

The Importance of Small Planktonic Copepods and Their Roles in Pelagic Marine Food Webs

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Jefferson T. Turner (2004) The importance of small planktonic copepods and their roles in pelagic marine food webs. *Zoological Studies* 43(2): 255-266. Small planktonic marine copepods (< 1 mm in length) are the most abundant metazoans on Earth. Included are adults and copepodites of calanoid genera such as *Paracalanus*, *Clausocalanus*, and *Acartia*; cyclopoid genera such as *Oithona*, *Oncaea*, and *Corycaeus*; planktonic harpacticoids of the genus *Microsetella*; and nauplii of almost all copepod species. Despite the abundance of small copepods, they have historically been undersampled due to the use of nets with meshes > 200-333 μm . Recent studies have shown, however, that when appropriate net meshes of 100 μm or less are used, small copepods vastly exceed the abundance and sometimes the biomass of larger ones. Failure to adequately account for small copepods may cause serious underestimations of zooplankton abundance and biomass, the copepod grazing impact on phytoplankton primary production, zooplankton-mediated fluxes of chemicals and materials, and trophic interactions in the sea. The feeding ecology of small copepods is less well-known than that of adults of larger copepod species, such as members of the genus *Calanus*. Further, most feeding information for small copepods is for coastal genera such as *Acartia*, rather than for offshore taxa. Although it is generally assumed that small copepods, including nauplii, feed primarily upon small-sized phytoplankton cells, most such information comes from rearing or feeding studies on limited laboratory diets. There have been few examinations of actual copepod feeding on mixed diets of natural phytoplankton and microzooplankton found in the sea, but some of those have produced surprises. For instance, some species of *Oithona* and *Paracalanus* and even nauplii of Arctic *Calanus* spp. may feed primarily as predators upon heterotrophic protists, rather than as grazers of phytoplankton. Also, nauplii of various tropical copepod species have been shown to feed upon bacterioplankton. Thus, numerous basic questions remain as to the feeding ecology and grazing/predation impact of small copepods in the sea. Despite limited knowledge of what small copepods eat, it is clear that many higher-trophic-level consumers eat them. Numerous studies have shown that copepod nauplii, *Oithona* spp., and other small copepods are important prey of fish larvae and other planktivores. Small copepods exhibit a variety of reproductive strategies to compensate for losses to their populations due to predation. These include having high fecundity and growth rates, when not limited by insufficient food; having high reproduction and growth rates at warmer temperatures; having limited motion and low respiration rates, allowing the investment of more energy in reproduction; and having extended longevity to maximize lifetime reproductive output. Thus, small copepods are important links in marine food webs, serving as major grazers of phytoplankton, as components of the microbial loop, and as prey for ichthyoplankton and other larger pelagic carnivores. Our present inadequate understanding of the true abundance, biomass, trophic ecology, and role of small copepods in biogenic fluxes precludes proper understanding of the ecology of the sea.
<http://www.sinica.edu.tw/zool/zoolstud/43.2/255.pdf>

Key words: Plankton, Copepods, Marine ecosystems.

Small planktonic marine copepods (< 1 mm in length) are undoubtedly the most abundant metazoans on Earth. Included are adults and copepodites of calanoid genera such as *Paracalanus*, *Pseudocalanus*, *Acartia*, and *Clausocalanus*; cyclopoid genera such as

Oithona, and *Oncaea* and *Corycaeus*; planktonic harpacticoids of the genus *Microsetella*; and nauplii of almost all copepod species. Because the early stages of all copepods include nauplii, even copepods that are comparatively large as adults are small when young.

Despite their overwhelming abundance and pivotal position in marine food webs, there is still comparatively less knowledge of these small copepods than for larger calanoid taxa such as members of the genus *Calanus* (Marshall and Orr 1955, Tande and Miller 1996 2000). This is particularly true for the feeding and reproductive ecology of small copepods. Nonetheless, there is a substantial body of literature indicating that small copepods are important prey items for larval fish and other zooplanktivorous consumers. Accordingly, this paper reviews the abundance of small planktonic marine copepods, their feeding ecology, their role as prey for predators at higher trophic levels, and aspects of reproductive biology which allow sufficient reproductive success to counter predation losses.

