17	0.21	0.23
(mm)	1	0.08	0.12	0.14	്0.21	0.22	0.22
Range of greatest					♀0.14-0.20	0.20-0.23	0.23-0.25
prosome width (mm)	1	0.08	0.11-0.14	0.14	്0.17-0.23	0.20-0.25	0.20-0.23

Microcalanus pusillus Sars, 1903

Notes:

1). From copepods sampled in the Firth of Clyde, western Scotland, in March 1974.

Two species of *Microcalanus* have been described in European waters, *M. pygmaeus* (Sars 1900) and *M. pusillus* Sars, 1903. They have the same general distribution and are morphologically very similar. The greatest difference between them is that the A1 reaches the furcae in *M. pygmaeus*, but only the genital somite in *M. pusillus*. Additionally, in *M. pygmaeus* the P1-P4 are slender and the distal spines on the P2-P4 exopods have finely serrated outer edges, while in *M. pusillus* the P1-P4 are comparatively short and broad and the distal spines on the P2-P4 exopods have coarsely serrated outer edges. Both species are listed as valid in the World Register of Marine Species (WORMS) website. Razouls *et al.* (2005-2012) also lists the two 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, calling into doubt their separate status. Specimens recorded from the Firth of Clyde by Marshall (1949) were identified by her as *M. pygmaeus*, but those sampled in the same general region in 1974 (table above) better fitted the description of *M. pusillus*. If genetical studies are carried out and indicate they are the same species, the name *M. pygmaeus* will take precedence.

The prosome is characteristically short, rounded and deep, and this shape is found even in the earliest stages. The number of free prosome somites in the Co6 adults is the same as in the related *Pseudocalanus elongatus*, so somite number in all other stages may be the same.

Microcalanus is one of the smallest gymnoplean copepods and tends to be found in highest numbers towards the sea bottom (Conway & Minton, 1976; Østvedt, 1955).

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	2	3/4	4/5	6	6/5	4
No. of free urosome							♀ 4
somites	1	2	2	2	3	4	₫5
No. of pairs of							
swimming legs	1	2+1	3+1	4+1	5	5	5
Mean total length						♀0.87	0.87
(mm)	2	0.35	0.46	0.55	0.72	്0.96	0.96
Range of total length						♀0.87	0.82-0.99
(mm)	2	0.32-0.37	0.42-0.48	0.49-0.59	0.65-0.76	് 0.96	0.96
Mean prosome length						♀0.70	0.69
(mm)	2	0.28	0.36	0.43	0.56	്0.73	0.73
Range of prosome						♀0.70	0.65-0.76
length (mm)	2	0.25-0.30	0.34-0.37	0.39-0.45	0.51-0.59	്0.73	0.73
Range of mean					♀0.46-0.54	0.59-0.65	0.66-0.73
prosome length (mm)	3*			0.46-0.47	∂0.57-0.60	0.70-0.74	0.73-079
Range of mean					♀0.46-0.56	0.55-0.63	0.62-0.85
prosome length (mm)	4*	0.24-0.30	0.30-0.38	0.39-0.49	്0.52-0.59	0.65-0.73	0.68-0.79
Mean prosome width						♀0.25	0.25
(mm)	2	0.10	0.13	0.15	0.20	് 0.28	0.28
Range of greatest						♀0.25	0.23-0.31
prosome width (mm)	2	0.10-0.11	0.11-0.14	0.13-0.17	0.17-0.23	∂°0.28	0.28

Paracalanus parvus (Claus, 1863)

*Values are the range of mean sizes of groups of copepods sampled on different dates.

Notes:

1). From Kraefft (1910) and copepods from the Northern North Sea in April 1974.

2). Co1-Co4 from the Northern North Sea in April 1974 and Co6 from the Firth of Clyde, western Scotland, in March 1974.

3). From copepods collected in the Firth of Clyde from July to October 1933 (Marshall, 1949).

4). From copepods collected off Plymouth throughout the year in 1947 (Digby, 1950).

The prosome and first pedigerous somite are fused from Co1 and the last two metasome somites become fused during development. Number of free prosome somites appears to be variable in Co2, Co3 and Co5 making this feature difficult to use in stage identification. In Co1-Co3 an additional pair of small rudimentary legs may be present, which are noted separately in the table (e.g. 2+1). If present, these additional legs only become developed close to their final structure after the next moult.

Although much smaller than *Calanus* spp, *Paracalanus parvus* has similar body proportions. The prosome is approximately three times the length of the urosome and these body proportions are found from early stages, helping to separate it from *Pseudocalanus elongatus*, which has a longer urosome in relation to prosome length. *P. parvus* can also be distinguished from *P. elongatus* by the lack of external serrations on the distal spine of P2-P4. Co4-Co6 3° are generally longer than Co4-Co6 3° . In Co5 3° the body shape is the same as the female but the P5 is the same length as the P4, much shorter in the female.

Eriksson (1973), working on the west coast of Sweden, gave the female prosome length range as 0.50-0.92 mm.

