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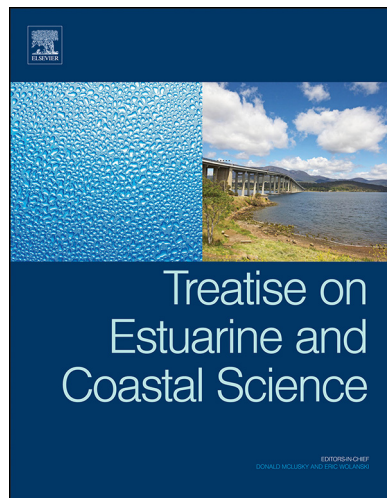
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## 6.05 Plankton Consumer Groups: Copepods

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### Abstract

The article examines the trophic relationships of mesozooplankton in coastal and estuarine systems. The first half of the article focuses on zooplankton feeding, including diet, nutrition, and feeding on toxic algae. The influence of diet on growth, reproduction, and secondary production is also covered. The second half of the article examines mesozooplankton as prey items for fish, gelatinous zooplankton, and other invertebrates. Finally, future directions of mesozooplankton research in neritic systems are presented.

### 6.05.1 Introduction

Copepods are likely the most abundant metazoans on Earth (Humes, 1994). Copepods are part of the phylum Arthropoda, class Crustacea, subclass Copepoda and number some 11 500 species as of 1993 (Humes, 1994). There are 10 orders of copepods (Mauchline, 1998), of which species belonging to those orders primarily found in pelagic coastal and estuarine waters will be considered. These orders include the Cyclopoida, Harpacticoida, and Calanoida, the latter order being the most widely studied (Mauchline, 1998). Calanoid copepods are abundant members of the plankton in both coastal and estuarine waters and serve as the vital trophic step linking primary production to fish. Fish feed on copepods during their larval and juvenile stages (Houde, 1989, 2008), a time when they are vulnerable to density-dependent, starvation mortality. This has been aptly named the 'critical period' and has been recognized for nearly a century (Hjort, 1914). A mismatch in time or space between larval fish and zooplankton prey may result in failure of a year-class of fish to recruit to the population (Cushing, 1974, 1975, 1990). While it is now recognized that many factors contribute to fish recruitment (Houde, 2008), the amount of zooplankton prey available to larval fish remains vital. Zooplankton also impact phytoplankton communities by direct grazing but more importantly by grazing microzooplankton,

often the primary consumers of phytoplankton (Burkill et al., 1987; Calbet, 2008). Thus, copepods may act to filter trophic variability (Runge, 1988) and are the gateway to primary production for higher animals in food webs.

This chapter gives an overview of the trophic ecology of copepods in estuarine and coastal waters. It begins with a brief overview of the diversity, species composition, abundance, biomass, and distribution of copepods in estuarine/coastal systems. The focus of this volume is trophic relationships; therefore, the majority of the chapter considers the role of copepods in food webs. The chapter examines the feeding patterns of copepods, including grazing, predation, and ingestion of detritus. Rates of copepod secondary production will be presented and this will transition into a discussion of copepod predators. Finally, the chapter concludes with some general remarks about the role of copepods in estuarine and coastal systems worldwide and examines future research directions.

### 6.05.2 Copepod Diversity, Species Composition, Abundance, Biomass, and Distribution

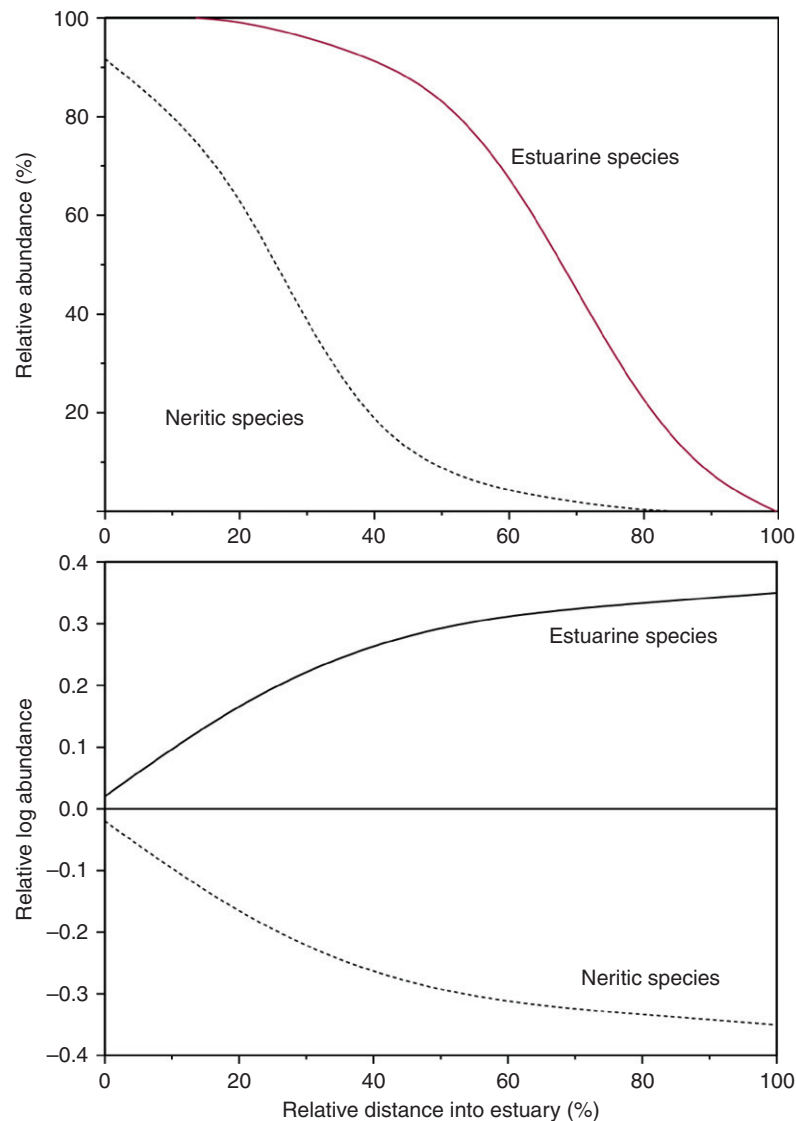
Copepod communities in estuarine waters have many general characteristics that are in contrast to communities found in the open ocean (Table 1). Estuarine communities have low species

**Table 1** A contrast of the characteristics of estuarine/coastal copepods versus open ocean copepods

| Characteristic    | Estuarine/coastal species | Open ocean species            |
|-------------------|---------------------------|-------------------------------|
| Species richness  | Low                       | High                          |
| Species diversity | Low                       | High                          |
| Abundance         | High                      | Low                           |
| Temperature range | Eurythermal               | Stenothermal                  |
| Salinity range    | Stenohaline               | Stenothermal                  |
| Feeding strategy  | Omnivory; few predators   | Less omnivory, more predation |

richness. Turner (1981) found a range of 6–23 zooplankton species in North American estuaries. This is in contrast to the 88 species found in the upper 500 m of the Sargasso Sea (Deevey and Brooks, 1977). The species diversity of estuarine and coastal systems also tends to be low, with one or a few species numerically dominant. The same, general pattern is observed in oceanic

systems; however, the species diversity and number of numerically dominant species is often much higher (McGowan and Walker, 1985). Two hypotheses may explain the low diversity of estuarine copepod assemblages. First, the salinity gradient that characterizes most estuarine systems is thought to determine the pattern of observed diversity (Figure 1). Bousfield et al. (1975)



**Figure 1** Relative abundance of estuarine and neritic copepod species as a function of distance into an estuary. Reproduced from Kimmerer, W.J., 1991. Predatory influences on copepod distributions in coastal waters. Bulletin of Plankton Society of Japan Special Volume, 161–174.

noted three distinct groups of zooplankton in the St. Lawrence estuary: (1) marine, coastal species that are found only in the seaward portion of the estuary; (2) truly estuarine species that are found in the mesohaline portion of the upper estuary; and (3) freshwater species that can be found in the oligohaline portion of the upper estuary. Most estuaries have variable ionic concentrations and osmotic pressure gradients that species must acclimate to over short periods. The ability to acclimate to these shifts requires specialized adaptations (Lee and Bell, 1999); thus, not all species are able to live in these areas. An alternative explanation is offered by Kimmerer (1991) who postulated that selective predation is the likely cause of low diversity in shallow, estuarine embayments. It is worth noting that Kimmerer (1991) only considered shallow, temperate bays with little or no salinity gradient. The observed distributions of copepods in estuarine and coastal systems may be a function of interactions between competing species and/or the influence of predators that has, to this point, been explained solely by salinity. This topic merits further investigation.

Estuarine copepod communities are dominated by very few species (Miller, 1983). Species composition varies

regionally and I have summarized the dominant species of copepods found in estuarine systems worldwide (Table 2). Temperate systems are typically dominated by copepods from the genus *Acartia* and several different species may be found depending on location (Table 2). Several other species are found in the brackish zone along with *Acartia*, including members of the genus *Oithona* (Table 2). The oligohaline portion of temperate estuaries is often dominated by *Eurytemora affinis* (Europe and North America) or *Sinocalanus* spp. (Asia), whereas subtropical or tropical estuaries contain *Pseudodiaptomus* spp. The mouths of estuaries contain fauna that more closely resemble neritic populations such as *Paracalanus* spp., *Parvocalanus crassirostris*, *Centropages* spp., and *Temora* spp. (Table 2). The heads of estuaries often contain freshwater-adapted species, such as *Acanthocyclops* spp. and *Diaptomus* spp. (Mouny and Dauvin, 2002).

Abundances of copepods vary significantly across systems. Estuaries and coastal areas are naturally mesotrophic to eutrophic and therefore have significant primary production to support large standing stocks of copepods compared to open ocean systems. In the open ocean, the average

**Table 2** Dominant species in selected estuarine systems by continent: Africa (AFR), Australia (AUS), Europe (EUR), North America (NA), and South America (SA)

| Location                                   | Continent | Dominant species  | Reference                         |
|--|-----------|---|-----------------------------------|
| Mpenjati Estuary                           | AFR       | <i>Pseudodiaptomus hessei</i> , <i>Acartia natalensis</i> , <i>Gastrosaccus brevifissura</i>  | Kibirige and Perissinotto (2003b) |
| Great Fish Estuary, Kariaga Estuary        | AFR       | <i>P. hessei</i> , <i>A. natalensis</i> , <i>Acartia longipatella</i>   | Grange et al., (2000)             |
| Senegal River Estuary                      | AFR       | <i>Acartia clausi</i> (dominant 98–100%), <i>Paracalanus</i> spp., <i>Clausocalanus</i> spp., <i>Corycaeus</i> spp., <i>Temora stylifera</i> and <i>Eucalanus</i> spp., <i>P. hessei</i>  | Champalbert et al. (2007)         |
| Chanjiang Estuary                          | ASIA      | <i>Monoculodes limnophilus</i> , <i>Schmackeria poplesia</i> , <i>Tortanus vermiculus</i> , <i>Labidocera euchaeta</i> , <i>Paracalanus parvus</i> , <i>Sinocalanus sinensis</i>  | Gao et al. (2008)                 |
| Bay of Bengal                              | ASIA      | <i>Arocalanus</i> spp., <i>Oithona</i> spp., <i>Corycaeus danae</i> , <i>Euterpina acutifrons</i> , <i>Paracalanus</i> spp., <i>Acartia</i> spp.  | Rakesh et al. (2006)              |
| Pearl River Estuary                        | ASIA      | <i>Acartia spinicauda</i> , <i>Acartiella sinensis</i> , <i>Pseudodiaptomus poplesia</i> , <i>L. euchaeta</i> , <i>Tortanus dextrilobatus</i> , <i>Penilia avirostris</i> , <i>Subeucalanus subcrassus</i> , <i>Calanus sinicus</i> , <i>Temora turbinata</i> , <i>Sagitta bedoti</i> , <i>Doliolum denticulatum</i> , <i>Oikopleura longicauda</i> | Li et al. (2006)                  |
| Zhelin Bay, S China                        | ASIA      | <i>Paracalanus crassirostris</i> , <i>Oithona brevicornis</i> , <i>Pendia avirostris</i>  | Dong et al. (2006)                |
| Cochin backwaters                          | ASIA      | <i>Labidocera pectinata</i> , <i>P. crassirostris</i> , <i>Paracalanus aculeatus</i> , <i>Acartia centrura</i> , <i>Acartia bowmani</i> , <i>Acartia bilobata</i> , <i>Centropages alcocki</i> , <i>Pseudodiaptomus serriacaudatus</i> , <i>Corycaeus</i> spp., <i>O. brevicornis</i>   | Madhu et al. (2007)               |
| Chikugo River estuary, Japan               | ASIA      | <i>Pseudodiaptomus inopinus</i> , <i>S. sinensis</i>  | Ueda et al. (2004)                |
| Darwin Harbour                             | AUS       | <i>Parvocalanus crassirostris</i> , <i>Bestiolina similis</i> , <i>Oithona aruensis</i>   | Duggan et al. (2008)              |
| Mangrove estuaries in NE Australia         | AUS       | <i>Oithona</i> spp., <i>P. crassirostris</i> , <i>Bestiolina similis</i> , <i>Acartia shininess</i> , <i>Pseudodiaptomus australiensis</i> , <i>P. baylyi</i> , <i>P. inflexus</i>  | McKinnon and Klumpp (1997)        |
| Wilson Inlet, Australia                    | AUS       | <i>Oithona simplex</i> , <i>Acartia simplex</i> , <i>Gladioferens imparipes</i>   | Gaughan and Potter (1995)         |
| Mondego Estuary, Portugal                  | EUR       | <i>Acartia tonsa</i> , <i>A. clausi</i> , <i>Diaptomus castor</i> , <i>Acanthocyclops robustus</i>  | Primo et al. (2009)               |
| North Adriatic Sea, Gulf of Trieste, Italy | EUR       | <i>P. avirostris</i> , <i>P. parvus</i> , <i>A. clausi</i> , <i>Oncaea</i> spp.   | Camatti et al. (2008)             |
| Gironde Estuary                            | EUR       | <i>Acartia bifilosa</i> , <i>A. tonsa</i> , <i>Eurytemora affinis</i>   | David et al. (2007)               |
| Bilbao and Urdaibai Estuary, Spain         | EUR       | <i>A. bifilosa</i> , <i>P. parvus</i> , <i>A. clausi</i>  | Uriarte and Villate (2005)        |