Abundance of small copepods

Despite the abundance of small copepods, they have historically been undersampled due to the use of nets with meshes $> 200\text{-}333\ \mu\text{m}$. Reasons why such coarse meshes have been employed are that (1) fine meshes frequently become clogged with phytoplankton when sampling in coastal waters where chain-forming diatoms can predominate (giving erroneous abundances for the zooplankton collected in such tows); and (2) zooplankton samples often come

from sampling programs targeting collection of fish larvae, which can frequently avoid slower-moving fine-mesh nets. However, recent studies have shown that when appropriate net meshes of $100\ \mu\text{m}$ or less are used, the abundance and sometimes the biomass of small copepods can vastly exceed those of larger ones. Included are studies from such disparate areas as Long Island estuaries (Turner 1982), the continental shelf (Turner and Dagg 1983) and slope (Roman et al. 1985) of the northeastern US, the Sargasso Sea (Roman et al. 1993), the continental shelf off the southeastern United States (Paffenhöfer 1985 1993, Paffenhöfer et al. 1995a), coastal and oceanic waters of Jamaica (Chisholm and Roff 1990, Webber and Roff 1995a b, Hopcroft et al. 1998a, Hopcroft and Roff 1998b), the North Sea (Nichols and Thompson 1991, Nielsen and Sabatini 1996), the Mediterranean (Siokou-Frangou et al. 1997, Calbet et al. 2001), the Red Sea (Böttger-Schnack 1988), the North Atlantic (Gallienne et al. 2001), the North and South Atlantic (Gallienne and Robins 1998), the equatorial Pacific (Roman and Gauzens 1997), coastal waters of Japan (Uye 1994, Liang and Uye 1996, Uye and Sano 1998, Uye et al. 2002), and Antarctica (Fransz 1988).

The baseline monitoring program associated with construction of the Boston Harbor sewage outfall (Turner 1994) highlighted the extreme numerical importance of small copepods, due to

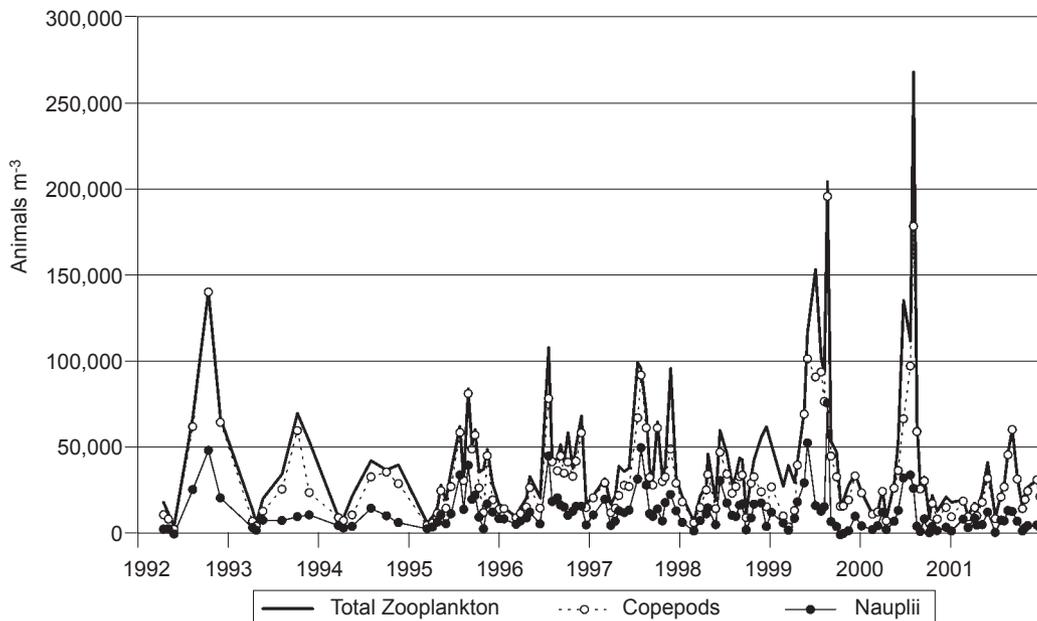


Fig. 1. Mean abundance for each survey of total zooplankton, copepods, and copepod nauplii from $102\text{-}\mu\text{m}$ mesh net vertical tow samples from stations in the "Nearfield" area near the Boston Harbor outfall in Massachusetts Bay, USA.

use of nets with meshes of 102 μm . This program has involved sampling 17 times a year in the nearfield region near the outfall (42.37°N, 70.78°W), and 6 additional times a year throughout adjacent regions of Boston Harbor, Massachusetts Bay, and Cape Cod Bay (41.85-42.32°N, 70.22-71.01°W) since 1992. Baseline data for zooplankton reveal that copepods and copepod nauplii comprise the major components of total zooplankton abundance (Fig. 1). Of the non-nauplii component of copepods, the most abundant components include adults and copepodites of *Oithona similis* (Fig. 2) and (mostly copepodites of) *Pseudocalanus/Paracalanus* (Fig. 3). For overall mean abundances in 1992-2001, copepods comprised 80% of total zooplankton, and of these copepods, 39% were nauplii, 34% were adults and copepodites of *Oithona similis*, and 13% were copepodites of *Pseudocalanus + Paracalanus* spp.

