- regional assessment of plankton biodiversity
- regional studies of responses to climate change
- as input variables to predictive modeling for fish stock and ecosystem management
- for construction and validation of new models comparing ecosystems of different regional seas.

The CPR survey has gathered nearly 70 years of data on marine plankton throughout the North Atlantic Ocean, and has recently extended into the North Pacific Ocean. Alister Hardy's simple concept in the 1920s has succeeded in providing us with a unique and valuable long-term data set. There is increasing worldwide concern about anthropogenic effects on the marine ecosystem, including eutrophication, overfishing, pollution, and global warming. The data in the CPR time-series is being used more and more widely to investigate these problems and now plays a significant role in our understanding of global ocean and climate change.

## See also

**Climate and Plankton. Copepods. Diversity of Marine Species. Ecosystem Effects of Fishing. Eutrophication. Exotic Species, Introduction of. Fish Larvae. Florida Current, Gulf Stream and Labrador Current. Gelatinous Zooplankton. Large Marine Ecosystems. North Atlantic Oscillation (NAO). North Sea Circulation. Ocean Colour from Satellites. Pelagic Fish. Phytoplankton Blooms. Plankton. Protozoa, Planktonic Foaminifera. Protozoa, Radiolarians. Satellite Remote Sensing of Sea Surface Temperatures. Shelf-sea and Slope Fronts.**

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# CONVECTION

*See* **DEEP CONVECTION; DOUBLE-DIFFUSIVE CONVECTION; OPEN OCEAN CONVECTION**

# COPEPODS

**R. Harris**, Plymouth Marine Laboratory, Plymouth, UK

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## Introduction

Copepods are microscopic members of the phylum Crustacea, the taxonomic group that includes crabs, shrimps and lobsters and is the only large class of arthropods that is primarily aquatic. The name copepod comes from the Greek words *kope* (an oar) and *podos* (foot), the majority of members of the group having five pairs of flat paddlelike swimming legs. About 10 000 species are currently known, and their numerical dominance as members of the marine plankton means that they are probably the most numerous metazoan – multicellular – animals on earth. In addition to forming a major component of marine plankton communities, copepods are also found in sea-bottom sediments, as well as associated with many marine plants and animals. They play

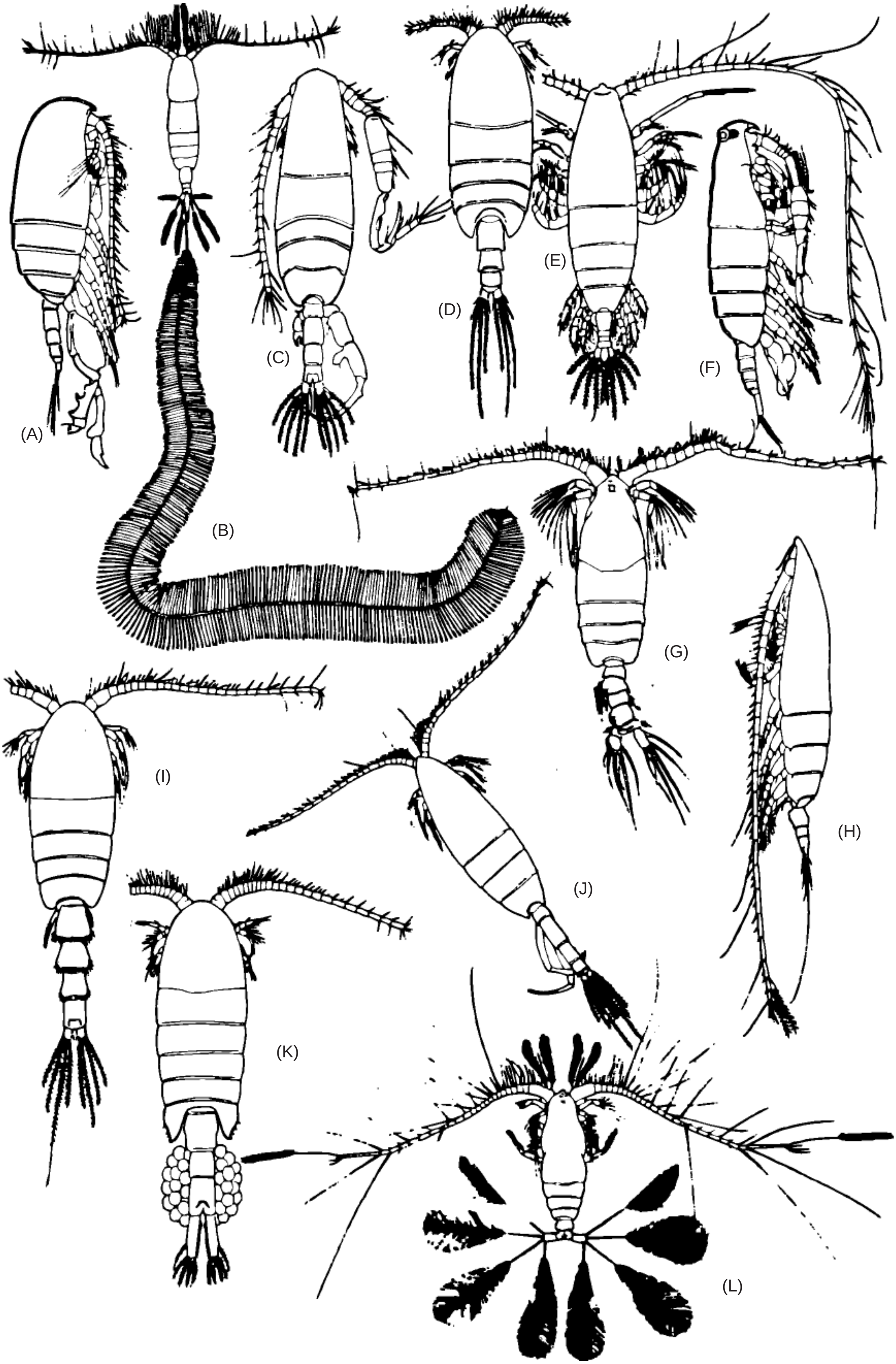

**Figure 1** The diversity of calanoid body form. (A) Diaixidae; (B) Calocalanidae; (C) Acartiidae; (D) Pseudocyclopidae; (E) Augaptilidae; (F) Pontellidae; (G) Metridinidae; (H) Eucalanidae; (I) Stephidae; (J) Euchaetidae; (K) Temoridae; (L) Calocalanidae. (Permission from Huys and Boxshall, 1991.)

a pivotal role in marine ecosystems by controlling phytoplankton production through grazing, and by providing a major food source for larval and juvenile fish. This article will place particular emphasis on the dominant group of planktonic copepods, known as the Calanoida (**Figure 1**), playing a central role in these processes in the world's oceans.