Acartia clausi Giesbrecht 1889

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	4	5	6	5	5	5
No. of free urosome					₽2*	3	3
somites	1	2	2	2	്3	4	5
No. of pairs of							
swimming legs	1	2+1	3+1	4	5	5	5
Mean total length					₽0.96	1.13	1.43
(mm)	1			0.73	് 0.94	1.08	1.28
Mean total length					₽0.88	1.06	1.13
(mm)	2	0.48	0.58	0.70	്0.93	1.04	1.16
Range of total length					♀0.84-0.93	1.01-1.10	1.04-1.18
(mm)	2	0.34-0.53	0.53-0.62	0.65-0.84	്0.90-0.99	0.98-1.27	1.04-1.32
Mean prosome length					₽0.69	0.83	0.87
(mm)	2	0.38	0.47	0.56	്0.72	0.82	0.87
Range of prosome					♀0.65-0.76	0.79-0.84	0.79-0.93
length (mm)	2	0.25-0.42	0.42-0.51	0.51-0.65	∂°0.70-0.76	0.79-0.93	0.79-0.99
Range of mean					♀0.64-0.79	0.75-0.96	0.85-1.17
prosome length (mm)	3 [§]	0.38^{\ddagger}	0.48^{\ddagger}	0.54-0.66	്0.64-0.75	0.74-0.89	0.82-1.00
Range of mean					♀0.59-0.76	0.67-0.86	0.83-1.12
prosome length (mm)	$4^{\$}$	0.33-0.43	0.43-0.52	0.50-0.60	്0.60-0.73	0.70-0.85	0.80-0.97
Mean prosome width					Q0.23	0.28	0.28
(mm)	2	0.14	0.16	0.19	്0.24	0.26	0.28
Range of greatest					♀0.20-0.23	0.25-0.31	0.25-0.31
prosome width (mm)	2	0.08-0.17	0.14-0.17	0.17-0.23	്0.23-0.25	0.23-0.33	0.25-0.31

*Gaudy (1962) gave the number of urosome somites in Co4 as three.

[§]Values are the range of mean sizes of groups of copepods sampled on different dates.

[‡]Means for July 1933 only.

Notes:

1). From Kraefft (1910) and Klein Breteler (1982).

2). From copepods sampled in the Firth of Clyde, western Scotland, in March 1974.

3). From copepods sampled in the Firth of Clyde from January to October 1933 (Marshall, 1949).

4). From copepods sampled off Plymouth from January 1947 to January 1948 (Digby, 1950).

Adult *Acartia* spp. are characterised by their slim prosomes, antennules bearing many long, flexible setae and the array of very fine, rigid setae on the furcae. The setae seem better able to survive sampling and preservation in all stages, compared to most other copepods. A prominent eyespot is usually visible, but can be bleached out by preservative. The body shape in early stages is reminiscent of the adult, but the anterior cephalosome is more rounded and the last metasome somites taper in more towards the urosome. In the earliest stages an additional pair of small but obvious rudimentary legs may be present, which are noted separately in the table (e.g. 2+1). If present, these additional legs only become developed close to their final structure after the next moult. In Co4 \bigcirc the P5 are short with fine setae and the genital somite is not swollen. In Co5 \bigcirc the genital somite is swollen, making it appear like a Co6 \bigcirc , but the genital apertures have not appeared and this somite is usually quite transparent. Additionally, the somites of the urosome are not as well defined as in the Co6 \bigcirc and the P5 are shorter, although they have long fine setae as found in the adult. In the Co5 \bigcirc the P5 are longer than in the Co5 \bigcirc , the urosome somites are not well defined and there is one more than in the Co5 \bigcirc .

Eriksson (1973), working on the west coast of Sweden, gave the female prosome length range as 0.56-1.16 mm.

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	4	5	6	6	6	6
No. of free urosome						♀3	3
somites	1	2	2	2	3	∂4	4
No. of pairs of							
swimming legs	1	2+1	3+1	4+1	5	5	5
Mean total length (mm)					♀0.88	1.23	1.45
	2	0.42	0.54	0.71	്0.84	1.14	1.38
Range of total length					♀0.79-0.96	1.17-1.29	1.27-1.62
(mm)	2	0.39-0.45	0.51-0.56	0.66-0.78	്0.81-0.87	1.01-1.32	1.27-1.47
Mean prosome length					♀0.67	0.92	1.13
(mm)*	2	0.31	0.41	0.56	്0.65	0.86	1.00
Range of prosome					♀0.60-0.72	0.84-1.01	0.96-1.27
length (mm)*	2	0.28-0.34	0.39-0.42	0.48-0.63	∂°0.63-0.66	0.78-0.96	0.90-1.08
Range of mean						♀0.71-1.09	0.86-1.37
prosome length (mm)*	3 [§]	0.35 [‡]	0.43 ‡	0.48-0.64	0.58-0.79	ð0.68-0.98	0.79-1.16
Mean prosome width					♀0.28	0.37	0.45
(mm)	2	0.15	0.17	0.23	് 0 .27	0.34	0.38
Range of greatest					Q0.25-0.33	0.33-0.42	0.36-0.53
prosome width (mm)	2	0.14-0.17	0.17	0.21-0.24	്0.27	0.30-0.39	0.34-0.39

Centropages hamatus (Lilljeborg, 1853)

*Measured to end of points on posterior metasome somite.

[§]Values are the range of mean sizes of groups of copepods sampled on different dates.

[‡]Mean for July 1933 only.

Notes:

1). From Klein Breteler (1982) and copepods sampled in the Firth of Clyde, western Scotland, in March 1974.