(Continued)

**Table 2** (Continued)

| Location  | Continent | Dominant species   | Reference                             |
|---|-----------|--|---------------------------------------|
| Genova Harbor, Ligurian Sea                       | EUR       | <i>P. parvus</i> , <i>A. clausi</i>  | Pane et al. (2005)                    |
| Schelde Estuary, Belgium                          | EUR       | <i>E. affinis</i> , <i>A. tonsa</i> , mysids,  | Tackx et al. (2004)                   |
| Arcachon Bay, France                              | EUR       | <i>A. bifilosa</i> , <i>A. tonsa</i> , <i>P. parvus</i> , <i>Oncaea venusta</i> , <i>P. avirostris</i>   | Vincent et al. (2002)                 |
| Seine Estuary                                     | EUR       | <i>Acartia</i> spp., <i>E. affinis</i> , <i>Temora longicornis</i>   | Mouny and Dauvin (2002)               |
| Po River delta, 2 lagoons                         | EUR       | <i>A. tonsa</i> ,  | Bressan and Moro (2002)               |
| Ems, Gironde, Westerschelde                       | EUR       | <i>A. bifilosa</i> , <i>E. affinis</i>   | Sautour and Castel (1995)             |
| Severn Estuary                                    | EUR       | <i>E. affinis</i> , <i>A. bifilosa</i> , <i>Centropages hamatus</i> , <i>Calanus helgolandicus</i>   | Collins and Williams (1981)           |
| Tampa Bay, FL                                     | NA        | <i>Oithona colcarva</i> , <i>A. tonsa</i>  | Badylak and Philips (2008)            |
| Pensacola Bay, FL                                 | NA        | <i>A. tonsa</i> , <i>Oithona</i> spp., <i>Clausocalanus furcatus</i>   | Murrel and Lores (2004)               |
| Waquoit Bay, MA                                   | NA        | <i>Acartia hudsonica</i> , <i>C. hamatus</i> , <i>E. affinis</i> , <i>A. tonsa</i>   | Lawrence et al. (2004)                |
| Punta Morales estuary, Gulf of Nicoya, Costa Rica | NA        | <i>Acartia lilljeborgi</i> , <i>P. parvus</i>  | Brugnoli-Olivera et al. (2004)        |
| Lower St. Lawrence Estuary                        | NA        | <i>Calanus finmarchicus</i> , <i>Calanus hyperboreus</i> , <i>Acartia</i> spp., <i>Oithona</i> spp., <i>Pseudocalanus</i> spp.   | Plourde et al. (2002)                 |
| Phosphorescent Bay, Puerto Rico                   | NA        | <i>Oithona</i> spp., <i>A. tonsa</i> , <i>Paracalanus</i> spp., <i>Pseudodiaptomus cokeri</i>  | Rios-Jara (1998)                      |
| Tomales Bay CA                                    | NA        | <i>A. tonsa</i> , <i>Acartia omorii</i> , <i>Calanus pacificus</i> , <i>Paracalanus quasimodo</i> , <i>Tortanus discaudatus</i> , <i>Pseudocalanus</i> spp. (OUTER) <i>Acartia hudsonica</i> , <i>Acartia californiensis</i> , <i>Centropages abdominalis</i> , <i>Pseudodiaptomus marinus</i> | Kimmerer (1993)                       |
| Hereford Inlet Estuary, NJ                        | NA        | <i>Oithona</i> spp., <i>Temora</i> spp., <i>Acartia</i> spp.   | Herman and Dapolito (1985)            |
| San Francisco Bay                                 | NA        | <i>Acartia</i> spp., <i>Oithona davisae</i> , <i>E. affinis</i> , <i>A. californiensis</i> , <i>Sinocalanus doerrii</i>  | Ambler et al. (1985)                  |
| Lower Delaware River Estuary                      | NA        | <i>A. tonsa</i> , <i>C. hamatus</i> , <i>T. longicornis</i> , <i>Pseudocalanus minutus</i> , <i>Pseudodiaptomus coronatus</i> , <i>Paracalanus</i> spp.  | Maurer et al. (1978)                  |
| Navesink River estuary, NJ                        | NA        | <i>A. tonsa</i> , <i>P. coronatus</i> , <i>E. affinis</i>  | Knatz (1978)                          |
| Wilmington River/Savannah River estuary GA        | NA        | <i>A. tonsa</i> , <i>Oithona</i> , <i>P. coronatus</i> , <i>E. acutifrons</i>  | Stickney (1975)                       |
| Bahia Blanca Estuary                              | SA        | <i>A. tonsa</i> , <i>Ewingella americana</i>   | Hoffmeyer et al. (2009)               |
| Sergipe Estuary, Brazil                           | SA        | <i>P. crassirostris</i> , <i>P. quasimodo</i> , <i>T. turbinata</i>  | Araujo et al. (2008)                  |
| Solis Grande, Uruguay                             | SA        | <i>A. tonsa</i> , <i>Oithona nana</i> , <i>O. simplex</i> , <i>P. parvus</i> , <i>P. crassirostris</i>   | Gomez-Erache et al. (2000)            |
| Pina estuary, Recife-Pernambuco Brazil            | SA        | <i>Favella ehrenbergi</i> (tintinnid), <i>Brachionus plicatilis</i> , <i>Oithona osvaldocruzi</i>  | Eskinazi-Sant'anna and Tundisi (1996) |
| Guarau River estuary SE Brazil                    | SA        | <i>Pseudodiaptomus richardi</i> , <i>A. lilljeborgi</i> , <i>Oithona hebes</i> , <i>P. crassirostris</i> , <i>Pseudodiaptomus acutus</i>   | Lopes (1994)                          |

abundance of copepods in the upper 100 m averages between 20 and 60 individuals  $m^{-3}$  (Mauchline, 1998). Abundances in estuaries may be extremely high during certain periods, for example, abundances of *E. affinis* can reach  $3 \times 10^6$  individuals  $m^{-3}$  (Heinle, 1972). Average abundance is more likely to range from 100 to 10 000 individuals  $m^{-3}$  (Table 3). General patterns of biomass and seasonality are difficult to summarize and are likely species specific. A cross section of the average abundance and biomass in several systems worldwide is presented in Table 3. Beginners in the field of biological oceanography are often taught that the general pattern in temperate systems consists of a spring bloom of phytoplankton followed by a gradual increase in zooplankton biomass as it tracks the bloom. This is observed in some estuarine systems; however, a recent study found that the classic spring and fall bloom cycles for phytoplankton were not found in estuaries (Cloern and Jassby, 2008). The peaks in phytoplankton biomass and primary production were system dependent and highly variable (Cloern and Jassby, 2008). Also, the timing of the peak was not consistent across systems, suggesting that the copepod response to peaks in

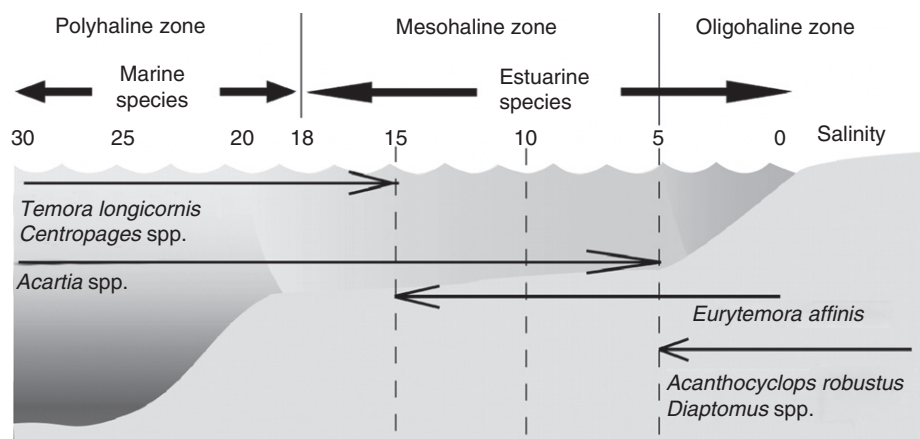
phytoplankton biomass and production is also likely to be highly variable (Cloern and Jassby, 2008).

Most studies examine copepod distribution in estuaries with respect to salinity. For example, the Seine River, France is characterized by a large salinity gradient and has a distribution of copepod species typical of temperate estuaries (Figure 2). Toward the seaward terminus of the estuary are neritic species that are found in fewer numbers at mid-range salinities (15–20; Figure 2). Truly estuarine species, *Acartia* spp., are located throughout the estuary (Figure 2). At the landward side of the estuary, more freshwater species are found, such as *Acanthocyclops robustus* and *Pseudodiaptomus* spp. (Figure 2). Congeners can also differ in salinity tolerance, as Lance (1963) found *Acartia tonsa* to be more tolerant of salinity than either *A. bifilosa* or *A. discaudata*. Salinity tolerance is also influenced by temperature, as found with *E. affinis* (Bradley, 1986). Some estuarine systems lack strong salinity gradients and therefore other factors may control distribution in these systems. These other factors include temperature, hydrographic features, food limitation, and predation.