## Taxonomy

There are 10 taxonomic orders of copepods, of which 9 have marine representatives. Of these the most important marine orders are the Calanoida, Cyclopoida, and Harpacticoida. Calanoid copepods are primarily pelagic, 75% of the known species are marine, and some are benthopelagic or commensal. The group includes the species *Calanus finmarchicus* (Gunnerus), a dominant component of North Atlantic boreal ecosystems, first named nearly 250 years ago as *Monoculus finmarchicus* by Johan Ernst Gunnerus, Bishop of Trondheim in Norway (**Figure 2**). The Cyclopoida include pelagic commensal and parasitic species (**Figure 3**). Harpacticoid copepods are predominantly marine, with only 10% of species being freshwater. Most are benthic, with a few pelagic and commensal representatives, they represent the most abundant component of the meiofauna after nematode worms. The Platycopoida and Misophrioida are primarily benthopelagic groups, the latter having two pelagic species. The Poecilostomatoida and Siphonostomatoida are commensal or parasitic groups. Finally, the Monstrilloida are exclusively marine, with parasitic juveniles, but a pelagic adult stage.

## Morphology

Most copepods are small, requiring study with a microscope. Small planktonic cyclopoids may be only 0.2 mm long and similarly harpacticoid copepods found in the interstitial space of sandy sediments are among the smallest Metazoa. In contrast, some large deep-sea calanoids, such as *Valdiviella*, may exceed 20 mm in length. *Calanus finmarchicus* is often said to be about the size of a grain of rice (**Figure 2**). Parasitic forms are generally larger than the free living copepods. For example, species of the genus *Penella*, which is parasitic on fish and whales, may be over 30 cm in length.

The body of a free-living copepod (**Figure 4**) is normally cylindrical, and is distinctly segmented. The head, which is the site of the median naupliar eye, is either rounded or may bear a pointed rostrum. The presence of at least two pairs of swimming legs is characteristic of nearly all copepods at some stage in their life cycle. Similarly, antennules with up to 27 (**Figure 5**) segments are general in the order, though segmentation may often be reduced. The body is divided into the prosome, which may be further subdivided into the cephalosome and metasome, and the urosome. The feeding appendages are on the cephalosome; in the calanoids these comprise, from anterior to posterior, the antennule, antenna, mandible, maxillulle, maxilla, and maxilliped (**Figure 6**). The swimming legs are attached to the metasome in adult calanoids, one pair for each of the five segments of the metasome. The urosome contains the genital and anal segments, and ends with the furca or caudal rami, a series of spines or fine hairs. Most copepods are pale and transparent, though some species, particularly those living at the sea surface or in the deep sea, may be pigmented blue, red, orange, or black.

The early developmental stages in the life history are the nauplii (**Figure 7**), with reduced numbers of appendages. In calanoids there are six naupliar stages, NI to NVI. Copepods, like all other Crustacea, molt by shedding their exoskeleton as they grow. Hence there is a molt between each naupliar stage. Molting from NVI involves a radical change in morphology (metamorphosis) to the first copepodite stage. The copepodites, of which there are normally six stages (CI–CVI) are like small adults, and gradually develop adult characteristics during successive molts. The adult stage is CVI, and no further molts occur.

## Distribution and Habitats

As has already been noted, copepods are probably the most numerous multicellular organisms on earth. They are found throughout the marine and estuarine environments of the world's oceans. Species inhabiting coastal and brackish waters have wider tolerances of environmental variables than, for example, deep sea copepods, which are specifically adapted to the special conditions of this environment. Generally, copepods are more abundant in coastal and productive upwelling environments than in the oligotrophic open ocean. Over the deep ocean, where the water column may extend to 8000 m, the abundance of copepods is highest in the surface layers, and then decreases almost exponentially. The number of species occurring in a particular environment varies. In some, for example brackish tide-pools, a single species may dominate. In contrast, assemblages in the open ocean normally exceed 100 species (**Figure 8**).

In addition to those that dominate the plankton, copepods also live in marine sediments, forming

**Figure 2** Gunnerus' sketches of *Calanus*. The smallest shows the natural size. (Permission from Marshall and Orr, 1955.)

a major component of the meiofauna. They are found in all sediments from muds to coarse sands, and from the intertidal zone to the deep ocean. Harpactocoids are the dominant copepod component of the meiofauna. This group is also abundant on intertidal and subtidal macroalgae.

Apart from free-living planktonic and benthic forms, almost half of the described species live in association with other marine animals. Copepods parasitize almost every phylum of marine animals, many as ectoparasites living on the external body surface, though others have exploited, for example, the internal surfaces of the gills of fish. In the majority of cases it is the adult copepods that are parasites, but the Monstrilloida are an exception, as the naupliar stages are internal parasites of polychaete worms and gastropod mollusks. The adults live in the plankton, but do not feed.

Specialized habitats include marine caves that are home to a number of platycopoid and calanoid species, all living in association with the bottom sediments. Other such hyperbenthic copepods, living close to the sediment surface, are also found throughout shallow and deep seas. Deep-sea hydrothermal vents also have an associated copepod fauna, which is only now being described.

Other interfaces in the marine environment that provide specialized habitats for copepods are the under ice environment in Polar regions, and the sea surface. The under-ice habitat supports a rich growth of microalgae, and in turn this food source is exploited by a large number of copepods. The sea surface habitat is that of the neuston, the group of animals and plants living in the extreme surface film. The calanoids of the family Pontellidae, such as members of the genera *Pontella* and *Anomalocera* are the commonest neustonic copepods. Many have strong blue pigmentation, which may be associated with protection against surface ultraviolet radiation, and also attachment structures on the back of the head by which the copepod suspends attached to the surface film. A few species can move with such vigor that they can hurl themselves out of the water, and a shoal of these creatures can appear like a rain shower on the surface of the sea.

## Feeding

The majority of planktonic copepods were originally thought to be exclusively herbivorous, filtering phytoplankton from sea water with the fine hairs of the mouth parts. In contrast, carnivorous copepods have more robust spines on the mouthparts. More recently it has been appreciated that many copepods are omnivores, feeding on a wide range of naturally occurring particulate material, phytoplankton, small planktonic animals of the microzooplankton, and detritus.