2). From copepods sampled in the Firth of Clyde in March 1974.

3). From copepods sampled in the Firth of Clyde from March to September 1933 (Marshall, 1949).

Centropages hamatus are easily distinguishable from most other copepod from Co4, as the last metasome somite is produced into two backwardly directed points. Prior to the development of these points, confusion could arise with early stages of *Pseudocalanus elongatus* and *Paracalanus parvus*, although in *C. hamatus* the metasome somites are less streamlined in profile when viewed dorsally, each rounded and bulging slightly. From Co4, *C. hamatus* of both sexes do not have spines on the basal segments of the A1 as found in *C. typicus*. In Co1-Co3 an additional pair of small but obvious rudimentary legs may be present, which are noted separately in the table (e.g. 2+1). If present, these additional legs only become developed close to their final structure after the next moult. Males can be distinguished from females from Co4 by the already swollen geniculate right antennule and asymmetric P5. Males do not have a spine on the swollen portion of the A1 from Co4, as found in *C. typicus*. Co1-Co3 of *C. typicus* and *C. hamatus* (illustrated by Oberg, 1906), are probably not easy to separate.

Eriksson (1973), working on the west coast of Sweden, gave the female prosome length range as 0.70-1.58 mm.

Centropages typicus Kröyer, 1849

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	4	5	6	6	6	6
No. of free urosome						Q3	3
somites	1	2	2	2	3	්4	4
No. of pairs of							
swimming legs	1	2+1	3+1	4+1	5	5	5
Mean prosome length						우0.88	1.20
(mm) *	1	0.29	0.38	0.50	0.65	്0.82	1.05

^{*}Measured to end of points on posterior metasome somite.

Notes:

1). From Lawson and Grice (1970).

Centropages typicus are easily distinguishable from most other copepods, as from Co4 the last metasome somite is produced into two backwardly directed points, more pronounced than in *C. hamatus*. Prior to the development of these points, confusion could arise with early stages of *Pseudocalanus* and *Paracalanus*, although in *Centropages* the metasome somites are less streamlined in profile when viewed dorsally, rounded and bulging slightly. From Co4, *C. typicus* of both sexes have spines on the basal segments of the A1, not found in *C. hamatus*. In the earliest stages an additional pair of small rudimentary legs may be present, which are noted separately in the table (e.g. 2+1). If present, these additional legs only become developed close to their final structure after the next moult. Males can be distinguished from females in Co4, as they have a swollen geniculate right antennule and asymmetric P5. They also have a small spine developed on segment 19 of the right antennule, not present in *C. hamatus*. This spine becomes quite robust by Co6. Co1-Co3 of *C. typicus* and *C. hamatus* (illustrated by Oberg, 1906) are probably not easy to separate.

Eriksson (1973), working on the west coast of Sweden, gave the female prosome length range as 1.10-1.64 mm.

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	4	5	6	6	6	5
No. of free urosome						₽ 3	2
somites	1	2	2	2	3	්4	5
No. of pairs of							
swimming legs	1	2	3	4	5	5	5
Mean total length						♀ 1.8	2.5
(mm)	1	0.6	0.7	0.9	1.2	∂1.7	2.4
Range of total length						♀ 1.6-1.9	2.3-2.7
(mm)	1		0.6-0.7	0.8-1.0	1.1-1.3	∂1.6-1.9	2.1-2.6
Mean prosome length						♀ 1.4	2
(mm)*	1	0.4	0.5	0.7	1.0	∂1.4	1.9
Range of prosome						♀ 1.3-1.5	1.9-2.2
length (mm)*	1		0.5-0.6	0.7-0.8	0.9-1.0	∂1.3-1.5	1.8-2.2
Mean prosome width						♀ 0.6	0.8
(mm)	1	0.2	0.3	0.3	0.4	්0.6	0.8
Range of greatest						♀ 0.5 - 0.6	0.7-0.8
prosome width (mm)	1		0.2-0.3	0.3-0.4	0.4-0.5	്0.5-0.7	0.7-0.8

Candacia armata Boeck, 1872

*Measured to end of points on posterior metasome somite.

Notes:

1). From copepods sampled off north-western Iberia in July 2005. The coarse mesh neuston net used for sampling retained too few Co1 to construct length ranges.

Candacia armata is a large predatory species and the maxilla is massively developed for grasping prey, obvious from Co1. The antenna and mandible are also very large with very long, strong setae, also obvious from Co1. The maxilliped is greatly reduced. The anterior cephalosome, between the antennules, is very square in dorsal view from Co1. From Co4 the points on the posterior of the last metasome somite are present. In Co4 they are quite small, pointing posteriorly close to the urosome, enlarging in subsequent stages. The sexes can be separated from Co4 when the P5 appears. The P5 are very rudimentary in Co4 and Co5, uniramous and symmetrical in the female, asymmetrical with the right limb bearing a simple endopod in the male. In the Co5 \bigcirc the first somite of the urosome is long and slightly swollen, while in Co5 \bigcirc it is shorter and narrower. Between Co5 and Co6 in both sexes the last two metasome somites fuse. Typical of the genus, black pigmentation may be present along the edges of the prosome somites and on the distal part of the P1-P5 from the earliest stages. Bernard (1965) gave the total length of Co1 as 0.50 mm.