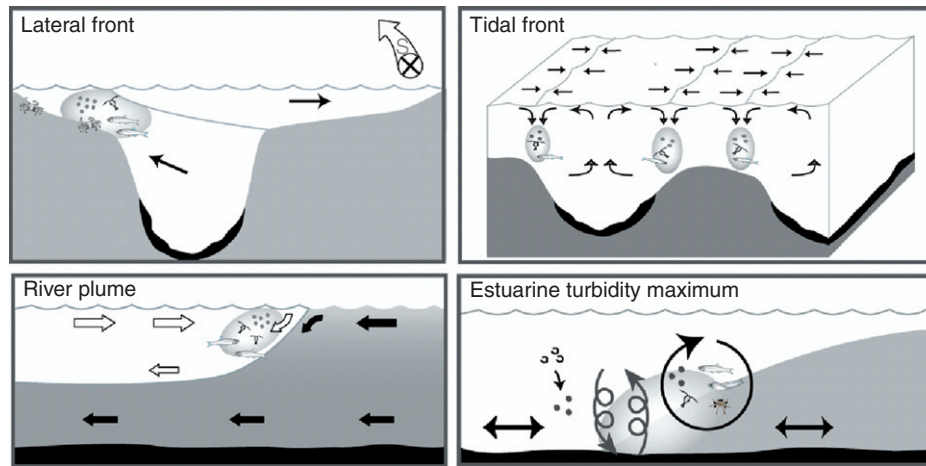
**Table 3** Total copepod abundance and biomass in selected systems by continent: Africa (AFR), Australia (AUS), Europe (EUR), North America (NA), South America (SA)

| Location  | Continent | Abundance (number m <sup>-3</sup> ) range                   | Biomass range   | Net mesh (μm)         | Reference                             |
|---|-----------|---|---|-----------------------|---------------------------------------|
| Mpenjati Estuary                                  | AFR       | 20–5.8 × 10 <sup>4</sup> <sup>a</sup>                       | 0.01–1.69 g DW m <sup>-3</sup> <sup>a</sup>                 | 90                    | Kibirige and Perissinotto (2003b)     |
| Senegal River Estuary                             | AFR       | 8.4–1.4 × 10 <sup>4</sup> <sup>b</sup>                      | 500–2.0 × 10 <sup>4</sup> ug-C m <sup>-3</sup> <sup>b</sup> | 200                   | Champalbert et al. (2007)             |
| Changjiang Estuary                                | ASIA      | 283–2094 <sup>a</sup>                                       |   | 505                   | Gao et al. (2008)                     |
| Bay of Bengal                                     | ASIA      | 819–3.5 × 10 <sup>4</sup> <sup>a</sup>                      | 7.1–160.2 mg DW m <sup>-3</sup> <sup>a</sup>                | 300                   | Rakesh et al. (2006)                  |
| Pearl River Estuary                               | ASIA      | 181–464 <sup>a</sup>  | 172–295 mg WW m <sup>-3</sup> <sup>a</sup>                  | 505                   | Li et al. (2006)                      |
| Cochin backwaters                                 | ASIA      | 49–4457 <sup>b</sup>  | 1.2–88 mg-C m <sup>-3</sup> <sup>a</sup>                    | 200                   | Madhu et al. (2007)                   |
| Darwin Harbour                                    | AUS       | 3.9 × 10 <sup>4</sup> –4.4 × 10 <sup>5</sup> <sup>b</sup>   | 52–1363 mg m <sup>-3</sup> <sup>a</sup>                     | 73                    | Duggan et al. (2008)                  |
| Mangrove estuaries in NE Australia                | AUS       | 3.5 × 10 <sup>4</sup> –8.8 × 10 <sup>5</sup> <sup>a</sup>   |   | Niskin bottle samples | McKinnon and Klumpp (1997)            |
| Wilson Inlet, Australia                           | AUS       | 2610–2.9 × 10 <sup>6</sup> <sup>a</sup>                     |   | 53                    | Gaughan and Potter (1995)             |
| Mondego Estuary, Portugal                         | EUR       | 21–1102 <sup>a</sup>  |   | 335                   | Primo et al. (2009)                   |
| Schelde Estuary, Belgium                          | EUR       | < 10 × 10 <sup>3</sup> –2.67 × 10 <sup>5</sup> <sup>a</sup> |   | 50                    | Tackx et al. (2004)                   |
| Arcachon Bay, France                              | EUR       | 1.6 × 10 <sup>4</sup> <sup>a</sup>                          |   | 200                   | Vincent et al. (2002)                 |
| Punta Morales estuary, Gulf of Nicoya, Costa Rica | NA        | 438–5877 <sup>b</sup>                                       |   | 280                   | Brugnoli-Olivera et al. (2004)        |
| Phosphorescent Bay, Puerto Rico                   | NA        | 5.6 × 10 <sup>4</sup> –2.29 × 10 <sup>5</sup> <sup>b</sup>  |   | 135                   | Rios-Jara (1998)                      |
| San Francisco Bay                                 | NA        | 4644–5.4 × 10 <sup>4</sup> <sup>c</sup>                     | 13.2–53.1 mg-C m <sup>-3</sup>                              | 64                    | Ambler et al. (1985)                  |
| Lower Delaware River estuary                      | NA        | 2730–9311 <sup>a</sup>                                      |   | 241                   | Maurer et al. (1978)                  |
| Sergipe Estuary, Brazil                           | SA        | 1.5–3.7 × 10 <sup>4</sup> <sup>a</sup>                      |   | 200                   | Araujo et al. (2008)                  |
| Solis Grande, Uruguay                             | SA        | 1097–6219 <sup>b</sup>                                      |   | 158                   | Gomez-Erache et al. (2000)            |
| Pina estuary, Recife-Pernambuco Brazil            | SA        | 2623–4.1 × 10 <sup>5</sup> <sup>a</sup>                     |   | 69                    | Eskinazi-Sant'anna and Tundisi (1996) |

<sup>a</sup> Total zooplankton community.<sup>b</sup> Copepods only.<sup>c</sup> *Acartia* spp. only.**Figure 2** Distribution of copepod species common to the Seine River Estuary, France. Reproduced from Mouny, P., Dauvin, J.C., 2002. Environmental control of mesozooplankton community structure in the Seine Estuary (English Channel). Oceanologica Acta 25, 13–22.

Temperature has a large impact on copepod biology. The growth rate of copepods is strongly temperature dependent (Huntley and Lopez, 1992; Hirst and Bunker, 2003), as is their development rate (McLaren et al., 1969). Water temperatures in estuaries do not form large gradients in the manner of

salinity, but do show considerable seasonal variability, depending on location. Most truly estuarine species are eurythermal; for example, *A. tonsa* can tolerate temperatures from –1 to 32 °C (Gonzalez, 1974), *E. affinis* from 0 to 30 °C (Bradley, 1978), *Sinocalanus tenellus* from 6 to 27 °C (Kimoto



**Figure 3** Conceptual diagram of physical features that aggregate copepods in estuarine and coastal systems. Reproduced from Roman, M.R., Zhang, X., McGilliard, C., Boicourt, W.C., 2005. Seasonal and annual variability in the spatial patterns of plankton biomass in Chesapeake Bay. *Limnology and Oceanography* 50, 480–492. Copyright (2005) by the American Society of Limnology and Oceanography, Inc.

et al., 1986), and *Oithona similis* at least from 4 to 25 °C (Castellani et al., 2005). Thus, temperature would not appear to be a major factor determining distribution of copepods within estuarine systems.

Hydrography shapes distributions of copepods within estuaries. Distributions are often patchy and related to hydrographic features. Roman et al. (2005) summarized these features for copepods in Chesapeake Bay, USA (Figure 3). Aggregations of copepods are found in areas of tidal energy dissipation, tidal fronts, and convergent eddies (Figure 3). Advective loss from estuarine systems is a function of either strong tidal currents or freshwater input and also serves to structure estuarine copepod communities. Many crustaceans, including copepods, appear to undergo vertical migrations in response to tidal changes in current direction (Ketchum, 1954; Cronin and Forward, 1979; Kimmerer and McKinnon, 1987b; Hough and Naylor, 1992; Kimmerer et al., 1998, 2002). The Columbia River system in Oregon, USA is an estuarine system with strong freshwater input and net seaward flow. As a result, the copepod *E. affinis* appears to undertake vertical migrations in order to avoid advective loss (Figure 4) (Morgan et al., 1997). This behavior maintains *E. affinis* in the oligohaline portion of the estuary and is in close proximity to the estuarine turbidity maximum (ETM) region. Another example of tidal migration is found in Westernport Bay, Australia. Westernport Bay is weakly stratified and *Acartia tranterii* found in the Western portion of the Bay are subjected to currents that switch direction on each tidal cycle (Kimmerer and McKinnon, 1987b). These copepods also undergo vertical migration in concert with the tides in order to avoid advective loss from the seaward portion of the bay (Kimmerer and McKinnon, 1987b).

### 6.05.3 Copepod Feeding

#### 6.05.3.1 Introduction

Research into the trophic ecology of estuarine copepods can be summarized by three basic questions: (1) What is the diet composition of estuarine copepods? (2) How does diet

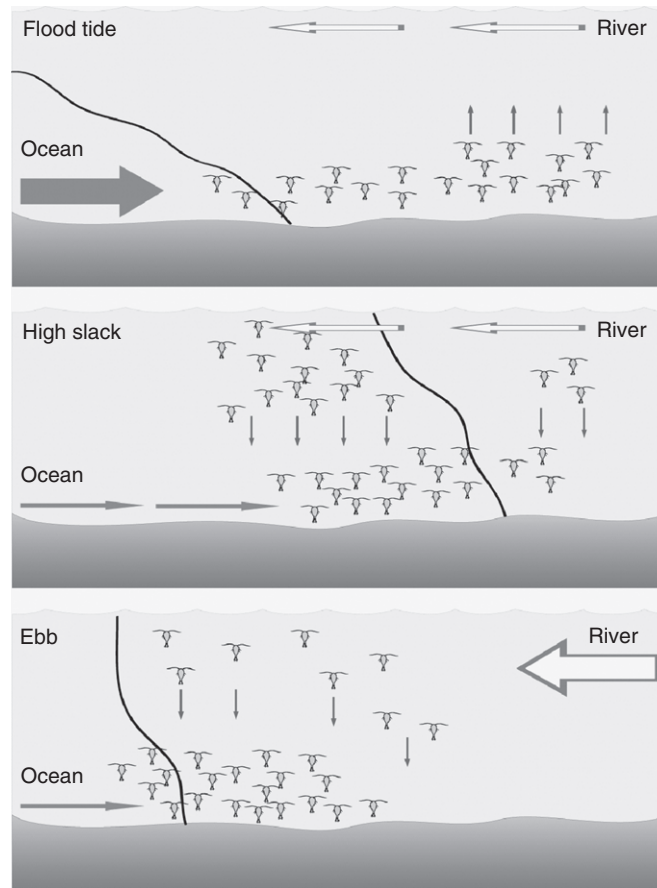
influence growth and reproduction? (3) What factors determine the secondary production of copepods? Put more simply, researchers are interested in what copepods feed upon to meet their nutritional and energy requirements; how these materials influence growth and reproduction; and what quantity and quality of material becomes available to higher trophic levels. Research into these questions has advanced considerably as estuarine copepods were once considered to be primarily herbivorous (Day et al., 1989), feeding on mixed assemblages of phytoplankton. It is now clear that the diets of most copepods are much more complex than simple herbivory (Kleppel, 1993). The classic food chain of phytoplankton to zooplankton to fish has been shown to be far less prevalent in estuaries and it is now widely recognized that copepods feed at multiple trophic levels. Estuarine copepods are best characterized as having evolved a generalist feeding strategy that takes advantage of the plentiful variety of food options present in estuarine and coastal systems. However, many species do show preferences for particular prey based on several factors, including prey size, availability, and quality.

#### 6.05.3.2 Diet Composition

Estuaries are often net heterotrophic systems that are meso- to eutrophic. Estuaries have zones of limited primary production despite sufficient nutrients (due to light limitation) as well as zones of high primary production. Thus, there exist within estuaries many potential pathways for copepod feeding and production. Based on these habitat characteristics, it is reasonable to assume that copepod diets in estuarine systems are not solely dependent upon phytoplankton. Indeed, copepod feeding studies suggest that diets are diverse and appear to have evolved to meet nutritional demands and optimize production (Kleppel, 1993; Gifford et al., 2007).

Phytoplankton in estuaries are typically dominated by diatoms and dinoflagellates (Day et al., 1989). Other groups may be important depending on location and season and these include cryptophytes, chlorophytes, and cyanobacteria (Day et al., 1989). The phytoplankton composition of individual





**Figure 4** Conceptual diagram tidal migration strategy of *Eurytemora affinis* to maintain position within the Columbia River Estuary, USA. Arrow size represents the magnitude of event. Reproduced from Morgan, C., Cordell, J., Simenstad, C., 1997. Sink or swim? Copepod population maintenance in the Columbia River estuarine turbidity-maxima region. *Marine Biology* 129, 309–317.

systems can vary widely, and literature relevant to each system should be consulted. General patterns of phytoplankton variability for estuarine systems are also difficult to summarize. Copepods in estuarine and coastal systems feed on a variety of phytoplankton species, including all of the groups listed above. There is an abundance of literature that focuses on copepod grazing of phytoplankton. Rather than review all of this literature, I will focus on how copepods affect the total phytoplankton stock.

Differences in the amount of phytoplankton grazed by copepods between systems can be large. Grazing impact on

standing stocks or total phytoplankton production can range from 0% to 100% (Table 4). This suggests that local factors must be examined in order to determine the amount of phytoplankton grazed. These numbers likely shift depending on local conditions, which often have seasonal components. Temperate estuaries display seasonality in terms of daily phytoplankton production removed. For example, White and Roman (1992b) found that in Chesapeake Bay 12–103% of daily phytoplankton stock was removed by mesozooplankton and that this number varied depending on season. Tan et al. (2004) found similar numbers in the

**Table 4** Grazing impact of copepods on phytoplankton standing stock from selected systems

| System                                   | Percent grazed        | References                        |
|--|-----------------------|-----------------------------------|
| Schelde Estuary, Belgium/The Netherlands | 0 <sup>a</sup>        | Lionard et al. (2005)             |
| Berre Lagoon, west Mediterranean         | <1 <sup>b</sup>       | Cervetto et al. (1995)            |
| Ebrie Lagoon, Ivory Coast                | 14 <sup>b</sup>       | Pagano et al. (2006)              |
| Kariega Estuary, South Africa            | 4.3–57.8 <sup>b</sup> | Froneman (2000, 2001)             |
| Neuse River Estuary, USA                 | 38–44 <sup>b</sup>    | Mallin and Paerl (1994)           |
| Mpenjati Estuary, South Africa           | 100 <sup>b</sup>      | Kibirige and Perissinotto (2003a) |

<sup>a</sup>Standing stock.