The feeding appendages are the antennules, antennae, mandibles, maxillules and maxillae (**Figure 5**). These are often considerably reduced in adult males, which may not feed. The mouth parts of ectoparasites are adapted for piercing or sucking. Internal parasites have often lost their mouth parts, and food is absorbed directly from the host. Among planktonic calanoids there are three general mouth part patterns, related to feeding ecology: the true filter-feeders, the omnivores, and the true carnivores. The antennules are particularly involved in carnivorous feeding, having sensory organs that function in prey detection.

Spacing between the hairs (the setae) of the maxillae has been considered to indicate the size of particles that can be filtered by a copepod (**Figure 9**). However, the model of copepod filter-feeding as a mechanical process depending on the morphological characteristics of the maxillae is no longer accepted. Direct studies of feeding behavior using high-speed microcinematography and video observations have shown that feeding behavior is complex, taking account of the viscous, low-Reynolds-number, environment that these small organisms inhabit. Feeding behavior, and adaptations of the appendages, enable copepods to exploit particles such as

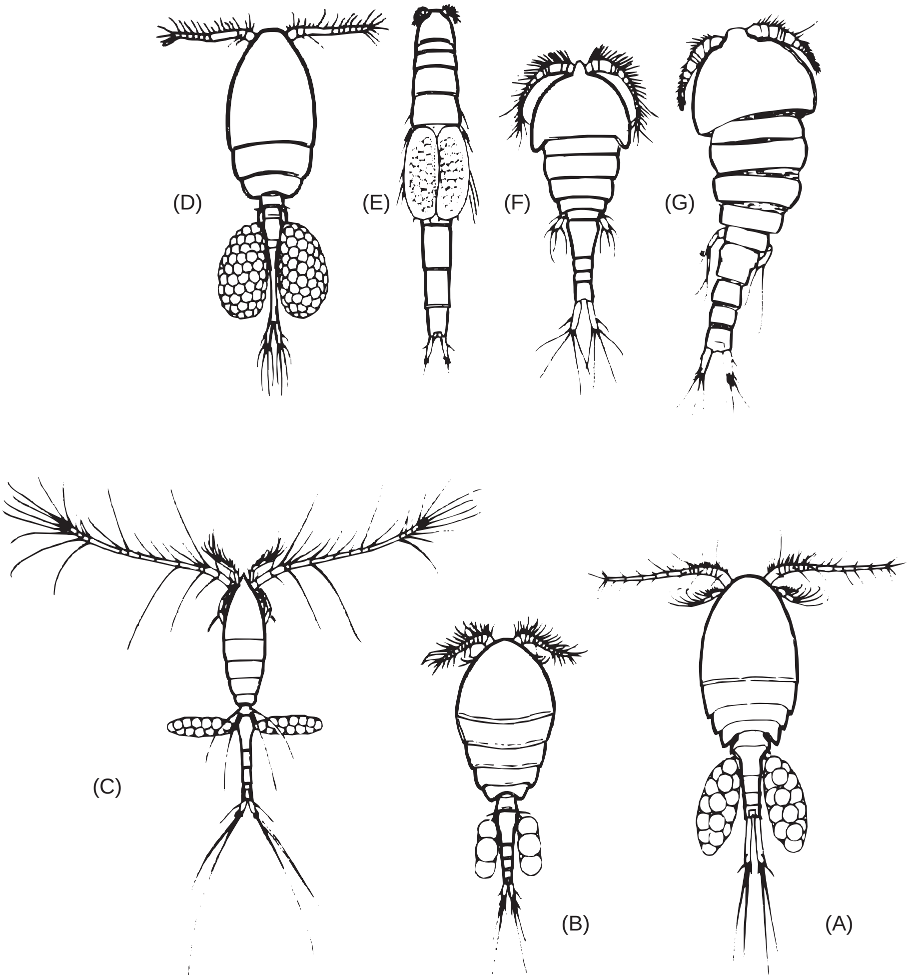

**Figure 3** The diversity of cyclopoid body form. (A) Cyclopidae; (B) Cyclopinidae; (C) Oithonidae; (D) Thespessiopsyllidae; (E) Asidicolidae; (F) Archinotodelphyidae; (G) Mantridae. (Permission from Huys and Boxshall, 1991.)

detritus and phytoplankton, a few micrometers in size, while at the other extreme they can feed on other members of the zooplankton such as other copepods, chaetognaths, and fish larvae. Particles may be rejected during the feeding process, resulting in food selectivity.

The feeding rate of planktonic copepods is dependent on type and size of food particle (**Figure 10**), as well as environmental factors such as temperature, light, and turbulence. The latter, in particular, can affect the rate of encounter between predator and prey.

## Growth and Development

Copepods grow by molting, as do all other Crustacea. Normally the nauplius stage NI hatches from the egg; naupliar growth involves five molts to the sixth nauplius (NVI), and then after metamorphosis to copepodite stage one (CI) there are a further five molts until the adult, CVI stage, is reached. In a few groups the egg hatches directly into one of the later naupliar stages, for example NII.

The development rate of copepod eggs is dependent on temperature within any one species. The relationship between development time $D$ (days) and temperature $T$ (°C) is generally described by the empirical equation [1], in which $\alpha$ and $b$ are fitted constants.

$$D = a(T - \alpha)^b \qquad [1]$$

Egg development times of egg sac-carrying groups are longer than those of free spawners.

A number of models of development have been applied to the naupliar and copepodite stages of copepods. Equiproportional development considers that the duration of each developmental stage is proportional to the egg development time, determined by the equation above, at the same temper-

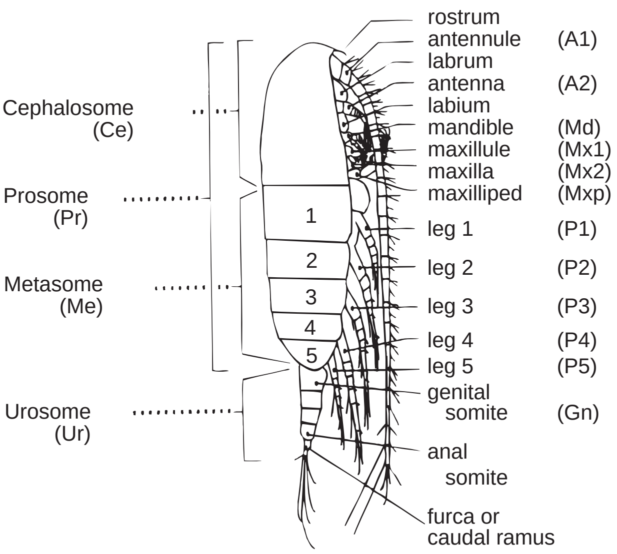

**Figure 4** Diagrammatic illustration of the external morphology and appendages of a female calanoid copepod. The metasome has five clearly defined segments, numbered 1–5; this species has five pairs of swimming legs and so these five metasome segments are synonymous with pedigerous segments 1–5. Legs 1–5 are the swimming legs. (Permission from Mauchline, 1998.)