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	4	5	6	6/5	5	5
No. of free urosome						Q3	3
somites	1	2	2	2	3	ి4	5
No. of pairs of							
swimming legs	1	2+1	3+1	4+1	5	5	5
Mean total length					♀0.88	1.22	1.54
(mm)	2	0.44	0.52	0.65	∂0.97	0.96	1.28
Range of total length					♀0.73-1.04	1.10-1.29	1.43-1.66
(mm)	2	0.42-0.45	0.50-0.53	0.56-0.74	∂0.84-1.07	0.87-1.04	1.13-1.46
Mean total length					♀ 0.98	1.25	1.54
(mm)	1			0.75	്0.92	1.31	1.56
Mean prosome length					♀0.61	0.81	1.04
(mm)	2	0.33	0.40	0.47	്0.64	0.66	0.83
Range of prosome					♀0.53-0.70	0.76-0.87	0.93-1.10
length (mm)	2	0.31-0.34	0.37-0.42	0.42-0.51	∂0.59-0.70	0.62-0.70	0.70-0.93
Range of mean					♀0.46-0.53	0.51-0.92	0.60-1.07
prosome length (mm)	3*	0.34 [§]	$0.40^{\$}$	0.41-0.58	്0.45-0.52	0.50-0.81	0.59-0.94
Range of mean					♀0.53-0.62	0.65-0.77	0.80-1.17
prosome length (mm)	4*	0.29-0.34	0.37-0.42	0.45-0.56	∂0.55-0.57	0.67-0.74	0.76-1.07
Mean prosome width					₽0.34	0.46	0.56
(mm)	2	0.19	0.22	0.27	്0.37	0.34	0.38
Range of greatest					Q0.28-0.42	0.42-0.51	0.48-0.59
prosome width (mm)	2	0.17-0.20	0.20-0.23	0.23-0.31	്0.31-0.45	0.31-0.37	0.31-0.42

Temora longicornis (O.F. Müller, 1785)

*Values are the range of mean sizes of groups of copepods sampled on different dates. [§]Mean for July 1933 only.

Notes:

1). From Kraefft (1910), Klein Breteler (1982) and Corkett (1967).

2). From copepods sampled in the Firth of Clyde, western Scotland, in March 1974.

3). From copepods sampled in the Firth of Clyde from April to September 1933 (Marshall, 1949).

4). From copepods sampled off Plymouth all year round in 1947 (Digby, 1950).

Co6 *Temora longicornis* have a characteristic kite-shaped prosome when viewed dorsally, deep and rounded when viewed laterally. The caudal furcae are very long, typical of the genus. From the earliest stages these characteristics are obvious, making them easy to separate from other copepodites. In Co1-Co3 an additional pair of small, rudimentary legs may be present, which are noted separately in the table (e.g. 2+1). If present, these additional legs only become developed close to their final structure after the next moult. In the Co53 the right antennule has a thickened section, already clearly geniculate, but shows some thickening from Co4.

Fusion of the last two metasome somites appears to take place either between Co3 and Co4 or more likely between Co4 and Co5, as in *Temora stylifera* (page 23). Corkett (1967) found a proportion of Co4 of both sexes with five or six prosome somites, suggesting incomplete fusion in some cases. Co4 $\stackrel{\bigcirc}{_{+}}$ usually have the same numbers of urosome somites as the Co5 $\stackrel{\bigcirc}{_{+}}$, but in the Co5 $\stackrel{\bigcirc}{_{+}}$ the first somite is longer and bulges slightly. The P5 in both Co5 $\stackrel{\bigcirc}{_{+}}$ and Co6 $\stackrel{\bigcirc}{_{+}}$ are quite similar. Males can be separated from females from Co4, as female limbs are symmetrical, gradually developing more spines between stages, while those of males are obviously asymmetrical. From the Co4, indications of the claw found on the right P5 in the Co6 $\stackrel{\wedge}{_{-}}$ is already present on the second P5 segment.

Eriksson (1973), working on the west coast of Sweden, gave the female prosome length range as 0.52-1.40 mm.

Temora stylifera (Dana, 1849)

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	4	5	6	5	5	5
No. of free urosome						Q 3	\$ 3
somites	1	2	2	2	3	്4	ే5
No. of pairs of							
swimming legs	1	2+1	3+1	4+1	5	5	5
Range of total length							♀1.4-1.9
(mm)*							∂1.4-1.5
Mean prosome length							
(mm)	2	0.35	0.40	0.52	0.67	0.85	

*From Rose (1933).

Notes:

1). From laboratory reared copepods (Carotenuto, 1999).

2). From copepods sampled in the Gulf of Marseilles (Gaudy, 1962).

From Co1-Co5 the cephalosome is broad and cloak-like, wider than the metasome, a feature less pronounced in the Co6. From Co1 the typical long furcae of this genus are also obvious and the last metasome somite extends posteriolaterally on both sides, like crude precursors of the metasome points that are fully developed in the adults (Gaudy, 1962; Carotenuto, 1999). It is unusual for copepods with metasome spines to show indications of them so early in development. In Co1-Co3 an additional pair of small, rudimentary legs may be present, which are noted separately in the table (e.g. 2+1). If present, these additional legs only become developed close to their final structure after the next moult. Co4 \bigcirc usually have the same numbers of somites as the Co5 \bigcirc , but in the Co5 \bigcirc the first urosome somite is longer and bulges slightly. Fusion of the last two metasome somites takes place between Co4 and Co5. The sexes can be separated from Co4, as described for *Temora longicornis* (page 22). Carotenuto (1999) illustrated the limbs of the Co4-Co6 stages of this species. Gaudy (1962) did not give information on the range of total length of individual stages, only mean prosome lengths of Co1-Co5.