Failure to adequately account for small copepods may cause serious underestimations of zooplankton abundance, biomass, and production, copepod grazing impact on phytoplankton primary production, zooplankton-mediated fluxes of chemicals and materials, and trophic interactions in the sea. A recent paper by Gallienne and Robins (2001) entitled: "Is *Oithona* the most important copepod in the world's oceans?" examined the effects of mesh selection on zooplankton abun-

dance, biomass, and production, and copepod grazing impact. Gallienne and Robins (2001) found that "A 200 μm mesh net is likely to catch only 7% of numbers between 200 μm and 20 mm body length. Because of the relationship of volume to body length, the effect on biomass of the loss of these very small organisms is considerably less, although one-third of the total biomass is still lost." Gallienne and Robins (2001) continued that "Estimated production from that proportion of biomass caught by the 200 μm mesh net ... owing to the decline in weight-specific growth with body size ... the effect of mesh selection on estimates of secondary production may be much worse than that on biomass only--33% of production will be measured using such a net sample." Gallienne and Robins (2001) then calculated that for "35 values for mesozooplankton grazing impact on primary production from studies in the literature over the last 20 years...in coastal seas, shelf seas, and sub-arctic, temperate, and equatorial oceanic waters from the Atlantic, Pacific, Indian, and Southern Oceans...the "global mean" grazing impact for the smallest mesh size is 35.44%...the mean mesh size in this class is just over 62 μm ," and "when recalculated for the mean mesh sizes for the other two size classes (120 and 211 μm), produces estimates that 62 and 30.2% of grazing impact would be characterized using these nets,

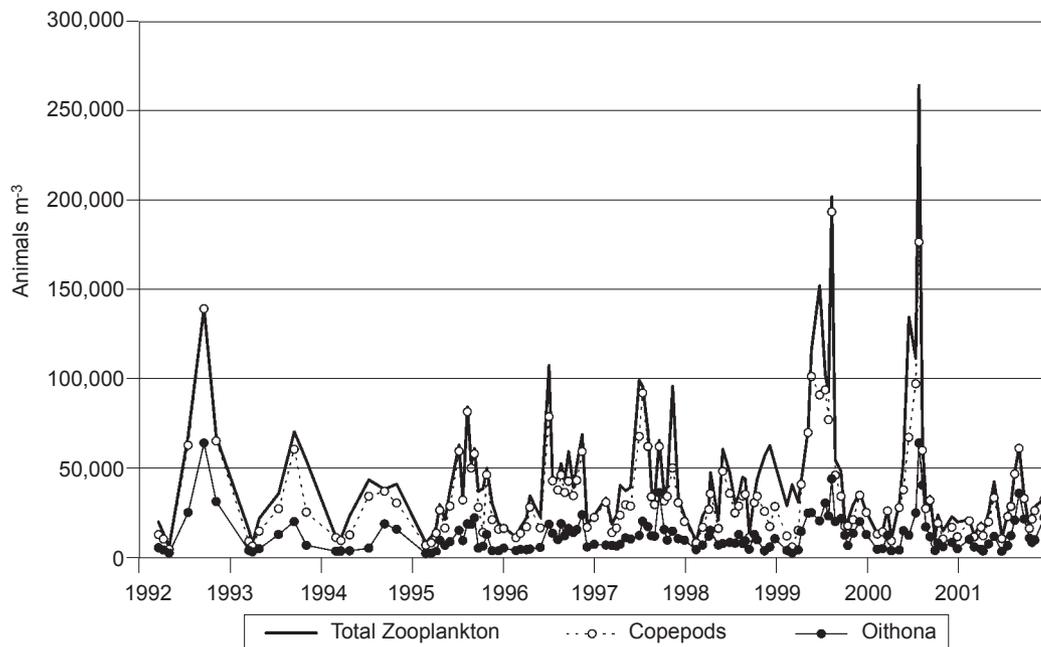


Fig. 2. Mean abundance for each survey of total zooplankton, copepods, and *Oithona similis* copepodites + adults from 102 μm -mesh net vertical tow samples from stations in the "Nearfield" area near the Boston Harbor outfall in Massachusetts Bay, USA.

yielding reduced “global mean” grazing impact values of 22.1 and 10.9% of primary production.” Gallienne and Robins (2001) concluded that “We are therefore left with a considerable proportion of the zooplankton size range (~200-800 μm length) whose biomass and grazing impact may exceed that of the 200 μm net mesozooplankton, but which is not represented in either the microzooplankton or the mesozooplankton in many studies.”