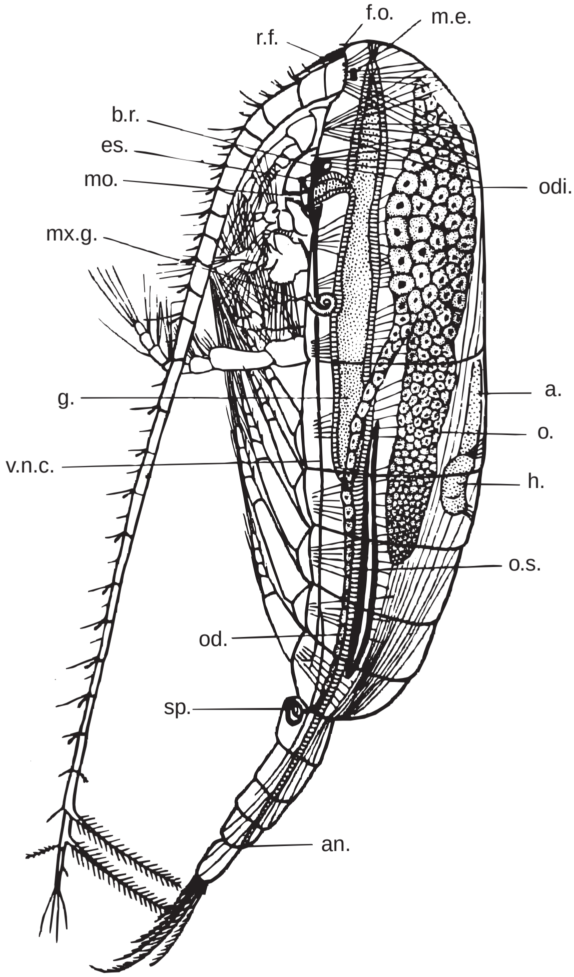

**Figure 5** Diagram of the internal anatomy of a female *Calanus* from the side. a., aorta; an., anus; br., brain; f.o., frontal organ; g., gut; h., heart; m.e., median eye; mo., mouth; mx.g., maxillary gland; o., ovary; o.di., oviducal diverticula; od., oviduct; es., esophagous; o.s., oil sac; r.f., rostral filament; sp., spermathecal sac; v.n.c. ventral nerve cord. (Permission from Marshall and Orr, 1955.)

ature. The isochronal model of development describes those species for which all stages have almost the same duration, and development proceeds linearly with time. In sigmoidal development, the development rate of the early naupliar stages is significantly slower, and the later copepodite stages also have a longer relative development duration.

Growth rates of copepods are temperature-dependent, and are most usefully expressed as the weight-specific growth rate (per day, $d^{-1}$), which is the increase in body weight per day as a proportion of the body weight of the developmental stage being considered (**Figure 11**). An adequate food supply, both quantitative and qualitative, is clearly necessary for proper development and growth. Ultimate body size, either as length or weight, is dependent on both temperature and food conditions. It has been suggested that for small planktonic copepods growth is optimized, and food is utilized more efficiently, at higher temperatures, whereas larger forms optimize growth and food utilization at lower temperature. This may explain some aspects of the geographical and vertical distribution patterns of copepods.

## Metabolism

Copepods have a variety of digestive enzymes in the gut, and there are both diel and seasonal changes in enzyme activity. In particular, overwintering animals in diapause may have considerably reduced digestive enzyme activity. The proportion of the ingested food that is assimilated, and therefore available for subsequent metabolism, ranges from 60% to 90% in herbivores, the remaining 10% to 40% being released as fecal pellets. The soluble excretory products of metabolism are generally excreted as ammonia or urea and dissolved phosphorus compounds, and this process is important in nutrient regeneration cycles supporting phytoplankton growth in marine ecosystems. There are no gills in free-living copepods, and respiratory exchange is supported by direct uptake of dissolved oxygen from sea water. Apart from in the calanoids