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1					5	5
No. of free urosome							Q3
somites	1	2	2	2	3	4	ð5
No. of pairs of							
swimming legs	1	2+1	3+1	4+1	5	5	5
Mean total length					Q1.32	1.92	2.53
(mm)	2	0.58	0.66	1.00	∂1.22	1.68	1.80
Range of total length					♀1.27-1.38	1.86-2.03	2.25-2.73
(mm)	2	0.56-0.59	0.70-0.82	0.93-1.04	∂1.15-1.29	1.60-1.77	1.80
Mean prosome length					₽0.93	1.31	1.69
(mm)	2	0.42	0.50	0.73	∂0.87	1.14	1.13
Range of prosome					♀0.87-0.96	1.29-1.35	1.49-1.80
length (mm)	2	0.42	0.51-0.59	0.67-0.79	∂0.82-0.93	1.07-1.21	1.13
Mean prosome width					Q0.33	0.47	0.62
(mm)	2	0.18	0.18	0.26	്0.30	0.42	0.45
Range of greatest					♀0.31-0.34	0.45-0.51	0.51-0.67
prosome width (mm)	2	0.17-0.20	0.20-0.23	0.23-0.28	്0.28-0.34	0.39-0.45	0.45

Metridia lucens Boeck, 1865

Notes:

1). Personal communication from J.A. Adams

2). From copepods sampled in the Northern North Sea in April 1974.

During development the last two metasome somites fuse. Apart from the very earliest stages, the urosome is approximately two thirds the length of the prosome. Between Co5Q and Co6Q there is a reduction from four to three urosome somites due to fusion. From Co1 there are rudiments of hooks at the base of the first segment of the endopod of the P2, becoming more clearly defined with each moult, a characteristic of this genus. In Co1-Co3 an additional pair of small rudimentary legs may be present, which are noted separately in the table (e.g. 2+1). If present, these additional legs only become developed close to their final structure after the next moult. In Co4 and Co5 the female can be distinguished from the male by its larger size and shorter and more symmetrical P5. A Co1 of 0.67 mm total length was sampled in the Celtic Sea in April 1983.

Pleuromamma abdominalis (Lubbock, 1856)

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	3	4	4	4	4	5*
No. of free urosome							₽3*
somites	1	2	2	2	3	4	ి5
No. of pairs of							
swimming legs	1	2	3	4	5	5	5*
Range of total length							♀ 2.4-4.36*
(mm)							J2.68-4.30
Mean prosome length							
(mm)	1	0.50	0.67	0.99	1.30	1.50	

*From Bradford-Grieve (1999)

Notes:

1). From copepods sampled in the Gulf of Marseilles (Gaudy, 1962).

The last two metasome somites are fused in adults and may be fused from Co1. Between Co5-Co6 \bigcirc there is a reduction from four to three urosome somites due to fusion. The Co6 \bigcirc has two large spines on the proximal segment of the A1, one straight the other curved, while the male has only tiny spines in this region. These large spines are present from Co2 (Gaudy, 1962), so presumably are present in all subsequent stages, but lost in Co5 or Co6 \bigcirc . The brown button on the side of the prosome, typical of the genus, appears in Co4. Gaudy (1962) drew the button on the left side in the only two late stages that he drew (Co4 and Co5), but in Co6 \bigcirc the button can be on either side (Rose, 1933), while in males it is on the left.

Gaudy (1962) did not give information on the range of total length of individual stages, only mean prosome lengths of Co1-Co5.

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	3	4	4	4	4	5*
No. of free urosome							₽ 3*
somites	1	2	2	2	3	4	്5
No. of pairs of							
swimming legs	1	2	3	4	5	5	5*
Range of total length							♀1.2-2.55* ♂1.5-2.25
(mm)							∂1.5-2.25
Mean prosome length							
(mm)	1	0.44	0.53	0.65	0.77	0.96	

Pleuromamma gracilis (Claus, 1863)

*From Bradford-Grieve (1999)

Notes:

1). From copepods sampled in the Gulf of Marseilles (Gaudy, 1962).

The last two metasome somites are fused in the adults and may be fused from Co1. Between $Co5^{\circ}_{\uparrow}$ and $Co6^{\circ}_{\uparrow}$ there is a reduction from four to three urosome somites due to fusion. There are no spines on the proximal part of the A1, as found in *Pleuromamma abdominalis* (above). The brown button, typical of the genus, appears in Co4 on the right (Gaudy, 1962) and is on the right in adults (Rose, 1933).

Gaudy (1962) did not give information on the range of total length of individual stages, only mean prosome lengths of Co1-Co5.