Anthropogenic activities such as coastal eutrophication may cause replacement of large copepods with small ones. Uye (1994) compared the copepod communities of 2 eutrophic embayments in Japan, Tokyo Bay, and Osaka Bay. In the more-eutrophic Tokyo Bay, the small cyclopoid *Oithona davisae* was the dominant copepod in Aug. 1989. In the less-eutrophic Osaka Bay, the larger copepods *Paracalanus* sp., *Calanus sinicus*, and *Corycaeus* spp. were dominant in June 1985. Uye (1994) compared his recent data from Tokyo Bay with a study by Yamazi (1955) using the same-mesh net (96 μm) used in 1948 when Tokyo Bay was less eutrophic. In the earlier study, the copepods *Acartia omorii*, *Paracalanus* sp., and *Microsetella norvegica* comprised a larger proportion of the copepod community in Tokyo Bay than 40 years later.

The main change contributing to the differ-

ences in copepod communities over 4 decades was a major increase in the relative proportion of *Oithona davisae* in Tokyo Bay. Uye suggested that nutrient loading of Tokyo Bay in the 1960s was responsible for a shift in the dominant phytoplankton from diatoms toward small flagellates, and since *O. davisae* does not eat diatoms, but feeds well upon small flagellates, this may have been a contributory factor. Also, bottom-layer anoxia in summer that accompanied increasing nutrient loading since the 1960s may have favored a copepod like *O. davisae* which carries its eggs in a clutch for long periods, rather than immediately shedding its eggs into bottom layers where they might be killed by anoxia. Uye (1994) suggested that the shift in the size structure of the copepod community in Tokyo Bay may also be related to observed declines in zooplanktivorous fish and increases in ctenophores and medusae during the same period.

Feeding ecology of small copepods

The feeding ecology of small copepods is less well-known than that of adults of larger copepod species, such as the genus *Calanus* (Marshall and Orr 1955). Most feeding information for small copepods is for coastal genera such as *Acartia*, rather than for offshore taxa. Although it is gener-

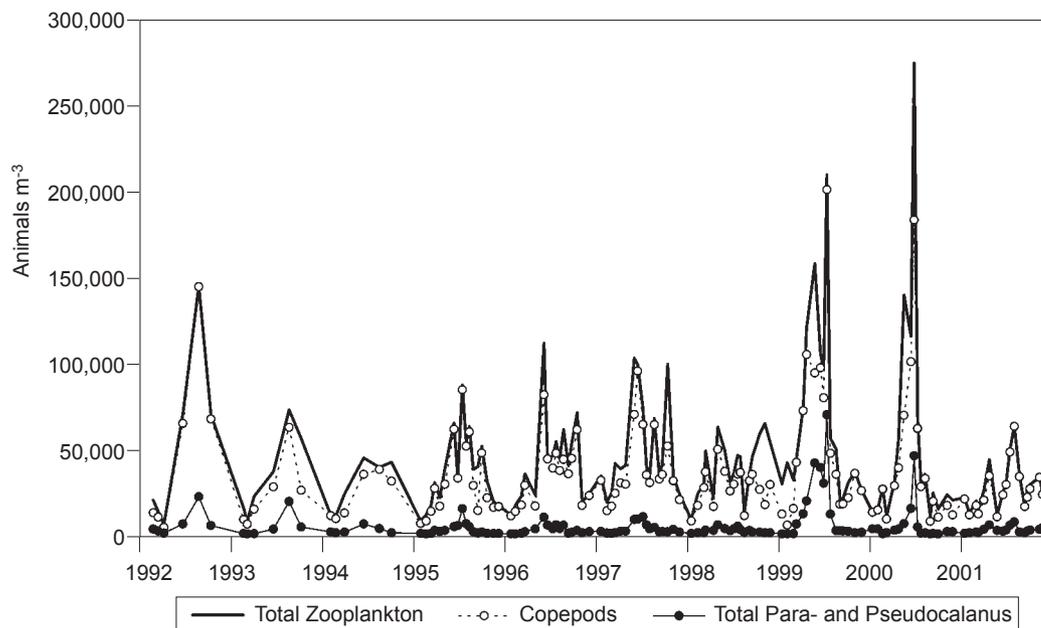


Fig. 3. Mean abundance for each survey of total zooplankton, copepods, and combined *Paracalanus* spp. + *Pseudocalanus* spp. adults + copepodites (most of which were *Pseudocalanus* spp. copepodites) from 102 μm -mesh net vertical tow samples from stations in the “Nearfield” area near the Boston Harbor outfall in Massachusetts Bay, USA.