<sup>b</sup>Total phytoplankton production.

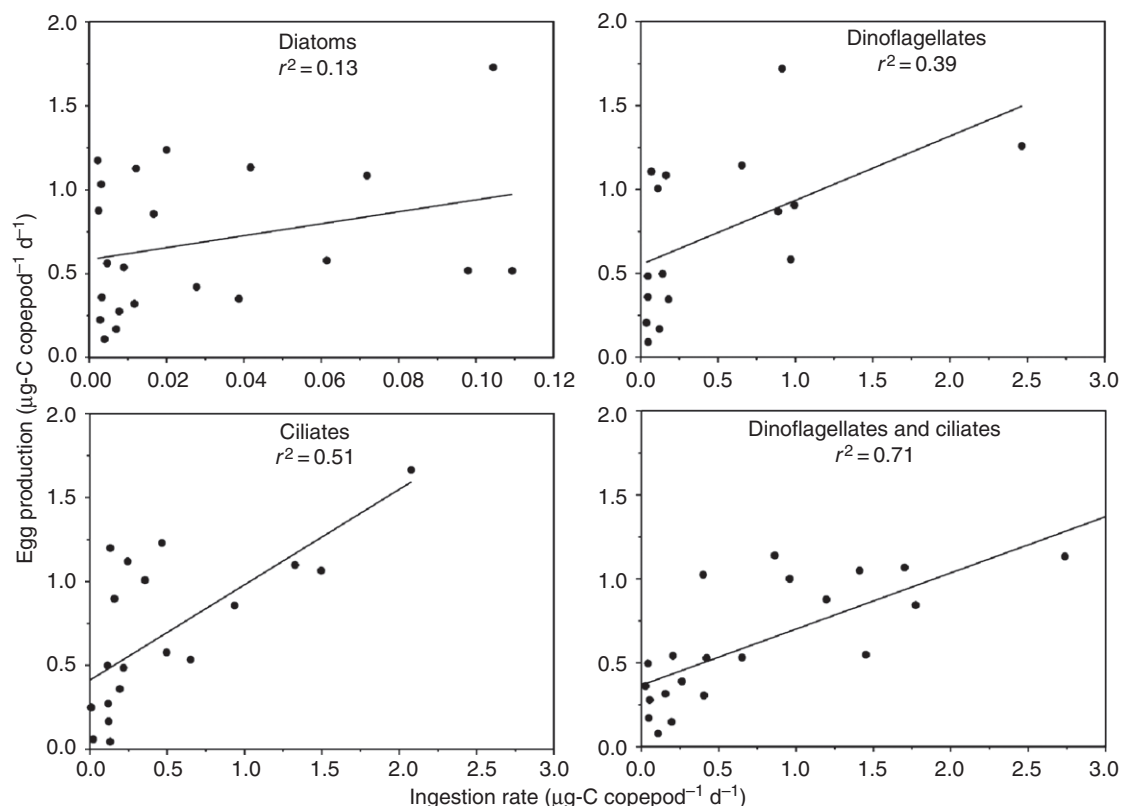
Pearl River Estuary, China where copepods removed 21% and 104% of daily phytoplankton production in winter and summer, respectively.

The majority of grazing on estuarine phytoplankton is often by microzooplankton (Dagg, 1995; Sautour et al., 2000). Microzooplankton consist of zooplankton 20–200  $\mu\text{m}$  in size (Sieburth et al., 1978) and are largely composed of heterotrophic flagellates, ciliates, dinoflagellates, and sarcodines (Gifford and Caron, 2000). Microzooplankton are critical components of copepod diets, enhancing copepod survival and growth and providing essential nutrients (Berk et al., 1977; Robertson, 1983; Stoecker and Capuzzo, 1990). Microzooplankton may also allow copepods to use bacteria and detritus as carbon sources – food sources that alone are inadequate or inaccessible to copepods directly (Tang and Taal, 2005). This phenomenon is known as 'trophic upgrading' and may also apply to algal food sources that are nutritionally deficient (Klein Breteler et al., 1999).

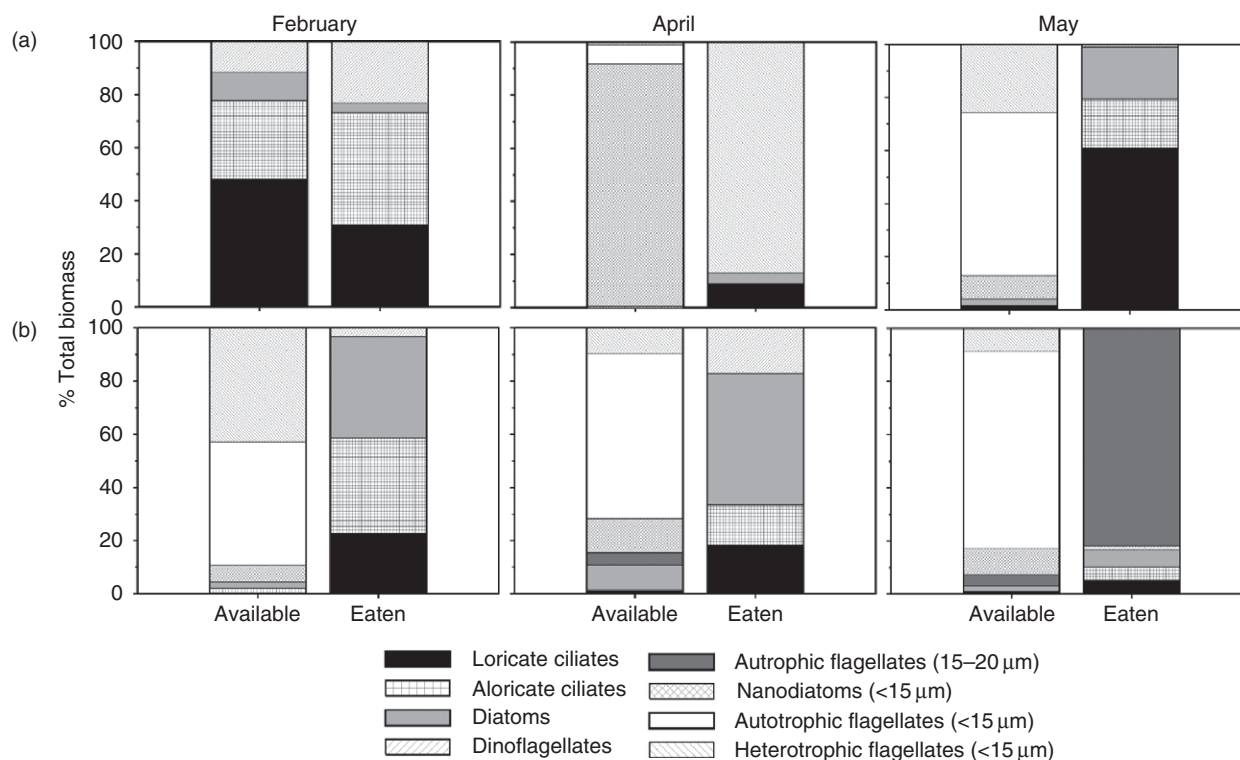
In most cases, copepods have higher clearance rates of ciliates compared to phytoplankton (Stoecker and Capuzzo, 1990). Kleppel et al. (1991) studied various coastal systems and found copepods fed preferentially on dinoflagellates and microzooplankton relative to diatoms. This preferential feeding resulted in a stronger relationship between ingestion rate and egg production (Figure 5). Copepods in the Bay of Villefranche, France were found to have a positive electivity index for ciliates and a negative index for diatoms and dinoflagellates (Wiadnyana and Rassoulzadegan, 1989). Based on

experimental work, Stoecker and Egloff (1987) concluded that microzooplankton are an important component of the diet of *A. tonsa* even when phytoplankton were in abundant supply. Fessenden and Cowles (1994) found that copepod clearance rates on ciliates were always in excess of those on phytoplankton, except during upwelling-induced diatom blooms off the Oregon coast. It is important to note that this general pattern may change based on the local microzooplankton and phytoplankton composition.

The ubiquitous *Acartia* spp. found in most temperate estuaries typically have a diverse diet (Paffenhof and Stearns, 1988; Rollwagen-Bollens and Penry, 2003; Diodato and Hoffmeyer, 2008), feed across a broad size range of particles (Richman et al., 1977; Tackx et al., 1995b), and are adapted to high food concentrations (Paffenhof and Stearns, 1988). One of the most thorough studies of diet composition of *Acartia* spp. was conducted in San Francisco Bay (Rollwagen-Bollens and Penry, 2003). The diet of *Acartia* spp. was examined in South Bay (a lagoon) and San Pablo Bay (a partially mixed estuary). Greater than 50% of *Acartia* spp. diet consisted of autotrophic biomass in South Bay (Rollwagen-Bollens and Penry, 2003). However, *Acartia* spp. were highly selective for ciliates and nanoflagellates and this selection was strongest under high food concentrations (Rollwagen-Bollens and Penry, 2003). Incubation studies revealed this selectivity clearly and the two locations differed based on prey composition and prey type consumed (Figure 6). Rollwagen-Bollens and Penry (2003)



**Figure 5** Egg production of the copepod *Acartia tonsa* as a function of dietary concentrations of diatoms, dinoflagellates, ciliates, and dinoflagellates and ciliates.  $r^2$  values are from linear regression. Reproduced from Kleppel, G.S., Holliday, D.V., Pieper, R.E., 1991. Trophic interactions between copepods and microplankton – a question about the role of diatoms. *Limnology and Oceanography* 36, 172–178. Copyright (1991) by the American Society of Limnology and Oceanography, Inc.



**Figure 6** Relative biomass of prey available versus eaten by *Acartia* spp. during 12-h incubations with unfiltered seawater from San Pablo Bay (a) and South Bay (b) in February, April, and May 2000. Available = % of total prey biomass available during incubation; eaten = % of total prey biomass consumed during incubation. Reproduced from Rollwagen-Bollens, G.C., Penry, D.L., 2003. Feeding dynamics of *Acartia* spp. copepods in a large, temperate estuary (San Francisco Bay, CA). *Marine Ecology Progress Series* 257, 139–158.

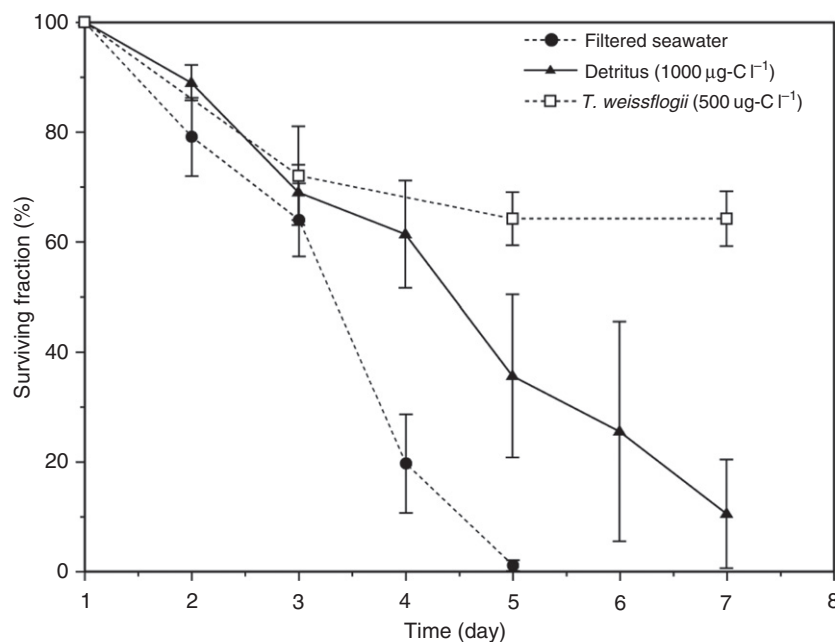
suggested that microzooplankton (ciliates and flagellates) are an important supplement to autotrophic biomass consumed and impact the overall amount of copepod production.