Pareuchaeta norvegica (Boeck, 1872)

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							₽ 4/5*
somites	1	3	4	4	4	4	්4
No. of free urosome							⊊4 [§]
somites	1	2	2	2	3	4	35
No. of pairs of					₽ 4	4	4
swimming legs	1	2+1	3+1	4+1	₫5	5	5
Mean total length					\$3.9	5.6	8.1
(mm)	1	1.2	1.7	2.3	∂3.7	5.4	6.0
Mean prosome length					Q2.9	4.3	6.1
(mm)	1	0.9	1.3	1.8	ి2.8	4.2	4.4

*Some authors draw partial fusion between the female cephalosome and first pedigerous somite, others complete fusion, forming a cephalothorax.

[§]Nicholls (1934) gave five somites in the female urosome, but according to Park (1994) there are only four, so there may sometimes be incomplete fusion of the genital double-somite.

Notes:

1). From Nicholls (1934).

This is a large copepod and the various developmental stages are correspondingly large. In all stages, in dorsal and lateral view, the anterior body comes to a point. The cephalosome and first pedigerous somite are fused in adults (perhaps only partially fused in females) and are possibly fused from Co1. The last two metasome somites are also fused and this may take place between Co2 and Co3. From Co1 the antennules bear the characteristic long, widely spaced, flexible setae, typical of Family Euchaetidae, which seem to survive sampling and preservation well. A single plumose seta is present on the penultimate segment of the antennules in all stages, but is sometimes snapped off. The maxilliped in later copepodite stages is massive and reaches its greatest development in the Co6 \bigcirc , being less developed in the Co6 \bigcirc . The size of this limb is associated with their mainly carnivorous diet and is obvious from Co1. In Co1-Co3 an additional pair of small, rudimentary legs may be present, which are noted separately in the table (e.g. 2+1). If present, these additional legs only become developed close to their final structure after the next moult. There are no P5 in females, so the sexes can be separated from Co4, as the male has a large, rudimentary and asymmetric P5.

Park (1994) gave female total length range as 7.7-8.5 mm, prosome length range as 5.5-6.0 mm; male total length range as 5.3-5.9 mm, prosome length range as 3.8-4.3 mm.

Euchaeta marina (Prestandrea, 1833)

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							₽ 4/5*
somites	1	3	4	4	4	4	්4
No. of free urosome							₽ 4*
somites	1	2	2	2 [§]	3	4	്5
No. of pairs of							4*
swimming legs	1	2	3	4	5	5	5
Range of total length							♀3.4-3.64 [‡]
(mm)							♀3.4-3.64 [‡] ♂2.88-3.20
Mean prosome length							
(mm)	1	0.67	0.85	1.20	1.45	1.93	

* From Rose (1933). Original descriptions show five somites in the female prosome, but Bradford (1974) only draws four, so there may sometimes be incomplete fusion of the genital double-somite. [§]Gaudy (1962) described two somites in the urosome of Co3, but drew three in his figure? [‡]From Park (1994).

Notes:

1). From copepods sampled in the Gulf of Marseilles (Gaudy, 1962).

Features described for the closely related *Pareuchaeta norvegica* also apply to this species. The cephalosome and first pedigerous somite are fused in the adults (perhaps only partially fused in females) and are possibly fused from Co1. The last two metasome somites are also fused and this may take place between Co2 and Co3. Males have an asymmetric P5 from Co4, missing in the female, so the sexes can be easily separated.

Gaudy (1962) did not give details of prosome lengths for $Co6 \text{Pd}^{-1}$.

SUPERORDER PODOPLEA: ORDER CYCLOPOIDA

It is considered that copepods that were previously in Order Poecilostomatoida should now be merged into Order Cyclopoida (Boxshall & Halsey, 2004). All cyclopoids include here have the same number of body somites: a prosome comprising a cephalosome and four free pedigerous somites, and urosome with five free somites in the female, six in the male. However, there are other cyclopoids with fewer somites, because of fusion. The major articulation of the body occurs between the fourth and fifth pedigerous somites. The first somite of the urosome is the fifth pedigerous somite and bears the P5 (usually much reduced and similar in both sexes). This somite is not present until the Co3, the P5 appearing on it in the Co4. None of the males included here have a geniculate A1, except in *Oithona* spp., where both are geniculate.

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	4	5	5	5	5	5
No. of free urosome						₽5	₽5
somites	1	2	2	3	4	35	ð6
No. of pairs of swimming							
legs	2	2	3	4	5	5	5
Range of total length							♀0.5-0.8
(mm)	3						∂ 0.48-0.6
Mean total length (mm)		♀0.20	0.32	0.38	0.48	0.52	0.55
_	4	്0.19	0.26	0.34	0.40	0.45	0.48
Length range to posterior							♀0.31-0.34
of first "abdominal"	5	0.15	0.19-0.20	0.23-0.24	0.25-0.27	0.28-0.31	♂?
somite (mm)*							

Oithona nana Giesbrecht, 1893

Values are the range of mean sizes of groups of copepods sampled on different dates.

Notes:

1). Number of somites and swimming legs for Oithona brevicornis (Uchima, 1979).

2). From Haq (1965a, as Oithonina nana).

3). From Rose (1933).

4). From Murphy (1923).

5). From copepods sampled off Plymouth from September to December 1947 (Digby, 1950).