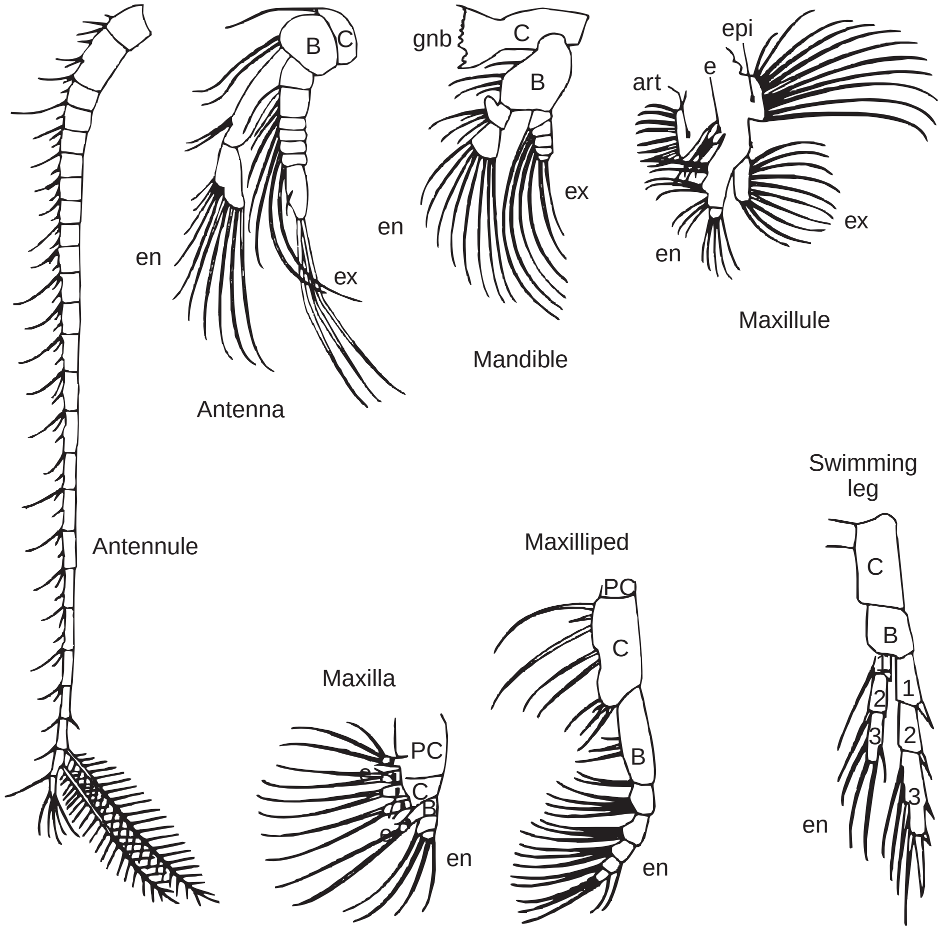

**Figure 6** Diagrammatic representations of the appendages of a calanoid copepod. The swimming legs usually have developed endopods and exopods with up to three segments, numbered 1–3 here. art, arthrite; B, basis; C, coxa; e, endite; en, endopod; epi, epipodite; ex, exopod; gnb, gnathobase; PC, praecoxa. (Permission from Mauchline, 1998.)

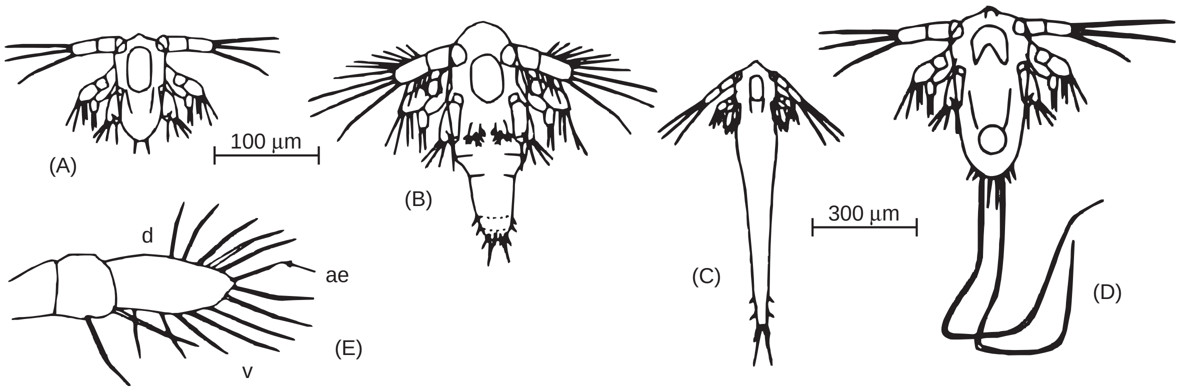

**Figure 7** Nauplii of calanoid copepods. (A) *Clausocalanus furcatus*, stage I (NI); (B) *Paracalanus aculeatus*, NV; (C) *Rhincalanus cornutus*, NIV; (D) *Euchaeta marina*, NVI; (E) antennule showing dorsal (d) and ventral (v) setae and terminal aesthetasc (ae). (Permission from Mauchline, 1998.)

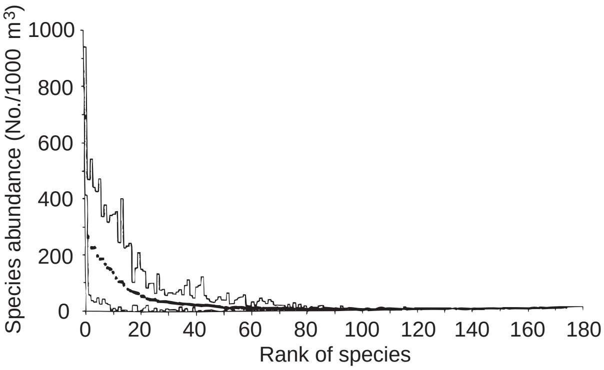

**Figure 8** Abundances of copepod species in the open Pacific Ocean showing the species order. Data points are the overall means. Gray bars show the range of seven individual cruise mean abundances per species. (Permission from McGowan JA and Walker PW (1985) Dominance and diversity maintenance in an oceanic ecosystem. *Ecological Monographs* 55: 113–118.)

**Figure 9** Left maxilla of *Calanus helgolandicus* female from the right. A, B and C represent the sizes of three algal cells: (A) *Nannochloris oculata*; (B) *Syracosphaera elongata*; (C) *Chaetoceros decipiens*. (Permission from Marshall SM and Orr AP (1956) On the biology of *Calanus finmarchicus* IX. Feeding and digestion in the young stages. *Journal of the Marine Biological Association of the United Kingdom* 35: 587–603.)

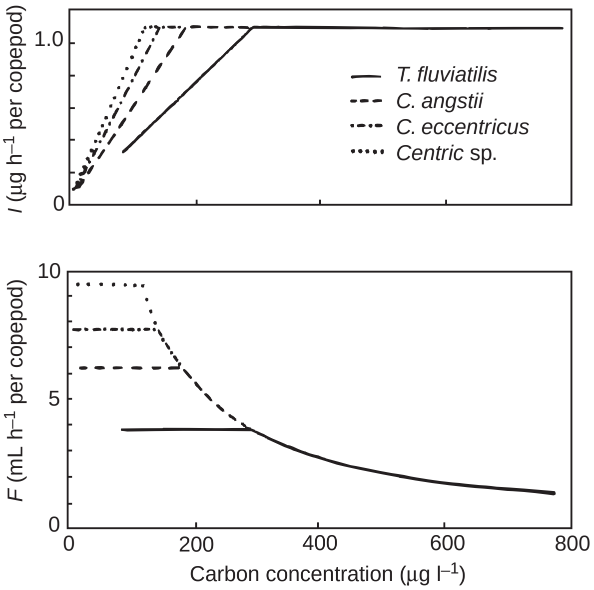

**Figure 10** The effect of size (species) and concentration (as carbon) of food particles on ingestion rate, *I*, and volume swept clear, *F*, of adult females of *Calanus*. (Permission from Frost BW (1972) Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus. Limnology and Oceanography* 17: 805–815.)

and some parasitic species there is no heart or circulatory system. Both respiration and excretion are closely coupled to feeding activity and often exhibit diel cycles.