The landward reaches of many estuaries are high turbidity and low primary production zones. These areas are called estuarine turbidity maxima (ETM) or maximum turbidity zones (MTZs) and often occur at the limit of salt intrusion (Schubel, 1968; Uncles and Stephens, 1993). The ETM zone of estuaries are retention zones with high abundances of particles and zooplankton, notably the copepods *E. affinis* (Roman et al., 2001) or *Sinocalanus sinensis* (Islam et al., 2005). Many researchers have noted the paradox between high copepod biomass in these areas and low phytoplankton production (Heinle et al., 1974, 1977a; David et al., 2006). This has led to research into the possible use of detritus (suspended organic matter) as a food source for estuarine copepods (Heinle et al., 1977b). The amount of algal production in the upper Patuxent estuary, USA was calculated to be much less than the carbon requirements of the population of *E. affinis* present (Heinle and Flemer, 1975), and grazing rates of *E. affinis* on phytoplankton in the Gironde Estuary, France were not sufficient to cover its nutritional requirements (David et al., 2006).

The suspended organic matter in the upper reaches of estuaries is thought to derive from seagrasses, marsh plants, or terrestrial sources (Heinle et al., 1977a, 1977b). Once it becomes suspended, it may be trapped in the ETM region and colonized by microbes. Heinle et al. (1977b) found that copepods (*E. affinis* and *Scottolana canadensis*) fed detritus did not survive unless the detritus had been colonized by microbes.

They hypothesized that ciliates were also important in transferring detrital energy to copepods through microzooplankton grazing on colonized microbes. The use of detritus as a food source by *A. tonsa* has been investigated as well. Roman (1984) found that *A. tonsa* could not grow from egg to adult on a detrital diet alone (Figure 7); however, diatom suspensions that were supplemented with detritus increased *A. tonsa* growth rates. Diodato and Hoffmeyer (2008) found that *A. tonsa* did consume detritus in the Bahia Blanca Estuary, Argentina, but preferentially grazed on microzooplankton and phytoplankton. A comparison of *E. affinis* and *A. tonsa* grazing was investigated in the Westerschelde, The Netherlands, and it was found that *A. tonsa* fed selectively on phytoplankton or microzooplankton, whereas *E. affinis* exhibited only occasional selectivity and gut contents suggested that particulate suspended matter was ingested (Tackx et al., 1995a). Both species were able to select dominant phytoplankton cells and *E. affinis* did feed on phytoplankton in addition to particulate matter based on gut pigment analysis (Tackx et al., 1995b, 2003). It appears that the use of detritus as a food source is a specialized adaptation of *E. affinis* that allows it to reach high abundances in the upper reaches of estuaries.

Output of organic material from estuaries into surrounding waters has also been examined as a food source for copepods. Stable isotope tracking in the Mississippi River, USA plume found up to 90% of zooplankton dietary carbon was derived from *in situ* phytoplankton production (Schlacher et al., 2009). This was in contrast to the lower reaches of the estuary where terrestrial- and estuarine-derived carbon comprised 47% of



**Figure 7** Survival of *Acartia tonsa* on filtered seawater, detritus derived from *Thalassia testudinum* and *Thalassiosira weissflogii*. Error bars represent the standard error of the mean of three replicates. Reproduced from Roman, M.R., 1984. Utilization of detritus by the copepod, *Acartia tonsa*. *Limnology and Oceanography* 29, 949–959. Copyright (1984) by the American Society of Limnology and Oceanography, Inc.

the zooplankton diet (Schlacher et al., 2009). McKinnon and Klumpp (1998) found copepods (*Oithona aruensis*, *Parvocalanus crassirostris*, and *Bestiolina similis*) associated with mangroves in northeast Australia were food limited much of the time, despite high standing stocks of potential foods. The authors speculated that intake of detritus and cannibalism may supplement the diet of copepods in this location. Food limitation may be related to the refractory nature of mangrove-derived organic matter. Suspended matter uptake was tracked in the Gautami Godavari estuary, India, a mangrove ecosystem. Zooplankton were found to feed upon the suspended matter pool derived from mangroves; however, local phytoplankton production appeared to be the most important source of carbon (Bouillon et al., 2000). It appears that only within estuarine and coastal embayments is land-derived detritus used as a carbon source.

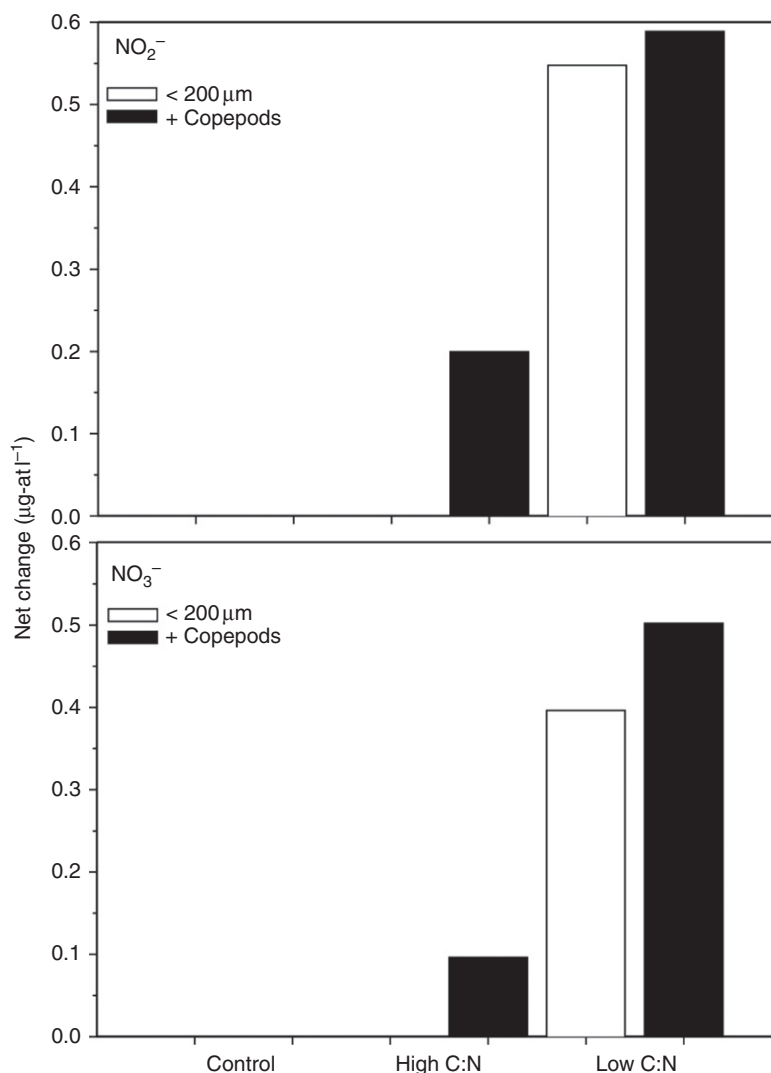
### 6.05.3.3 Nutrition: Macronutrients

Copepod feeding provides not only energy but also biochemicals used in catabolism and metabolism. Copepod nutrition in estuarine and coastal systems is often thought of as relating to individual nutrients, such as nitrogen (N) and phosphorus (P) (Kleppel, 1993). Investigations focus on copepod carbon:N:P ratios, where the limiting nutrient is that in least supply or that used least efficiently (Elser and Hassett, 1994). Also important to copepod nutrition are essential fatty acids (Anderson and Pond, 2000), as many species cannot synthesize particular fatty acids and must acquire them through diet (Muller-Navarra, 2008). Many of these investigations have been focused on freshwater and marine zooplankton and less so on neritic species (Anderson and Hessen, 1995). Copepod nutrition in estuaries is largely understudied compared to freshwater and

marine systems. Stoichiometric investigations into copepod nutrition may yield important insights into the structuring of trophic transfer to fish in these systems; however, studies must be careful to include other important diet components beyond C, N, and P (Tang and Dam, 1999).

Nitrogen limitation is thought to impact copepods by limiting growth and this has been shown off the coast of southern California, USA in studies of the copepod *A. tonsa* (Checkley, 1980). *Acartia tonsa* fed a mixture of algal prey (diatom *Thalassiosira weissflogii*; prymnesiophyte *Emiliana huxleyi*; and dinoflagellate *Aureodinium pigmentosum*) that were N-limited showed reduced growth and development compared to *A. tonsa* fed N-replete algal prey (Jones et al., 2002). Copepods from this experiment also actively selected dinoflagellates over N-depleted diatoms presumably due to the latter being less susceptible to N depletion during growth (Jones et al., 2002). A study in Buzzards Bay, Massachusetts, USA revealed that N assimilation by phytoplankton was lower than the estimated zooplankton daily ration (Roman, 1980). This result suggests that zooplankton in this system must supplement their diets with other sources of nitrogen, presumably from microzooplankton or detritus (Roman, 1980). However, this may not be the case in many estuarine systems where excess nitrogen loading occurs and P limitation may be more prevalent. Phosphorus limitation of copepods has not been rigorously assessed, as nitrogen is often the more limiting nutrient in marine and neritic environments (Elser et al., 2007).

Copepods may also alter the environment through the release of micronutrients. Extremely high grazing rates can impact the rate at which phytoplankton fix carbon – a phenomenon that appears to be related to the form of nutrient released by the grazers (ammonium versus particulate organic nitrogen)



**Figure 8** Net changes in nitrite ( $\text{NO}_2^-$ ) and nitrate ( $\text{NO}_3^-$ ) in experiments with filtered (200  $\mu\text{m}$ ) seawater and copepods ( $10\text{ l}^{-1}$ ) added after 24-h incubation. Control treatments had no nutrient addition; high C:N treatments had  $\text{C:N} \leq 10$ ; low C:N treatments had  $\text{C:N} \geq 4$ . Reproduced from Miller, C.A., Glibert, P.M., Berg, G.M., Mulholland, M.R., 1997. Effects of grazer and substrate amendments on nutrient and plankton dynamics in estuarine enclosures. *Aquatic Microbial Ecology* 12, 251–261.

(Collos et al., 2005). This was further explored in a mesocosm study that found the addition of copepods to mesocosms resulted in the loss of phytoplankton through direct grazing, but also a stimulation of phytoplankton production through copepod excretion of nitrogen (Miller et al., 1997). Copepod grazing increased nutrient regeneration and phytoplankton removal by microzooplankton (Figure 8) (Miller et al., 1997). A more recent study showed that the diet of copepods can impact the stoichiometry and form of micronutrient excretion (Saba et al., 2009). The copepod *A. tonsa* was fed either a ciliate *Oxyrrhis marina* or *Gyrodinium domibans* (carnivory), a diatom *T. weissflogii* (herbivory) or a mixture (omnivory). *Acartia tonsa* released the highest amount of ammonium ( $\text{NH}_4^+$ ) when exhibiting carnivory and the lowest amount when exhibiting omnivory. It was determined from these experiments that copepod diet plays an important role in determining the amount and composition of N and P available to phytoplankton and bacteria (Saba et al., 2009).

#### 6.05.3.4 Nutrition: Fatty Acids

A growing area of interest is the role of fatty acids, both as essential nutrients and food web markers (Dalsgaard et al., 2003). Fatty acids comprise the essential portion of triglycerides and wax esters, the majority of which are polyunsaturated fatty acids (PUFAs) such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) (Berge and Barnathan, 2005). PUFAs are almost exclusively synthesized by plants and must be acquired from phytoplankton by copepods (Brett and Muller-Navarra, 1997). Thus, they can serve as indicators of algal food quality. Limited investigations into the role of fatty acids in estuarine and coastal copepods have been conducted, but considerable work has been done in the polar regions (Mayzaud et al., 1998; Budge et al., 2008) and in freshwater lakes (Brett and Muller-Navarra, 1997; Kainz et al., 2004; Ventura, 2006).

As mentioned previously, 'trophic upgrading' may allow some copepods to acquire essential fatty acids from



phytoplankton indirectly, through the consumption of microzooplankton (Klein Breteler et al., 1999; Veloza et al., 2006). Trophic upgrading may vary considerably across predator–prey relationships. Klein Breteler et al. (2004) found no evidence of trophic upgrading when the copepods *Temora longicornis* or *Pseudocalanus elongatus* were fed the ciliate *Strombidium sulcatum* raised on the green alga *Dunaliella* spp. Also, lab and field differences in zooplankton fatty acid composition may exist where laboratory-reared zooplankton have different fatty acid signatures from field zooplankton that may be food limited (Muller-Navarra, 2006).