It was difficult to interpret number of body somites in different stages of *Oithona nana* from the key and crude illustrations in Murphy (1923), and they did not always appear to follow a logical sequence. Because of this, somite number for *O. brevicornis* from Uchima (1979), which is assumed to be the same, has been included here. Haq (1965a) only gave information for Co1 *O. nana* (as *Oithonina nana*) and the somite number and number of swimming legs were the same as in Co1 *O. brevicornis*.

Murphy (1923) was able to separately measure total body length for both males and females from Co1, as copepods were individually laboratory reared from the egg stage. Females were larger than males, but this would not be a reliable method to separate the sexes prior to them becoming adults. Digby (1950) used the same method to measure *O. nana* as Marshall (1949) used to measure *O. similis*, "from the tip of the cephalothorax to the end of the first abdominal segment". This is assumed to mean that measurements were to the end of the cephalosome in Co1 and Co2 and to the end of the first somite of the urosome from Co3, when this somite first appears.

Oithona similis Claus, 1866

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome			_	_	_	_	_
somites	1	4	5	5	5	5	5
No. of free urosome						₽5	₽5
somites	1	2	2	3	4	්5	්6
No. of pairs of swimming							
legs	1	2	3	4	5	5	5
Range of total length							♀0.73-0.96
(mm)	2						്0.59-0.70
Length range to posterior							♀0.52-0.59
of first "abdominal"	3	$0.29^{\$}$	$0.35^{\$}$	0.37-0.42	0.42-0.48	0.47-0.55	്0.49-0.56
somite (mm)*							
Length range to posterior							♀0.43-0.53
of first "abdominal"	4	0.20-0.24	0.25-	0.31-0.38	0.35-0.44	0.41-0.50	∂ ⁰ .43-0.49
somite (mm)*			0.31				

* Values are the range of mean sizes of groups of copepods sampled on different dates.

[§]Mean for July 1933 only.

Notes:

1). Number of somites and swimming legs for O. brevicornis (Uchima, 1979).

2). From Rose (1933; as Oithona helgolandica).

3). From copepods sampled in the Firth of Clyde, western Scotland, from January to October in 1933 (Marshall, 1949).

4). From copepods sampled off Plymouth all year round in 1947 (Digby, 1950).

Details of the number of swimming legs and number of prosome and urosome somites in *Oithona similis* were not available, so were assumed to be the same as in *O. brevicornis* (Uchima, 1979). Certainly the number of swimming legs in Co1 *O. similis* given by Gibbons & Ogilvie (1933; as *O. helgolandica*) was two. Both Marshall (1949) and Digby (1950) measured *O. similis* stages "from the tip of the cephalothorax to the end of the first abdominal segment". This is assumed to mean that measurements were to the end of the cephalosome in Co1 and Co2 and to the end of the first somite of the urosome, from Co3 when this somite first appears. Marshall (1949) considered that sex in *O. similis* could only be determined in the adult.

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	5	5	5	5	5	5
No. of free urosome						₽4	5
somites	1	1	2	3	4	₫5	6
No. of pairs of							
swimming legs	1	2+2	3+1	4+1	5	5	5
Total length range						♀0.50-0.59	0.49-0.76
(mm)	1	0.22	0.25-0.32	0.36-0.42	0.33-0.49	∂0.55	0.37-0.58

Oncaea waldemari Bersano & Boxshall, 1996 ["1994"]

Notes:

1) From copepods collected in the English Channel in September 1979, August to October 1980 and from laboratory reared specimens (Malt, 1982; as *Oncaea media* forma *minor* Sewell, 1947).

There is only one somite in the urosome of the Co1 (Malt, 1982), compared to two as found in most copepods. Also unusual, there are two additional pairs of small rudimentary legs, which are noted separately in the table (e.g. 2+2). These additional legs comprised single lobes with a spine and two setae on the first leg and a spine and three setae on the second. In Co2 the one additional leg is also a single lobe with a spine and possible also a seta. In Co3 the additional leg comprises a single seta on the first urosome somite, representing the P5. In Co4, the P5 is basically the same as in the Co3. In the Co5 \bigcirc , each side of the P5 is more developed, consisting of a tiny cylindrical segment bearing a distal seta and a separate seta. The P5 of the Co53 is similar, but the cylindrical segment is instead a swollen protuberance. In both adults, the structure of the P5 is similar to the Co5. The P6 only become obvious in the Co6. In the Co6 $^{\circ}$ they are a pair of small lobes, situated anterior to the midpoint on the dorsal surface of the genital somite, each armed with a tiny spine. In the Co63 the P6 consists of genital lappets protruding on the dorsal margin of the genital somite, not obvious in the Co5 $\cancel{\circ}$. The Co5 $\cancel{\circ}$ has four urosome somites, an unusual number in a cyclopoid copepods that has the typical number of five free urosome somites in the Co6^{\bigcirc}. Urosome number does not usually change between Co5 and Co6 $\stackrel{\circ}{\downarrow}$ because of fusion of the genital double somite, but this feature of four urosome somites in Co5 $\stackrel{\bigcirc}{\downarrow}$ O. waldemari has been noted in other oncaeids (Nishibe, 2005).