## Reproduction

Mating behavior follows a generally similar sequence in all copepods. Initially the male is attracted to the female, often by chemical attractants, pheromones (**Figure 12**), Then the male captures the female, adjusts to the mating position, and finally transfers and attaches a package of sperm, the spermatophore, to the female. Most species of planktonic calanoids lay their eggs directly into the water. However, harpacticoids and cyclopoids usually carry the eggs in a single or paired egg sacs and a number of calanoid genera, for example *Euchaeta*, *Eurytemora*, and *Pseudocalanus* also carry egg sacs. Individual eggs are usually spherical, ranging in size from 0.2 to over 0.6 mm, the eggs within egg sacs often being relatively larger than those that are freely spawned. Females of some freely spawning species, when well fed, produce over 100 eggs in a day. The daily rates of egg production expressed as a proportion of the female body weight are around 0.17 for copepods carrying their eggs, and 0.2 for free spawners. The lifetime fecundity of egg sac-bearers is lower than that of the free spawners; the latter have been observed in laboratory studies to produce over 2000 eggs in a female's lifetime.

A number of groups, including calanoids of the families Acartiidae, Centropagidae, Temoridae, and Pontellidae, produce resting eggs, often distinguishable from the normal eggs by having a thicker outer coating. These diapause eggs sink to the seabed and may become buried in bottom sediments until

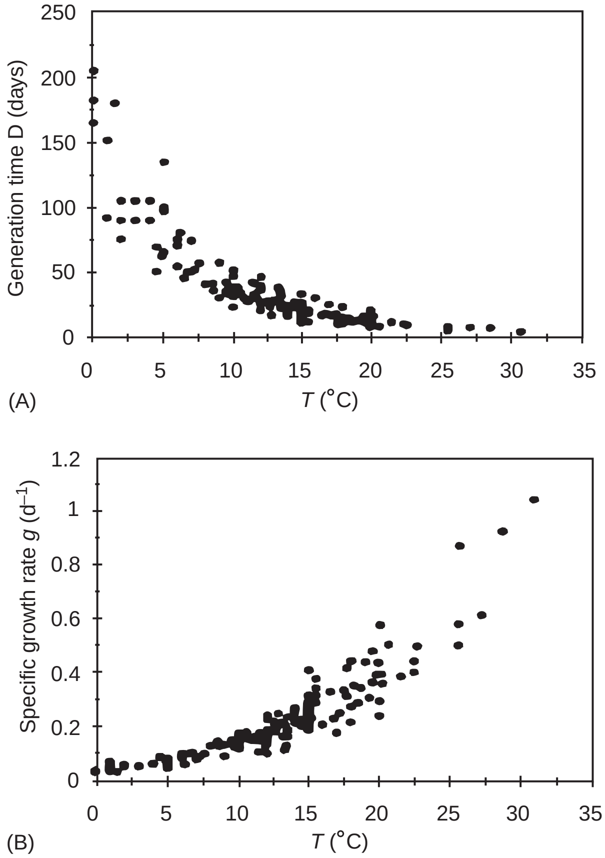

**Figure 11** (A) The generation *D* time (days) of different species of copepods related to environmental temperature *T* (°C). The relationship is described by the equation $D = 128.8\,e^{-0.120T}$ (B) The specific growth rate *g* ($d^{-1}$) of species of copepods calculated from the weight of egg and the adult and the generation time of each species and related to environmental temperature *T* (°C). The equation for the relationship is $g = 0.0445\,e^{0.111T}$. (Permission from Huntley ME and Lopez MDG (1992) Temperature-dependent production of marine copepods: a global synthesis. *American Naturalist* 140: 201–242.

conditions are appropriate for hatching. It has been estimated that diapause eggs may remain viable in sediment, capable of hatching, for up to 40 years.

## Behavior

Perhaps the most striking aspect of the behavior of planktonic copepods is that of diel vertical migration. This behavior, characteristic of most planktonic organisms, involves the population remaining at depth during the daytime. As night falls, the copepods actively migrate upward to spend some hours in the surface during the hours of darkness, before descending at dawn to the original daytime depth (**Figure 13**). Although this is a general phenomenon, there are many variations, depending both on species, and the influence of environmental factors.

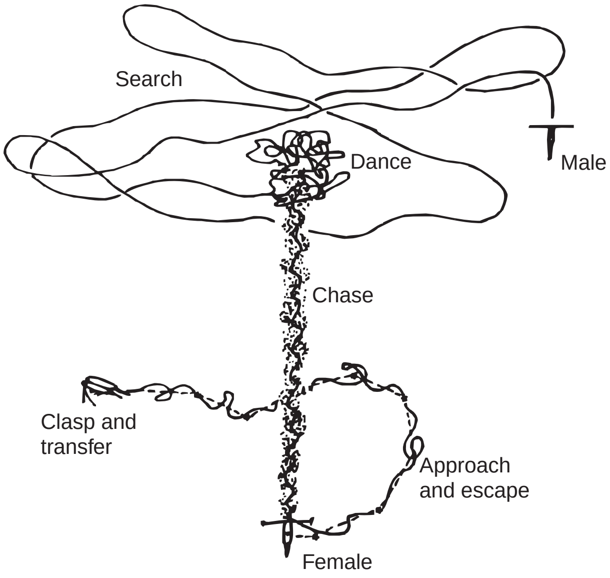

**Figure 12** *Calanus marshallae.* A conceptual interpretation of mate-attraction–mate-search behavior. The sequence of events is (1) a female generates a vertical pheromone trail; (2) a male is alerted by pheromone to females in the general vicinity and swims in smooth loops of mostly horizontal orientation; (3) on crossing a pheromone trail, the male performs a dance (or sometimes does not); (4) the male chases down the pheromone trail to the female; (5) the female jumps away repeatedly with the male pursuing, sometimes bumping her; and (6) a mating clasp is established and a spermatophore is transferred from the male to the female. (Permission from Tsuda A and Miller CB (1998) Mate-finding behaviour in *Calanus marshallae. Philosophical Transactions of the Royal Society of London*, series B 353: 713–720.

Light is the dominant environmental factor controlling diel vertical migration, with populations following diel changes in light intensity, isolumes (layers of constant light intensity). Predator avoidance related to light is thought to be one of the major adaptive advantages of diel vertical migration. By migrating to deeper darker layers by day, copepods minimize mortality from visual predators, in particular fish. Predator avoidance has to be balanced against the need to feed and, as the phytoplankton is concentrated in the surface layers, migration to the surface by night is generally associated with active feeding, diel cycles of digestive enzyme activity, and diel feeding rhythms. Where invertebrate predators detecting prey nonvisually are dominant, the phasing of migration may be reversed.