ally assumed that small copepods, including nauplii, feed primarily upon small-sized phytoplankton cells (Marshall and Orr 1955, Uye and Kasahara, 1983, Berggreen et al. 1988), most such information comes from rearing or feeding studies on limited laboratory diets (as reviewed by Turner 1984a 2000). There have been few examinations of actual copepod feeding on mixed diets of natural phytoplankton and microzooplankton found in the sea, and some of those have produced surprises.

There is increasing evidence that some small copepods feed primarily as predators upon heterotrophic protists, rather than as grazers of phytoplankton (reviewed by Stoecker and Capuzzo 1990, Gifford and Dagg 1991, Kleppel 1993, Turner and Roff 1993, Verity and Paffenhöfer 1996, Paffenhöfer 1998a, Turner 2000). Included are adults of the small copepod genera *Acartia* (Turner and Anderson 1983, Stoecker and Sanders 1985, Stoecker and Egloff 1987, Gifford and Dagg 1988), *Oithona* (Nakamura and Turner 1997, Lonsdale et al. 2000, Granéli and Turner 2002), and *Paracalanus* (Suzuki et al. 1999), and even nauplii of Arctic *Calanus* spp. (Turner et al. 2001).

While bacterioplankton are generally considered too small to be efficiently ingested by most adult copepods, nauplii of various copepod species have been shown to feed upon bacterioplankton (Turner and Tester 1992, Roff et al. 1995). The importance of bacterivory by copepod nauplii in nature remains unresolved.

Other copepods, including small species, appear to feed as carnivores or detritivores upon metazoan, organic macroaggregates, or detrital prey. Cyclopoids such as *Corycaeus* spp. appear to feed primarily as carnivores upon copepod nauplii (Turner et al. 1984, Landry et al. 1985). *Oncaea mediterranea* has been observed to feed upon particles and organisms attached to marine snow (Alldredge 1972, Ohtsuka and Kubo 1991), and Antarctic *Oncaea curvata* can feed upon entire gelatinous *Phaeocystis* colonies (Metz 1998). *Acartia tonsa* can feed upon macrophyte or phytoplankton detritus (Roman 1977 1984), and *Oithona similis* feeds on fecal pellets of other zooplankton (Gonzalez and Smetacek 1994).

Thus, it seems that most copepods, both large and small, feed as omnivores, ingesting a variety of autotrophic and heterotrophic, protozoan and metazoan, and live and dead food sources. Omnivory has been revealed from analyses of hard parts such as diatom and dinoflagellate thecae, tintinnid loricae, and fragments of crustacean

carapaces in contents of fecal pellets of small copepods of the genera *Paracalanus* (Turner 1984b 1991), *Acartia* (Turner 1984c 1991), *Oncaea*, *Corycaeus*, and *Oithona* (Turner 1986 1991). Omnivory is also apparent from quantitative feeding studies of the removal of both thecate and athecate phytoplankton and heterotrophic protist cells by various small copepods of the genera *Acartia*, *Oncaea*, and *Oithona* (Turner and Tester 1989a b, Turner and Granéli 1992, Turner et al. 1998).

Many of the mechanisms of copepod feeding have been elucidated by laser cinematographic techniques pioneered by J. Rudi Strickler, referred to during Geoff Boxshall's maxilliped lecture at this conference as "Rudi's revolution." Although many cinematographic studies have focused upon larger copepods of the genera *Eucalanus* (Alcaraz et al. 1980, Koehl and Strickler 1981, Paffenhöfer et al. 1982, Price et al. 1983, Price and Paffenhöfer 1986a, Paffenhöfer and Lewis 1990), *Centropages* (Cowles and Strickler 1983, Costello et al. 1990, Marrasé et al. 1990, Hwang et al. 1993 1994, Hwang and Strickler 1994), *Calanus* (Turner et al. 1993), and *Euchaeta* (Yen and Strickler 1996), others have examined feeding by adults of small copepod genera, including *Acartia* (Paffenhöfer and Stearns 1988), *Paracalanus* (Paffenhöfer et al. 1995b), *Oithona* (Hwang and Turner 1995, Paffenhöfer et al. 1996, Paffenhöfer and Mazzocchi 2002), and *Clausocalanus* (Mazzocchi and Paffenhöfer 1999), as well as naupliar stages of larger copepods of the genera *Eucalanus* (Price and Paffenhöfer 1986b, Paffenhöfer and Lewis 1989), *Centropages*, and *Temora* (Paffenhöfer et al. 1996).