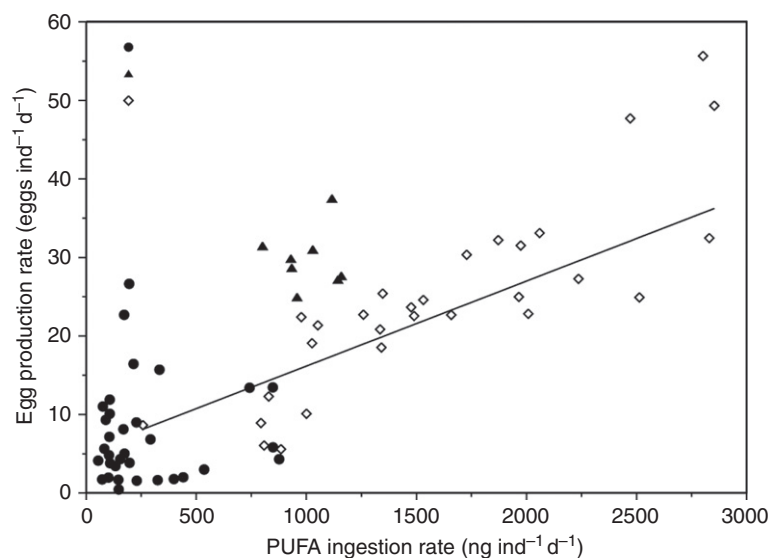
Several experiments have shown the importance of fatty acids to estuarine and coastal copepods. *Acartia tonsa* fed a variety of diets from heterotrophic ciliates (*S. sulcatum* and *Mesodinium pulex*) and a dinoflagellate (*Gymnodinium dominans*) to autotrophic cryptophyte (*Rhodomonas salina*), and a dinoflagellate (*Gymnodinium sanguineum*) showed clear differences in their fatty acid contents (Broglia et al., 2003). Egg production rates of *A. tonsa* were highly correlated to ingestion rate on *R. salina*, a species high in PUFA (Figure 9) (Broglia et al., 2003). A similar result was found in the copepod *T. longicornis* in the North Sea where food quality was directly linked to fatty acid composition of prey algae (Arendt et al., 2005).

Fatty acids have also been used as tracers of trophic interactions in copepods. Ederington et al. (1995) fed *A. tonsa* the bacterivorous ciliate (*Pleuronema* spp.) or the diatom (*T. weissflogii*). Ciliate-fed copepods had significant amounts of fatty acids diagnostic of bacteria, indicating that direct transfer of fatty acids from bacteria to ciliates is possible (Ederington et al., 1995). The ciliate diet may not provide copepods with adequate nutrition alone, but lipids unique to bacteria and ciliates are found in copepods and thus trophic transfer from bacteria to copepods does occur (Ederington et al., 1995). Several studies have traced the fatty acids of phytoplankton to copepods. Napolitano et al. (1997) found fatty acids from phytoplankton to be present in

*A. tonsa* in higher amounts after blooms in the Bahia Blanca Estuary, Argentina. Copepods in the Schelde Estuary, Belgium/The Netherlands were found to consume phytoplankton as 75% of their diet based on fatty acid profiles (Van den Meersche et al., 2009). This study also used stable isotopes, which indicated that 41% of copepod diets were from phytoplankton and copepods appeared to receive little carbon from bacteria (Van den Meersche et al., 2009). A study of the cycling of organic material in the Kariaga Estuary, South Africa revealed that mesozooplankton used both phytoplankton and detritus as food (Richoux and Froneman, 2008). Fatty acids can also track trophic transfer from phytoplankton to fish, through zooplankton. In the northwest Mediterranean, a fatty acid analysis revealed that small anchovy (*Engraulis encrasicolus*) fed on zooplankton and the dominant phytoplankton present, Prymnesiophytes (Rossi et al., 2006). Larger anchovy had fatty acid profiles similar to zooplankton – profiles that matched feeding on the less prevalent diatoms and dinoflagellates (Rossi et al., 2006).

#### 6.05.3.5 Feeding on Toxic or Unpalatable Food

A rise in the number of toxic or unpalatable phytoplankton blooms, termed harmful algal blooms (HABs), has been reported over the past few decades (Hallegraeff, 1993; Anderson et al., 2002; Sellner et al., 2003; Glibert et al., 2005a, 2005b). The main interest in these blooms is the effect on human health, particularly for the more toxic species (Anderson et al., 2002; Glibert et al., 2005a). These blooms tend to be more prevalent in coastal and estuarine systems that are heavily populated and subjected to high nutrient input (Anderson et al., 2002; Glibert et al., 2005b). Excess nutrients are often blamed for the increasing occurrence of HABs, but nutrients tell only one side of the story and grazing of these blooms must be considered (Smayda, 2008). Two main avenues of inquiry seem to dominate grazing studies: (1) What is the role of copepod grazers in formation of these blooms, for



**Figure 9** Egg production and polyunsaturated fatty acid (PUFA) ingestion rates of *Acartia tonsa* on diets of heterotrophs (*Mesodinium pulex*, *Strombidium sulcatum*, *Gymnodinium dominans*, *Rhodomonas salina*, and *Gymnodinium sanguineum*). Line is a linear regression fit for the *R. salina* data. Reproduced from Broglia, E., Jonasdottir, S.H., Calbet, A., Jakobsen, H.H., Saiz, E., 2003. Effect of heterotrophic versus autotrophic food on feeding and reproduction of the calanoid copepod *Acartia tonsa*: relationship with prey fatty acid composition. *Aquatic Microbial Ecology* 31, 267–278.



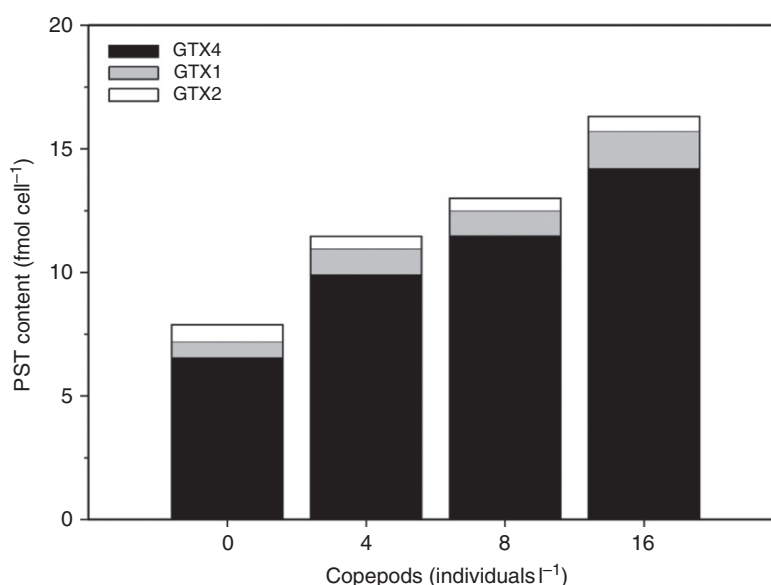
example, is it because species are toxic or simply nutritionally deficient? Alternatively, do these phytoplankton species produce physiological effects in copepods that reduce grazing and lead to bloom formation? (2) How do these blooms impact the transfer to higher trophic levels?

Feeding studies indicated that reduced grazing and fecundity often occur when copepods are fed toxic dinoflagellate species, though the results are far from unequivocal. Also unclear is whether algal species are directly toxic or nutritionally insufficient. Grazing by *A. tonsa* on the red tide dinoflagellate *Karenia brevis* showed that *A. tonsa* had lower ingestion rates and offspring production, but this was not due to toxicity but rather a chemical component lacking in *K. brevis* (Breier and Buskey, 2007). The same was true for *A. tonsa* feeding on the dinoflagellate *Prorocentrum minimum* (Colin and Dam, 2003) and *A. clausi* feeding on *Alexandrium lusitanicum* (Dutz, 1998). In both cases, the copepod species grazed the dinoflagellates at high rates, but egg production appeared to be reduced and this was attributed to nutritional deficiency and not toxicity (Dutz, 1998; Dam and Colin, 2005). A study that examined four species of copepods (*A. hudsonica*, *Centropages hamatus*, *Eurytemora herdmani*, and *Calanus finmarchicus*) feeding on several *Alexandrium* spp. of varying toxicity revealed that toxicity deterred feeding only when *Alexandrium* spp. reached high cell concentrations, and even under these conditions, grazing still occurred (Teegarden et al., 2008). Other studies have found dinoflagellate species that produce toxins that protect them from grazing. For example, Waggett et al. (2008) found that *Karlodinium veneficum* produced toxins that reduced ingestion rates of *A. tonsa*. Evidence has been found for the induction of toxicity in *Alexandrium minutum* by waterborne cues from the copepod *A. tonsa* (Selander et al., 2006). Grazing by *A. tonsa* induced *A. minutum* to produce up to 2.5 times more toxin than controls (Figure 10) and this resulted in more resistance to grazing (Selander et al., 2006). The mechanism for this toxicity may be antiproliferative. Ianora et al. (2004b)

fed *Alexandrium tamarense* to the copepod *Temora stylifera* and both egg production and hatching success were reduced, with egg viability dropping to 0 after 24 h of feeding. Extracts of *A. tamarense* blocked fertilization success of incubated sea urchin eggs; thus, these compounds are likely causing copepod eggs to go unfertilized (Ianora et al., 2004b).

Diatoms also appear to have an impact on copepod reproduction (Uye, 1996; Miralto et al., 1999; Ianora et al., 2003), though the subject is still under debate (Miralto et al., 1999; Irigoien et al., 2002; Ianora et al., 2004a). Diatom blooms frequently occur in temperate estuarine and coastal systems with high nutrients and often go ungrazed. This was assumed to be because copepods could not track these blooms due to low growth and lower temperatures; however, Ianora et al. (2004a) suggested it may be due to inhibition of copepod reproduction by diatom aldehyde production. This was based on arrested development and high mortality of *Calanus helgolandicus* fed a monoalgal diet of *Skeletonema costatum* (Ianora et al., 2004a). By contrast, Irigoien et al. (2002) found no correlation between copepod egg hatching success and diatom biomass or abundance in 12 globally distributed systems. Diatom impacts on coastal and estuarine species have been tested in laboratory and field situations. Exudates from three reportedly toxic diatoms (*T. weissflogii*, *T. rotula*, and *Phaeodactylum tricornutum*) had no effect on egg hatching in the copepod *A. tonsa* during lab incubations (Tang and Dam, 2001). A field test of the effect of diatoms on copepods was conducted in Dabob Bay, USA. Egg hatching success and naupliar survival of *Calanus pacificus* were reduced during *T. weissflogii* blooms (Pierson et al., 2005). However, these impacts appear to only last for short periods during blooms (Pierson et al., 2005), and the majority of *C. pacificus* losses in Dabob Bay was due to predation and advection (Pierson et al., 2007).

Aside from dinoflagellates and diatoms, other toxic algal species have been studied with respect to copepod feeding.



**Figure 10** Cell-specific content of gonyautotoxin (GTX; 1, 2 and 4 fmol<sup>-1</sup> cell) in *Alexandrium minutum* exposed to direct grazing from *A. tonsa*. Error bars represent the standard error of the mean of three replicates. Reproduced from Selander, E., Thor, P., Toth, G., Pavia, H., 2006. Copepods induce paralytic shellfish toxin production in marine dinoflagellates. *Proceedings of the Royal Society B – Biological Sciences* 273, 1673–1680.

The toxic prymnesiophyte *Prymnesium patelliferum* induced low egg production and high mortality in *E. affinis* (Koski et al., 1999) and reduced feeding and fecundity in *A. clausi* (Nejstgaard and Solberg, 1996). Cyanobacteria (*Nodularia spumigena* and *Aphanizomenon flos-aquae*) blooms in the Gulf of Finland were largely avoided by *A. tonsa* and *E. affinis* (Sellner et al., 1994). The cyanobacterium *N. spumigena* was found to have little impact on a zooplankton assemblage (*E. affinis*, *Synchaeta* spp., *A. bifilosa*, and the cladoceran *Bosmina longispina maritima*) in a mesocosm experiment (Schmidt et al., 2002). All species were able to reproduce successfully, though *A. bifilosa* showed some impaired recruitment (Schmidt et al., 2002).