Vertical migratory behavior involves active swimming. Most copepods swim by rapid beating of the appendages, the antennae, mandibular palps, the maxillules, and the maxillae. In some species of planktonic calanoids, such as the genera *Metridia, Centropages*, and *Temora*, these movements result

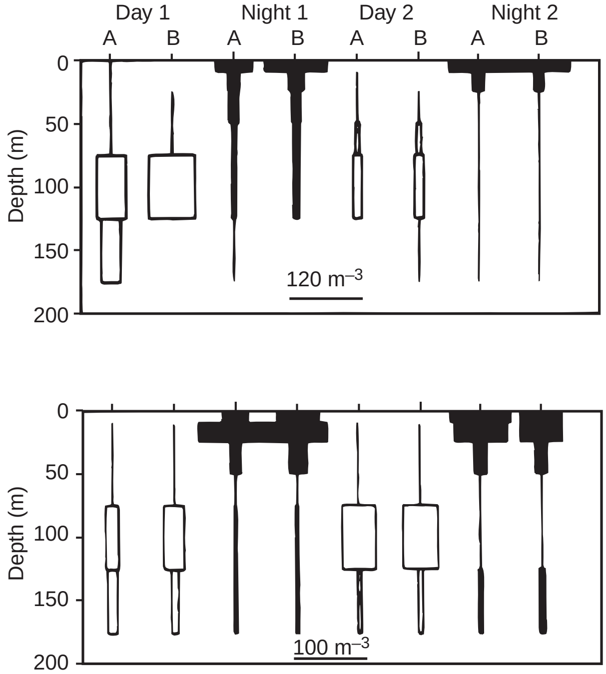

**Figure 13** Vertical distribution of adult females of *Calanus pacificus* (A) and *Metridia lucens* (B), 5 and 6 August 1986. (Permission from Dagg MJ, Frost BW and Walser WE Jr (1989) Copepod diel migration, feeding, and the vertical flux of pheopigments. *Limnology and Oceanography* 34: 1062–1071.)

in a smooth continuous swimming behavior. In others, periods of active swimming are interspersed with inactivity when the animal sinks. This hop-and-sink behavior is characteristic of *Calanus finmarchicus*. Rapid jumping, often as a predator-avoidance behavior, involves strong strokes of the antennules and the swimming legs. This results in very rapid jumps, which propel the copepod several body lengths from the source of stimulus. The benthic harpacticoids and some cyclopoids crawl over or burrow through sediment. The thoracic limbs are used in crawling, and this is accompanied in harpacticoids, by sideways undulations of the body.

Nauplii use three pairs of appendages in swimming: the antenules, the antennae, and the mandibles. Three swimming behaviors have been recognized; a slow gliding motion propelled by the antennae and mandibles; a rapid darting behavior driven by all three pairs of appendages beating together; a cruise and pause behavior.

Swimming and feeding behaviors are interdependent in herbivores, omnivores, and carnivores. Swimming speeds of planktonic calanoids generally range from 1 to 20 mm s$^{-1}$ which is equivalent to 1–5 body lengths per second. Estimates based on field studies of oceanic diel vertical migrators, such as *Pleuromamma*, range from 10 to 50 mm s$^{-1}$, representing the ability of such copepods to migrate at rates in excess of 100 m h$^{-1}$.

The predominant sensory mechanisms are mechanoreception and chemoreception, and receptor structures are found on the antennules. The antennules, particularly of males, are covered with sensory structures, aesthetascs, which are important in detecting water movement, food, predators, and potential mates. Detection of mechanical stimuli appears only to operate over short distances, often less than one body length. Chemoreception probably operates over longer distances and is involved in mate detection and response to food concentrations and to predators.

Many planktonic copepods are bioluminescent. The families Megacalanidae, Lucicutiidae, Heterohabdidae, Augaptilidae, and Metridinidae have luminescent glands that produce luminous glandular secretions. The number of light organs varies from 10 to 70, and they may be distributed widely over the body surface. The function of copepod bioluminescence is not certain. It may deter predators in the dark water column of the deep sea, and may act as a warning signal between individuals of the same species.

## Life Histories

Copepods inhabit a wide range of environments, from the tropics to the Polar regions, and from the intertidal zone to the deep ocean, and their life histories accordingly vary considerably. In the tropics and subtropics there is no seasonality in breeding, most species breeding continuously. An exception to this pattern occurs in the upwelling system off the Gulf of Guinea, and in the Benguela Current off south-west Africa, where the dominant calanoid, *Calanoides carinatus* enters a diapause resting stage, at copepodite stage CV, at the end of the cold season and sinks to colder water until the next season. At high latitudes, diapause and overwintering strategies are the dominant responses to the highly seasonal environment (**Figure 14**). Breeding periods are restricted, often only one generation is produced each year, and growth and development rates are slowed. The most common diapause stage is copepodite CV. Animals in this state overwinter in deep water with delayed development and reduced respiration and excretion rates, usually do not feed, and often show reduced digestive enzyme activity and changes in the digestive epithelium of the gut. Metabolism is sustained by the extensive lipid