Cinematographic observations suggest that different taxa of small calanoid copepods, as well as different developmental stages of the same copepod species can have different patterns of behavior for acquiring food and avoiding predators. Paffenhöfer (1991) concluded that *Acartia tonsa* has a strong mechanosensory capability to perceive hydrodynamic disturbances, which helps it avoid predators and capture mobile prey such as nauplii and ciliates. There were few behavioral differences between *A. tonsa* nauplii, copepodites or adults. Conversely, copepodite and adult stages, but not nauplii of *Paracalanus* spp. may be able to use chemoreception to perceive phytoplankton cells at long distances and at low cell concentrations, and to direct these cells toward mouthparts using a feeding current which can increase velocity at low food concentrations (Paffenhöfer 1991,

Paffenhöfer et al. 1996). Paffenhöfer (1991) also suggested that the slow gliding motion produced by the feeding current of *Paracalanus* may also make it less hydrodynamically conspicuous to predators than the jerky motion of *Acartia*. *Clausocalanus furcatus* females move continuously along convoluted small loops, occasionally interrupted by sudden rapid somersaults (Mazzocchi and Paffenhöfer 1999). This behavior suggests a foraging strategy of rapidly exploring small volumes of water, leading to efficient capture or rejection of motile dinoflagellate cells. There also appear to be considerable interspecific differences between nauplii of different calanoid species in terms of escape behavior and intermittent versus continuous feeding currents; such differences were also intraspecific, being exhibited by different stages of nauplii and copepodites of the same species (Paffenhöfer 1991, Paffenhöfer et al. 1996). There are also quantitative differences in rates of ingestion of different sizes of algal cells, at different cell concentrations, for different stages of *Paracalanus* (Paffenhöfer 1984a b).

The motion of cyclopoids is much more intermittent than that of most calanoids (Hwang and Turner 1995, Paffenhöfer et al. 1996, Svendsen and Kiørboe 2000, Paffenhöfer and Mazzocchi 2002). This applies not only to adults, but also to nauplii and copepodites of the species examined thus far (Paffenhöfer 1998b). Members of the genera *Oncaea* and *Oithona* do not create a feeding current such as that of many calanoids, and they feed primarily upon motile prey (Paffenhöfer 1993, 1998b). Thus, they spend much of their time motionless, and then rapidly lurch toward hydrodynamic disturbances created by the motion of prey, which are detected at great distances. This conclusion is supported by gut and fecal pellet content and experimental observations showing that Oithonidae feed upon copepod nauplii (Lampitt 1978, Lampitt and Gamble 1982, Turner 1986, Landry and Fagerness 1988, Nakamura and Turner 1997), and motile protozooplankton such as autotrophic and heterotrophic microflagellates, dinoflagellates, and ciliates (Uchima and Hirano 1986, Uchima 1988, Nakamura and Turner 1997). Members of the Oncaeidae also feed upon motile flagellates and dinoflagellates (Turner and Tester 1989b, Paffenhöfer 1993, Paffenhöfer et al. 1996). Although diatoms have been detected in gut or fecal pellet contents of the Oithonidae and Oncaeidae from subtropical (Turner 1986 1991) and polar (Hopkins and Torres 1989) waters, there are other indications that diatoms may not be opti-

mal or even suitable prey for members of these families (Uchima and Hirano 1986, Uchima 1988).

In summary, small copepods have a varied and wide repertoire of feeding strategies, and these undoubtedly contribute to their ubiquitous abundance in the sea. However, numerous basic questions remain regarding the feeding ecology and grazing/predation impact of most small copepods in the sea.