A general consensus on the interaction between copepods and toxic or harmful algal species is difficult to reach (Turner and Tester, 1997). Copepods appear to respond differently to different strains of the same species, and major negative effects of toxic species only occur under high concentrations or when copepods are fed monocultures of toxic strains. The impact of toxic species on trophic transfer is also difficult to summarize. Large blooms of toxic or nutritionally deficient species will clearly limit trophic transfer; however, these events are likely to be ephemeral in nature and may only be important for brief periods. Minor blooms may be avoided and given the large variety of food resources present in estuarine and coastal systems, the ability of copepods to endure blooms of short duration is likely increased. Also, it is likely that many toxic species may bloom when microzooplankton populations are directly impacted by copepod grazing, creating so called 'windows of opportunity' (Stoecker et al., 2008). Clearly, if the trend toward more frequent blooms of HAB species continues, this area of research will be a focus for copepod ecologists.

### 6.05.3.6 Cannibalism

Marine copepods have been reported to be cannibalistic, particularly in the genus *Calanus* (Kang and Poulet, 2000; Ohman et al., 2002; Bonnet et al., 2004). *Calanus* spp. cannibalizes nauplii, juveniles, and eggs (Kang and Poulet, 2000; Basedow and Tande, 2006; Neuheimer et al., 2009). Cannibalism appears to become important under high densities and in the absence of predators (Uye and Liang, 1998). The degree of cannibalism present in copepod populations is of importance in that it may cause an underestimation of the amount of copepod production reaching higher trophic levels (Shirobokova and Pechurkin, 2003; Mitra, 2009). Data on the relative importance of cannibalism in most population studies remain scarce.

Several investigations into the occurrence of cannibalism have been conducted in estuarine and coastal systems. Liang and Uye (1996) reported cannibalism of eggs by the copepod *Acartia omorii* in Fukuyama Harbor, Japan. Cannibalism in this location appeared to be driven by high abundance, biomass, and production combined with the absence of predation (Uye and Liang, 1998). A study on the effect of overcrowding on *Centropages typicus* discovered that increasing densities caused cannibalism of eggs (Miralto et al., 1996). Copepods from a mangrove system in northeastern Australia are often faced with food limitation despite high food

concentrations. McKinnon and Klumpp (1998) suggested that cannibalism would be important in copepod diets under these food conditions. An ingestion rate of  $1.4\text{--}7.1$  nauplii female<sup>-1</sup> d<sup>-1</sup> was calculated for *A. lilljeborgi* in Cananeia Lagoon, Brazil (Ara, 2001). It is difficult to place this rate into context given the relative scarcity of data on cannibalism. Cannibalism is likely important to copepod populations in estuarine and coastal systems at times given locally high abundances; however, high food concentrations in most locations might offer an alternative to cannibalism. Thus, more studies are needed to determine the exact role of cannibalism.

### 6.05.3.7 Impact of Diet on Copepod Growth and Reproduction

The impact of diets on growth and reproduction has long been a focus of copepod research. Much of this research arises with the question of whether or not food is limiting in nature. It has long been postulated that temperature is the primary factor determining growth rates of calanoid copepods (McLaren, 1978; Huntley and Lopez, 1992). Temperature alone can explain up to 90% of variance in growth rates and these rates are independent of body size (Huntley and Lopez, 1992). Despite the fact that many laboratory studies appear to show food limitation, this result suggests that food limitation is not likely occurring in nature (Huntley and Boyd, 1984). Huntley and Boyd (1984) further concluded that food limitation would be less likely in coastal systems due to enhanced primary production found in these areas. Others contradict the view presented by Huntley and Lopez (1992). Most growth rates of copepods are below the theoretical maximum predicted by temperature alone; thus, there are few occasions where temperature-dependent growth is realized (Kleppel et al., 1996). Food limitation occurs in the environment at times (Kleppel et al., 1996) and likely limits copepod growth, particularly as temperature increases (Hirst and Bunker, 2003). This was corroborated by measurements made of 17 species of copepods off Kingston Harbor, Jamaica. Egg production was found to be frequently limited by food resources in a size-dependent manner for these species (Hopcroft and Roff, 1998). Thus, egg production rates (see below) may underestimate somatic growth rates in tropical systems (Hopcroft and Roff, 1998).

Egg production rate (EPR) is often used as an indicator of somatic growth as adult females do not increase appreciably in size and apportion much of their resources to egg production (Sekiguchi et al., 1980; McLaren and Leonard, 1995). Egg production rates (Table 5) appear to be closely linked to food resources, as will be discussed below and thus serve as another important proxy for food limitation. Also, many characteristics of organisms vary with body size, including growth rates (Brown et al., 2004). The role of body size cannot be discounted when examining food limitation in copepods as it can be a powerful predictor of production and biomass relationships (Banse and Mosher, 1980; Kerr and Dickie, 2001). For example, EPR is most closely related to body size for adult, broadcast spawners (e.g., *Acartia* spp.), and not temperature as compared to sac spawners (e.g., *E. affinis*), which follow temperature more closely (Hirst and Lampitt, 1998). The remainder of this section explores the relationships between food quantity and quality and copepod growth and reproduction. The relevant question is

**Table 5** Egg production rates of estuarine and coastal species

| Species                     | Location           | EPR (eggs female <sup>-1</sup> d <sup>-1</sup> )         | Reference                      |
|-----------------------------|--------------------|--|--------------------------------|
| <i>Acartia tonsa</i>        | Narragansett Bay   | 25.3–45.9  | Durbin et al. (1983)           |
| <i>Tortanus discaudatus</i> | Narragansett Bay   | 4.3–51.5   | Lawrence and Sastry (1985)     |
| <i>A. tonsa</i>             | Long Island Sound  | 8.7–56.6   | Bellantoni and Peterson (1987) |
| <i>A. tonsa</i>             | Terrebonne Bay     | 1.0 <sup>a</sup> –50.7 <sup>b</sup>                      | White and Dagg (1989)          |
| <i>Centropages typicus</i>  | Gulf of Naples     | <20 to >100  | Ianora and Buttino (1990)      |
| <i>Acartia clausi</i>       | Gulf of Naples     | <5 to 25   | Ianora and Buttino (1990)      |
| <i>C. typicus</i>           | Skaggerak          | 91   | Peterson et al. (1991)         |
| <i>Temora longicornis</i>   | Skaggerak          | 6  | Peterson et al. (1991)         |
| <i>Acartia longiremis</i>   | Skaggerak          | 6  | Peterson et al. (1991)         |
| <i>Acartia hudsonica</i>    | Narragansett Bay   | 2.1 <sup>a</sup> –11.4 <sup>b</sup>                      | Durbin et al. (1992)           |
| <i>A. tonsa</i>             | Los Angeles Harbor | 0.06–0.24 µg-C µg <sup>-1</sup> female C d <sup>-1</sup> | Kleppel (1992)                 |
| <i>A. tonsa</i>             | Chesapeake Bay     | 0.2–0.7 µg-C µg female C d <sup>-1</sup>                 | White and Roman (1992a)        |
| <i>Eurytemora affinis</i>   | Lake Ohnuma, Japan | 2.1–5.3 <sup>a</sup>                                     | Ban (1994)                     |
| <i>E. affinis</i>           | Lake Ohnuma, Japan | 19–34 <sup>b</sup>                                       | Ban (1994)                     |
| <i>A. tonsa</i>             | Long Island Sound  | 5–53   | Dam et al. (1994)              |

<sup>a</sup> Starved.<sup>b</sup> Fed.

whether the growth and reproduction of copepods in estuarine and coastal waters is primarily determined by temperature and body size or whether food resources play an important role.

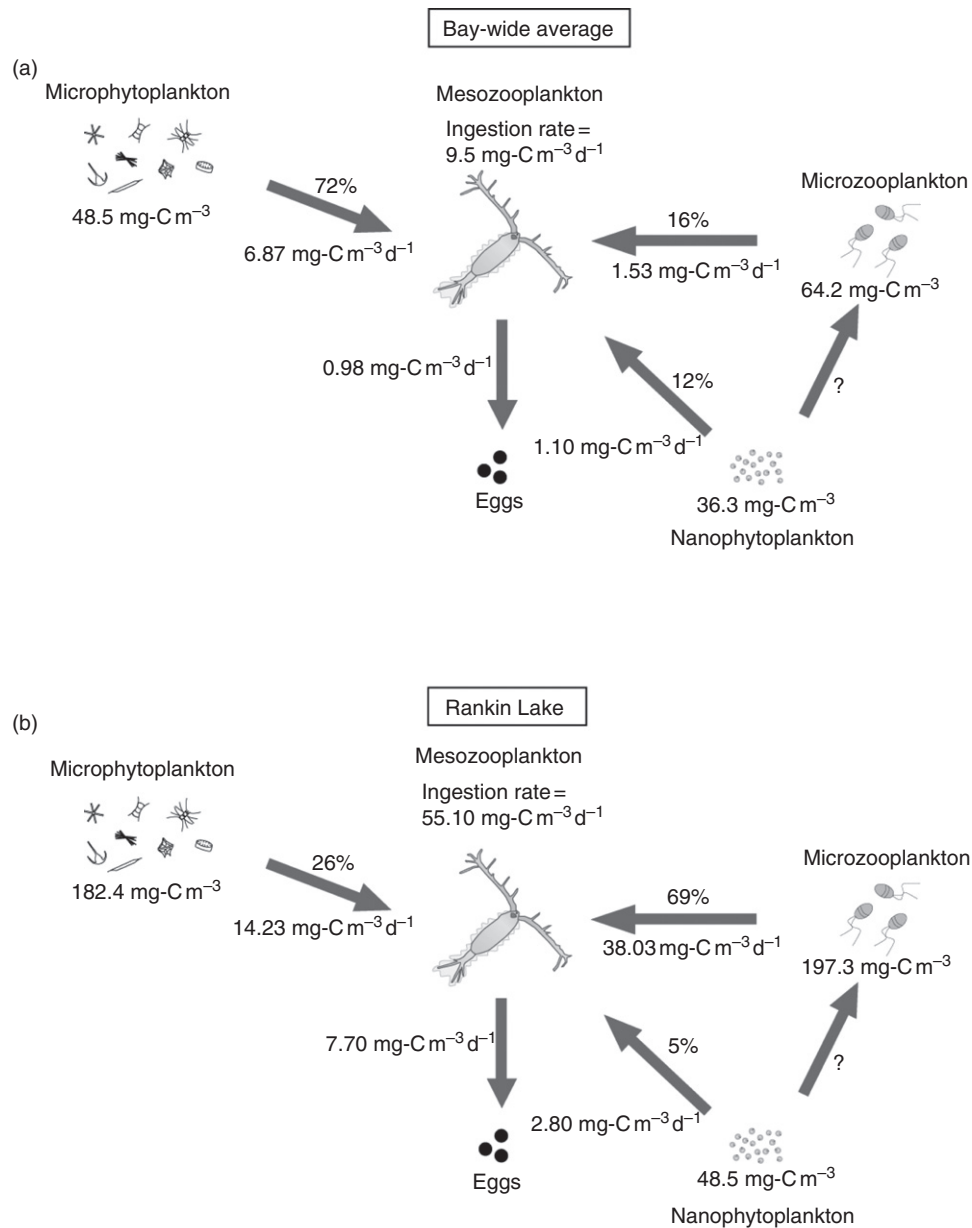
The vast majority of studies on copepod growth and reproduction in estuarine and coastal systems combines measurements of growth, egg production, and body size. Perhaps the best examples of these studies have been conducted on the genus *Acartia*. Egg production rates in *A. tonsa* from East Lagoon, USA were examined and temperature was positively correlated with EPR and salinity was negatively correlated with EPR (Ambler, 1985). Further investigation found that EPR was also correlated to food quantity and quality, with EPR correlated to higher C:N ratios in the diet and increasing chlorophyll (Chl) concentrations (Ambler, 1986). Temperature was the dominant factor over the course of the season, but over shorter timescales, food quality, quantity, and salinity may influence *A. tonsa* as much as temperature (Ambler, 1986). In Long Island Sound, New York, USA, the size of phytoplankton grazed (>10 µm fraction) appeared to be most related to EPR (Bellantoni and Peterson, 1987; Dam et al., 1994). EPR was lowest (8.7 eggs female<sup>-1</sup> d<sup>-1</sup>) when 0.5 µg l<sup>-1</sup> of Chl was in this fraction and highest (56.6 eggs female<sup>-1</sup> d<sup>-1</sup>) when 5.5 µg l<sup>-1</sup> of Chl was in this fraction (Bellantoni and Peterson, 1987). Additionally, maximum EPR was observed when as low as 0.85 µg l<sup>-1</sup> of Chl was found in the >10 µm fraction (Bellantoni and Peterson, 1987). EPR rates of *A. tonsa* may be decoupled from food availability. In the Rio de la Plata, Argentina, food availability was moderate to high, but quality was low (as measured by Chl *a*:phaeopigment ratios <1) resulting in low EPR rates (1.7–7.5 eggs female<sup>-1</sup> d<sup>-1</sup>) (Calliari et al., 2004). EPR rates for *A. tonsa* off Southern California, USA were more dependent upon temperature than food supply and egg production was related to food quality and not quantity (Kleppel, 1992).