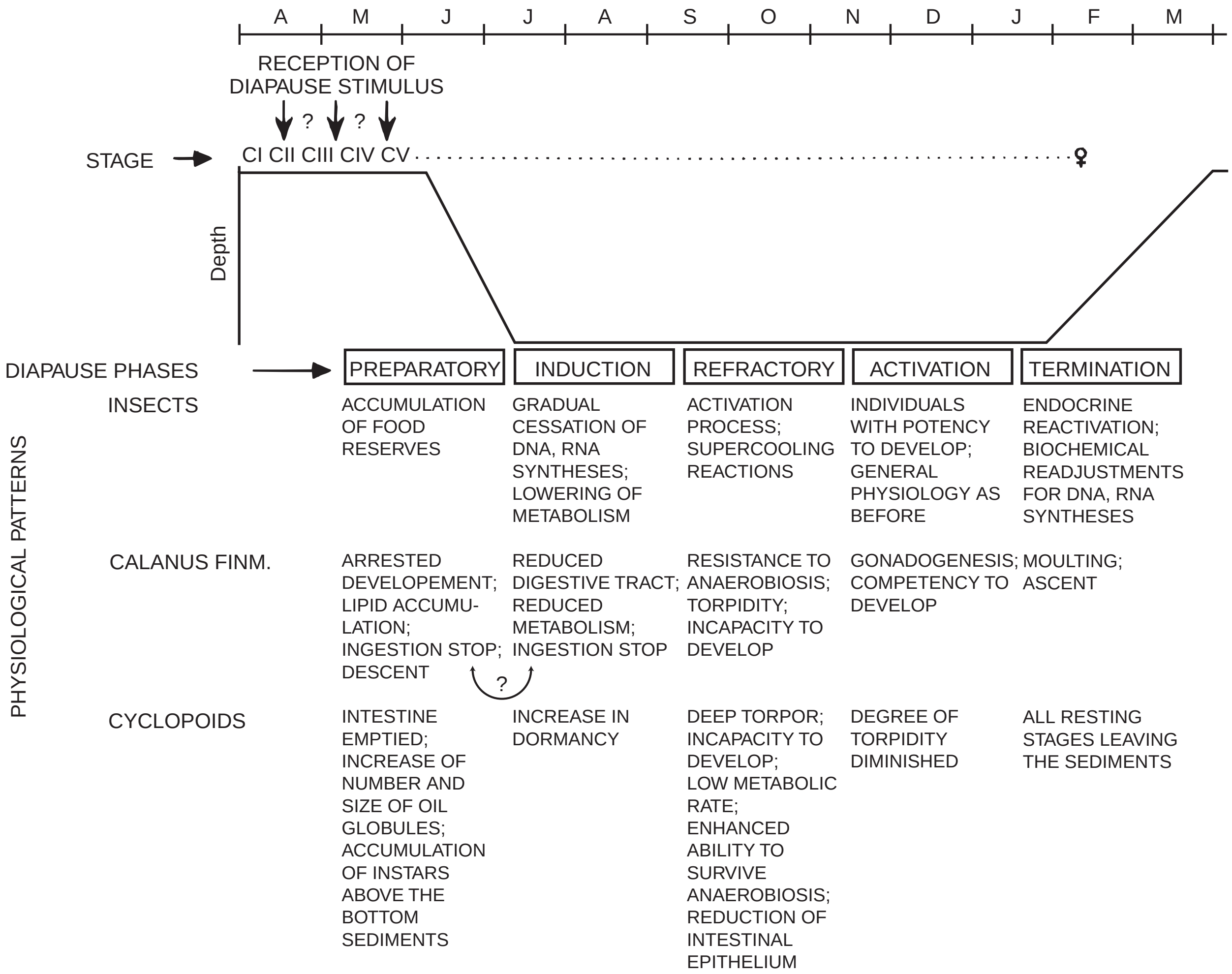

**Figure 14** Generalized pattern of seasonal ontogenetic migration and physiological changes during overwintering of *Calanus finmarchicus* in relation to diapause phases in insects and comparison with insect and cyclopoid diapause. (Permission from Hirche H-J (1996) Diapause in the marine copepod, *Calanus finmarchicus* – a review. *Ophelia* 44: 129–143.)

reserves, which in high-latitude copepods may exceed 75% of the total body weight, and these reserves give the body a brilliant red coloration in some species. Lipid stores can fuel egg laying in the spring before the spring phytoplankton bloom in species such as *Calanus glacialis* and *Calanus hyperboreus*, ensuring that the resultant nauplii are able to exploit the spring pulse of phytoplankton production.

In the bathypelagic environment of the deep sea below 500 m, copepods do not undertake diel vertical migration, and there is reduced seasonality with depth. The life histories of deep sea copepods are relatively little known, but the majority probably breed continuously throughout the year, with slow development rates and long generation times, reflecting the low-temperature environment.

## Copepods as Pests

Some copepods are economically important pests. An example is the salmon louse *Lepeophtheirus salmonis* (Krøyer), which may have significant impact on the economics of salmon aquaculture. The copepods breed rapidly in the high fish densities of the salmon cages and may kill the fish either directly or by causing skin damage that in turn makes the fish susceptible to disease. Gill-parasitic copepods such as *Lernaeocera* may have significant effects on commercial fish species, and the shellfish parasites such as *Myticola intestinalis* may also have economic effects.

## Biogeochemical Role

The production of fecal pellets by copepods is an important source of sedimented material for benthic organisms and plays a significant role in nutrient cycling and in vertical flux of biogenic elements to the deep ocean. Fecal pellet production rates of actively feeding copepods may exceed ten pellets per hour. Such rates, combined with the abundance of copepods in some ecosystems, mean that a significant component of the small particulate food captured is transformed into much larger packages represented by the fecal pellets. These may have sinking rates greater than $100\,\mathrm{m\,d^{-1}}$, the rate being dependent both on size and composition, derived from the diet, of the pellets. Many of these rapidly sinking pellets may exit the surface layers of the ocean, and either reach the seafloor of the continental shelves or enter the bathypelagic zone. This pellet flux is so great that sinking pellets may form a significant part of the diet of other members of the plankton, including copepods, and of benthic organisms.

## Role in the Ecosystem

Planktonic copepods, through their grazing activity, are one of the major controls on the growth of phytoplankton, and quantitative understanding of grazing processes is central to modeling marine ecosystem dynamics. Similarly, copepods play a pivotal role in nutrient cycles, by excreting dissolved nitrogen and phosphorus compounds, which are then utilized by phytoplankton to support growth, and hence primary production.

Pelagic cyclopoid and calanoid copepods form the first link in the marine food chain that leads from the single-celled plants of the phytoplankton to the fishes and marine mammals that form the exploitable living resources of the world's oceans. Nauplii through to adult stages of copepods are the typical food of nearly all larvae of commercially exploited marine fish. Some adult fish, such as herring, continue to feed on them. Similarly, the harpacticoid copepods of the meiofauna are a food source for bottom-feeding flatfish.

Copepods have been subjected to limited commercial exploitation. Although they are extremely abundant, their small size makes direct harvesting impractical. Limited fisheries for *Calanus* species, in areas of high coastal abundance, have provided dietary supplements for salmon aquaculture and for pet food.

## See also

**Biogeochemical Data Assimilation. Carbon Cycle. Continuous Plankton Recorders. Fish Feeding and Foraging. Fish Larvae. Fish Migration, Vertical. Gelatinous Zooplankton. Lagrangian Biological Models. Large Marine Ecosystems. Meiobenthos. Nitrogen Cycle. Ocean Gyre Ecosystems. Optical Particle Characterization. Particle Aggregation Dynamics. Plankton. Plankton and Climate. Polar Ecosystems. Population Dynamics Models. Temporal Variability of Particle Flux. Trapped Particulate Flux. Upwelling Ecosystems. Zooplankton Sampling with Nets and Trawls.**

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