Small copepods as prey items for larger zooplanktivores

Despite limited knowledge of what small copepods eat, it is clear that many higher-trophic-level consumers eat them. Numerous studies have shown that copepod nauplii, *Oithona* spp., and other small copepods are important prey of fish larvae, and other planktivores. Turner (1984a) reviewed information from 40 studies published between 1918 and 1983 on gut contents of 76 species of fish larvae from most oceans of the world. Those studies revealed that small copepods and their developmental stages were usually the most frequently recorded prey of larval fish. Included were adults, copepodites, and particularly nauplii of the copepod genera *Acartia*, *Calanus*, *Centropages*, *Paracalanus*, *Temora*, *Corycaeus*, *Oithona*, and *Oncaea*, and harpacticoids such as *Microsetella*. Most studies of larval fish feeding published since 1984 continue to document the importance of small copepods as fish prey. Several examples are mentioned below. Lough and Mountain (1996) found that the gut contents of larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) from Georges Bank were dominated by nauplii and copepodites of *Oithona similis* and *Pseudocalanus* spp. Sundby and Fossum (1990) found that the diet of first-feeding Arcto-Norwegian cod larvae was > 90% nauplii of *Calanus finmarchicus*. Conway et al. (1998) found that calanoid and cyclopoid nauplii were the preferred prey of European anchovy (*Engraulis encrasicolus*) larvae in the northwestern Adriatic. Copepod nauplii have also been shown to be important components of the diets of larvae of spot *Leiostomus xanthurus* (Govoni and Chester 1990), redfish *Sebastes* spp. (Anderson 1994), Arctic cod *Boreogadus saida*, and sand lance *Ammodytes* sp. (Fortier et al. 1995), walleye pollock *Theragra chalcogramma* (Hillgruber et al. 1995), Atlantic mackerel *Scomber scombrus* (Fortier and Villeneuve 1996), and summer flounder *Paralichthys dentatus* (Grover 1998). Ringuelette et al.

(2002) have showed that *Calanus nauplii* were dominant prey of larvae of the Atlantic mackerel (*Scomber scombrus*) in the Gulf of St. Lawrence, and that high abundance of nauplii during certain years may promote unusual success of the mackerel year-class during those years.

Why are small copepods so abundant?

Despite extensive predation upon small copepods by larval fish, carnivorous zooplankton such as chaetognaths, ctenophores, and medusae, and cannibalism by larger copepods, small copepods manage to out-reproduce losses due to predation. They do so by a combination of attributes related to reproductive success, examples of which are presented below.

A species of *Paracalanus* is ubiquitously abundant throughout the year in Japanese coastal waters, where it is often the most abundant copepod in terms of biomass and production (Uye et al. 1986, Liang and Uye 1996). Its abundance is related to high egg production and rapid per-stage growth rates, which increase with increasing temperature up to high summer field temperatures, indicating temperature acclimation (Uye 1991, Uye and Shibuno 1992). Thus, even though predation upon *Paracalanus* eggs and nauplii is high (< 7% of eggs produced survive to nauplius stage III; Liang and Uye 1996), this survival was sufficient to maintain the population. *Paracalanus* egg production rates appear to be limited by availability of phytoplankton food in some cases (Checkley 1980a b), but not in others (Checkley 1980, Uye and Shibuno 1992).

The small harpacticoid copepod, *Microsetella norvegica* is widely distributed throughout the ocean, and occurs throughout the year in the Inland Sea of Japan over a temperature range of 9-27°C (Uye et al. 2002). Although present year-round, it only reproduces during the May to November warm season. Proportions of adult females bearing egg sacs varied from 23% to 57%, and the number of eggs per sac varied from 6 to 16, but the duration time from egg laying to adulthood was temperature dependent, ranging from 14 to 32 d over a temperature range of 20-27°C. This strategy of reproduction mainly during the warmer season results in enormously high abundance levels, which accounted for 87% of total copepod abundance near the end of the reproductive period in October. The population persists during the cold period as overwintering adults in the water column. Although *M. norvegica*

has a much lower specific growth rate at 20°C than 7 sympatric copepod species in the Inland Sea of Japan, its extraordinary abundance during the warmest period of the year is related to mid-summer temperatures of > 25°C, which are lethal to other dominant copepod species, but which promote temperature-induced higher fecundity and specific growth rates in *M. norvegica* (Uye et al. 2002). Thus, *M. norvegica* dominates copepod abundance and biomass in the Inland Sea of Japan during the warmest periods of the year because temperatures that may be lethal to its competitors favor its reproduction.