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							
somites	1	5*	5	5	5	5	5
No. of free urosome						₽4	5
somites	1	1*	2	3	4	ð5	6
No. of pairs of							
swimming legs	1	2+2*	3+1	4+1	5	5	5
Total length range						♀0.36-0.48	0.46-0.69
(mm)	1		0.28	0.28-0.34	0.32-0.36	Å0.34-0.40	0.38-0.44

Monothula subtilis (Giesbrecht, 1893)

*Malt (1982) did not have any Co1 copepodites, so they are assumed to be the same as *O*. *waldemari*.

Notes:

1) From copepods collected in the English Channel in September 1979, August to October 1980 and from laboratory reared specimens (Malt, 1982; as *Oncaea subtilis*).

The number of body somites, pairs of swimming legs etc. are the same as for *Oncaea waldemari*. In the $Co5^{\circ}_{\circ}$ the developing genital lappets on the dorsal margin of the genital somite are much more pronounced than in *O. waldemari*. Few Co4 were caught by Malt (1982), possibly because this is a short duration stage and therefore infrequently caught in the plankton.

SUPERORDER PODOPLEA: ORDER HARPACTICOIDA

In adults the A1 is short, double-geniculate in males. The prosome typically comprises a cephalosome fused to the first pedigerous somite forming a cephalothorax, and three further free pedigerous somites. The major articulation of the body occurs between the fourth and fifth pedigerous somites (the tenth and eleventh body somites) as in all podopleans, so the first somite of the urosome bears the fifth pair of swimming legs. The urosome is usually of five free somites in female, six in male, but some species (not included here) have only three free somites in both sexes (fifth pedigerous, genital and anal). The separation between prosome and urosome is usually not as obvious as in gymnoplean and cyclopoid species. Both sexes have six pairs of swimming legs, but the P6 is usually rudimentary in females.

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							4
somites	1	3	4	4	4	4	්4
No. of free urosome							♀ 5
somites	1	2	2	3	4	4	්6
No. of pairs of							
swimming legs	1	2+1	3+1	4+1	4+1	5	5
Mean total length							₽0.49
(mm). Spring	1	0.30	0.35	0.38	0.41	0.41	്0.43
Mean total length							♀0.57
(mm). Summer	1	0.31	0.36	0.39	0.42	0.43	്0.46

Microsetella norvegica (Boeck, 1865)

Notes:

1). From Diaz & Evans (1983) and Hirakawa (1974).

Both Diaz & Evans (1983) and Hirakawa (1974) stated that the last pair of swimming legs in Co1-Co4 were rudimentary (noted in the table as e.g. 2+1), but their illustrations show reasonably well formed limbs, not as well developed as the other limbs present, but certainly not as rudimentary as the limbs sometimes found in other Co1-Co3 copepods.

Diaz & Evans (1983) considered that males and females could not be distinguished before the adult stage. However, Björnberg (1972) describing the copepodite stages of *Microsetella rosea* considered that the sexes could be separated from Co4, using details of the P5. Number of body somites and swimming legs in *M. rosea* were the same as in *M. norvegica*, and from Co1-Co4 rudimentary legs were also noted.

Euterpina acutifrons (Dana, 1847)

	Notes	Co1	Co2	Co3	Co4	Co5	Co6
No. of free prosome							₽4
somites*	1	3	4	4	4	4	∱4
No. of free urosome							₽5
somites*	1	2	2	3	4	4	∂6
No. of pairs of							
swimming legs	1	2+1	3+1	4+1	4+1	5	5
Mean total length					Q0.49	0.55	0.67
(mm). [§]	1	0.32	0.37	0.42	്0.46/0.49	0.49/0.57	0.53/0.68
Mean prosome length					♀0.20	0.22	0.27
(mm). [§]	1	0.16	0.17	0.17	്0.18/0.20	0.19/0.22	0.19/0.24

* Somite number deduced from the text of Haq (1965b) and from adult illustrations (Sars (1921). [§]Males from stage Co4 were measured separately for a small and a large sub-set of specimens.

Notes:

1). From specimens reared in the laboratory (Haq, 1965b).

Haq (1965b) stated that the last pair of swimming legs in Co1-Co4 were rudimentary (noted in the table as e.g. 2+1) and one-segmented, becoming two-segmented following the next moult, but an illustration of a Co4 urosome showed reasonably well formed limbs. It was also considered that sex could be determined from Co4, as a tiny P6 becomes apparent only in the male.

Regression equations of total length and prosome width on prosome length for selected gymnoplean species.

The following regression equations can be used for estimating total length (TL) from prosome length (PL) and prosome width (PW) from PL.

Species	Equation			
	TL = -0.0140 + 1.2859 CL			
Calanus finmarchicus	CW = 0.0134 + 0.2860 CL			
	TL = -0.0754 + 1.4335 CL			
Pseudocalanus elongatus	CW = 0.0115 + 0.3760 CL			
	TL = -0.0221 + 1.3441 CL			
Microcalanus pusillus	CW = -0.0095 + 0.4701 CL			
	TL = -0.0920 + 1.6064 CL			
Temora longicornis	CW = 0.0305 + 0.4958 CL			
	TL = -0.0305 + 1.3227 CL			
Acartia clausi	CW = 0.0247 + 0.2944 CL			
	TL = -0.0187 + 1.3508 CL			
Centropages hamatus	CW = 0.0294 + 0.3630 CL			
	TL = -0.1251 + 1.5677 CL			
Metridia lucens	CW = -0.0061 + 0.3689 CL			

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