Under conditions of unvaryingly warm (28°C) temperatures in Jamaican waters, copepodite growth rates (Hopcroft et al. 1998b) and egg production rates (Hopcroft and Roff 1998a) for several small copepods appeared to be limited by phytoplankton food resources, but growth rates of nauplii were not (Hopcroft and Roff 1998b). Instantaneous growth rates for nauplii, copepodites, and adults were generally < 1.0 d⁻¹, and small cyclopoids appeared to grow more slowly than small calanoids of comparable size.

Cyclopoid copepods, particularly *Oithona similis*, are ubiquitously abundant in epipelagic waters throughout the world, over a wider range of temperatures and salinities than any other copepod species from coastal to oceanic and tropical to temperate to polar waters (Nishida 1985). In some locations, such as Massachusetts Bay, this species is the most abundant copepod year-round, over a temperature range sometimes exceeding 25°C (Turner 1994). What are the factors contributing to such extraordinary abundance?

In addition to obvious eurythermal and euryhaline capabilities, *Oithona similis* is broadly omnivorous. It feeds upon a variety of phytoplankton, heterotrophic protist, and copepod nauplius food sources, but primarily on ciliates and heterotrophic dinoflagellates (Nakamura and Turner 1997 and references therein). Nielsen and Sabatini (1996) found that specific egg production rates by *O. similis* in the North Sea were correlated to the abundance of heterotrophic protozooplankton rather than to chlorophyll as with co-occurring *Paracalanus* spp. Thus, the ability of this copepod to exploit the lower portion of the food size spectrum, which is more coupled to the microbial loop than to phytoplankton blooms, may contribute to *O. similis*' ability to maintain an almost-continuously stable population.

Oithona similis also has low respiration rates (Marshall and Orr 1966, Nakamura and Turner

1997), which like those of other congeners, appear to be minimally affected by temperature (Lampitt and Gamble 1982, Hiromi et al. 1988). Low respiration coupled with infrequent intermittent movement (Paffenhöfer 1993, Hwang and Turner 1995) might result in energy savings that can be channeled into reproduction.

On an optimum diet, *O. similis* has development and growth that are nearly exponential, and similar to juvenile growth in some calanoids (Sabatini and Kiørboe 1994). Although egg production in the Kattegat of Denmark was limited by food availability (measured as chlorophyll) in summer, and controlled by temperature in winter, the seasonal variation in fecundity and population biomass was less than for co-occurring calanoid genera which undergo dramatic seasonal fluctuations (Sabatini and Kiørboe 1994). This relatively constant fecundity and biomass results in *O. similis* contributing most to overall copepod biomass in the Kattegat during marginal periods, such as fall when predation mortality is high, and winter when food is scarce (Sabatini & Kiørboe 1994) and egg hatching rates are low due to cold temperatures (Nielsen et al. 2002).

The small cyclopoid, *Oithona davisae*, is often the most abundant copepod in several eutrophic Japanese coastal embayments (Uye and Sano 1995, and references therein). This is partly due to temperature-dependent specific egg production rates (Uye and Sano 1995) and naupliar and copepodite growth rates (Uye and Sano 1998), both of which are high in summer.

The high abundance of another small cyclopoid, *Oncaea mediterranea*, off the southeastern coast of the US may also be largely related to successful reproduction (Paffenhöfer 1993). Under favorable food conditions, growth rates of copepodites were exponential ($r = 0.26$), and reproductive rates ($5.3 - 13.3$ nauplii d^{-1}) were high. These parameters coupled with long female longevity (29 - 41 d) mean that *O. mediterranea* females have a lifetime reproductive output that approximates that of co-occurring small calanoids such as *Paracalanus* spp., which reproduce at higher daily rates, but over shorter lifetimes. Similarly, the small co-occurring cyclopoid *Oithona plumifera* reproduced at a lower rate (3.8 nauplii d^{-1}) than *O. mediterranea*, but over a longer lifespan (71 d).

Thus, small copepods employ a variety of strategies to maximize reproduction and survival in order to overcome likely substantial losses due to predation and other factors.

Conclusions

Small copepods are abundant and are important links in marine food webs. They serve as major grazers of phytoplankton, as components of the microbial loop (Turner and Roff 1993) by preying upon bacterioplankton and heterotrophic protists, and as prey for ichthyoplankton and other larger pelagic carnivores. Small copepods exhibit various reproductive and feeding strategies which help to maximize population size, in order to counter heavy losses due to predation. Accordingly, small copepods can become extremely abundant, and presumably exert substantial feeding impact on their prey, but such data are scarce. Our present inadequate understanding of the true abundance, biomass, trophic ecology, and roles of small copepods in biogenic fluxes precludes a proper understanding of the ecology of the sea.

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