EPR of *A. tonsa* was found to correlate with temperature, microzooplankton biomass, and C:N ratio of suspended particulate matter and not phytoplankton biomass, ingestion or production in Chesapeake Bay, USA (White and Roman, 1992a). Furthermore, the amount of phytoplankton C was only able to support *A. tonsa* growth 50% of the time, suggesting that diet was related to growth and EPR (White and Roman,

1992a). A comprehensive examination of the role of diet in egg production of *A. tonsa* has been conducted in Florida Bay, USA. *Acartia tonsa* diet was found to consist of microzooplankton and dinoflagellates and only 1–6% of primary production was removed from the water column (Kleppel et al., 1998). The result was low EPR (5.8 eggs female<sup>-1</sup> d<sup>-1</sup>). Further investigation into diets of *A. tonsa* at this location revealed that EPR was closely related to seston protein content and the transfer of lipids from the diet to eggs increased exponentially with decreasing seston lipid content (Kleppel and Hazzard, 2000). This, combined with an egg production efficiency of only 10% (egg production C/ingested C), suggests that low EPR rates are a function of both food limitation (in some areas) and food quality (in others) (Kleppel and Hazzard, 2000). Egg production was found to vary directly in relation to the concentration of 18:3ω-3 fatty acid, the only ω-3 fatty acid found in the eggs (Hazzard and Kleppel, 2003). A comparison of two locations in this area is shown in Figure 11.

Other copepods in *Acartia* genus have also been investigated. *Acartia lilljeborgi* from a lagoon near Sao Paulo, Brazil had EPR rates that increased linearly with Chl *a* concentrations. Food limitation of *A. hudsonica* was detected in Narragansett Bay, USA during early summer, but impacted body weight more than egg production (Durbin et al., 1992). In Long Island Sound, USA, *A. hudsonica* EPR was found to correlate strongly to specific fatty acids, leading Jonasdottir et al. (1995) to conclude that Chl and ciliates exert control on EPR through chemical composition. Neither temperature nor Chl *a* was able to predict *A. grani* EPR in Malaga Bay, Spain (Rodriguez et al., 1995). Instead, egg production of collected females was influenced by the amount and quality of food (Rodriguez et al., 1995). EPR was found to be most strongly influenced by phytoplankton availability as well as ciliates in *A. hongii* studied in Kyeonggi Bay, Korea (Youn and Choi, 2007).

Studies on *E. affinis* have centered on the role of suspended particulate matter versus phytoplankton effects on the EPR. EPR and body size of *E. affinis* vary with temperature and food concentration (Ban, 1994). A reduction in food availability resulted in lower amount of eggs per clutch in this population found in Lake



**Figure 11** Conceptual diagram of a diet of *Acartia tonsa* in (a) Florida Bay and (b) Rankin Lake. Values associated with each microzooplankton or phytoplankton category represent biomass in carbon (C). Percentages associated with each arrow represent the percent dietary C for *A. tonsa* feeding on a given food source. Values associated with each arrow represent the ingestion (or egg production) rate for a given food source. The '?' indicates that the amount of C transferred is uncertain. Note the differences between the Florida Bay (a) and Rankin Lake (b) values. Rankin Lake had experienced seagrass die-offs and nuisance algal blooms. Reproduced from Kleppel, G.S., Burkart, C.A., Houchin, L., Tomas, C., 1998. Egg production of the copepod *Acartia tonsa* in Florida Bay during summer. 1. The roles of food environment and diet. *Estuaries* 21, 328–339.

Ohnuma, Japan (Ban, 1994). A similar result was found for *E. herdmani* in the Cornwallis Estuary, UK, where summer eggs were 27% smaller than winter eggs and this was hypothesized to be a function of food shortage (Crawford and Daborn, 1986). Another egg-carrying copepod, *Euterpina acutifrons*, also reduces its egg number, possibly to increase egg size, under food-limiting conditions (Diaz et al., 2003). An analysis of *E. affinis* EPR in the Gironde, Westerschelde, and Elbe showed that EPR varied with temperature and was impacted by high suspending particulate matter (Gasparini et al., 1999). When suspended particulate matter reaches very high levels, the amount of phytoplankton

in the guts decreases and EPR also decreases (Gasparini et al., 1999). Some intake of phytoplankton appears necessary to maintain egg production in *E. affinis*.

### 6.05.3.8 Secondary Production

Research into copepod trophic relationships often culminates in estimates of secondary production, considered an important goal in zooplankton research (Runge and Roff, 2000). Secondary production estimates the copepod biomass created from food assimilated over some time period and depends on



biomass and growth rate (Huntley and Lopez, 1992). Knowledge of copepod production rates is critical for determining the amount of biomass available for higher trophic levels. It also determines, in part, the proportion of primary production that is transferred. Estimation of secondary production in copepods is not straightforward and data necessary to make estimates are often difficult to measure (Kimmerer, 1987; Poulet et al., 1995). This has to do with the underlying assumptions necessary to calculate secondary production, assumptions that are discussed at length elsewhere (Rigler and Downing, 1984; Poulet et al., 1995). As with growth rate, it can be assumed that egg production is a proxy for secondary production (Kiorboe and Johansen, 1986), an approach that has support (Berggreen et al., 1988). In this brief section, I present an overview of research into copepod secondary production in coastal and estuarine systems.

The most widely studied genus in estuarine systems, in terms of production, is *Acartia*. Production of *A. tonsa* in Narragansett Bay, USA was found to be strongly related to temperature (Durbin and Durbin, 1981), and this is often the case under food-saturating conditions in other species (Peterson et al., 1991). *Acartia tonsa* in this system had high production, measuring  $19\text{--}22.9\text{ mg-C m}^{-3}\text{ d}^{-1}$  (Durbin and Durbin, 1981), though subsequent investigation into egg production and body size found evidence of food limitation (Durbin et al., 1983). Rates of production for several congeners of *Acartia* (*A. grani*, *A. clausi*, and *A. discaudata* var. *mediterranea*) in Malaga Harbor, Spain was  $13.1\text{ mg-C m}^{-3}\text{ d}^{-1}$  (Guerrero and Rodriguez, 1997). A population of *A. omorii* in Ilkwang Bay, Korea had values that ranged from  $33.5$  to  $221\text{ mg-C m}^{-3}\text{ d}^{-1}$  and the authors of this study concluded that plankton in the diet were more important than temperature (Kang et al., 2007).

A comprehensive examination of the secondary production of *A. tranteri* was conducted in Westernport Bay, Australia (Kimmerer and McKinnon, 1987a). Secondary production of *A. tranteri* was  $130\text{ mg C m}^{-3}$ , and this was estimated to be only 1% of primary production. This suggested that *A. tranteri* was a minor component of the Bay energy budget compared to the benthos (Kimmerer and McKinnon, 1987a). Copepod production in the Solent, UK was found to be a small fraction of primary production as well. The area was dominated by *Acartia* spp. as well as *Temora longicornis*, *Centropages hamatus*, *Paracalanus parvus*, and *Pseudocalanus elongatus* (Hirst et al., 1999). Copepod annual production was  $32.2\text{ mg-C m}^{-3}\text{ yr}^{-1}$  and this was only 0.5% of the total primary production compared to ciliate annual production, which was 33% of annual primary production (Hirst et al., 1999). Annual production of copepods was between 21% and 177% of ciliate production, highlighting the important role ciliates played in transferring primary production to copepods (Hirst et al., 1999). The copepod community of the Skagerrak, Denmark had a combined production rate of  $3\text{--}8\text{ mg-C m}^{-3}\text{ d}^{-1}$  (Peterson et al., 1991). Community production in this area was thought to be food limited based on egg production, which was below maximum for several species (*Centropages typicus*, *Calanus finmarchicus*, *Paracalanus parvus*, *A. longiremis*, and *T. longicornis*) (Peterson et al., 1991).

Secondary production of copepods in the upper reaches of estuaries has also been researched. Trophic transfer in this region may be independent of phytoplankton primary production; thus, other food resources may influence copepod

production. This was indeed the case in the Westerschelde, The Netherlands. A comparison of secondary production rates of the copepods *A. tonsa* and *E. affinis* found that yearly production of both communities was comparable, with *A. tonsa* producing  $5\text{ g C m}^{-2}\text{ yr}^{-1}$  and *E. affinis* producing  $6\text{ g-C m}^{-2}\text{ yr}^{-1}$  (Escaravage and Soetaert, 1995). In the southern Kattegat, Denmark, it was concluded that *in situ* phytoplankton production provided adequate carbon for only short periods of the year and nutritional demands of the copepods must be met by other sources (Kiorboe and Nielsen, 1994). As in Westernport Bay, the copepods appeared to play a minor role in the carbon budget of the Westerschelde, as only 6% of all carbon consumed passed through the copepod food web (Escaravage and Soetaert, 1995). Peitsch (1995) concluded that *E. affinis* populations in the Elbe Estuary, Germany were food limited based on higher production rates in enclosures versus organisms collected *in situ*.

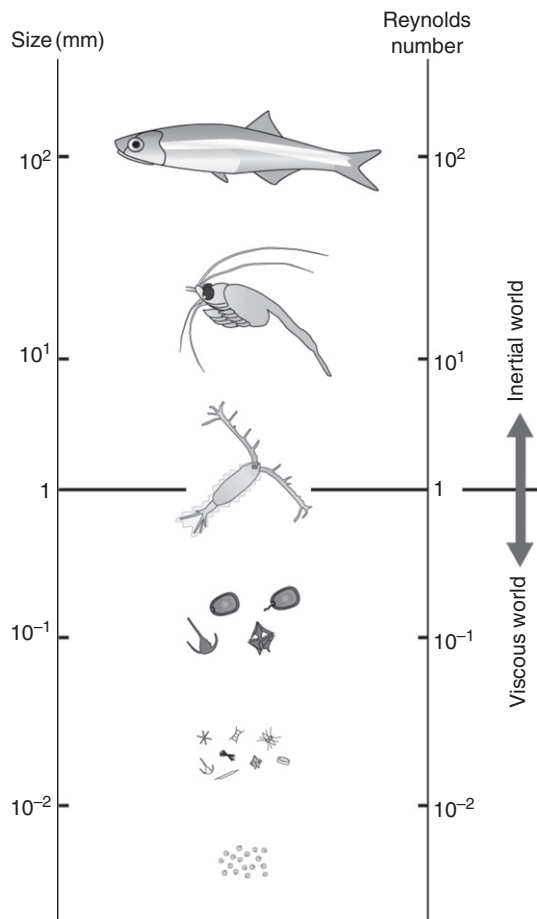
Based on limited available data, it appears that the secondary production of copepod biomass in coastal and estuarine systems is a mere fraction of primary production. This would be expected based on dietary studies that show the importance of microzooplankton as a food resource. The addition of a trophic level between phytoplankton and copepods would reduce the amount of material transfer to copepods. Assuming 10% loss per trophic level, the estimates of 1% by Kimmerer and McKinnon (1987a) and 0.5% by Hirst et al. (1999) appear to support an omnivorous copepod diet. During phytoplankton bloom conditions where copepods are relying on algae as a primary food source, productivity rates are likely to increase and a larger fraction of primary production will be transferred to copepods. The rest of the time, copepod communities in estuarine and coastal systems should see transfer rates from primary production around 1% or less.

## 6.05.4 Predation on Mesozooplankton

### 6.05.4.1 Introduction

Copepods form a major portion of the diet of a variety of organisms. Most papers that discuss copepods typically open with a general statement about the critical role that copepods play in food webs, citing their role in transfer of primary production to higher trophic levels. As discussed in the previous section, the classical food-web view has been significantly updated; however, copepods remain an important step in the transfer of primary production, though it may not be a direct transfer in many instances. An interesting note by Naganuma (1996) points out that copepods bridge the inertial and viscous worlds (Figure 12). This advantageous position allows copepods to occupy the top trophic position in the viscous world (Naganuma, 1996). In addition, if fish had to feed directly on the primary consumers of phytoplankton, such as ciliates and flagellates, they would be hampered by a size difference of 100 times. In the words of Naganuma (1996), "Eating a piece of bread is much easier than eating wheat grains one by one!"

Consumers impact copepod communities in a variety of ways. They can affect population dynamics by driving mortality rates, as predation is considered to be the primary source of mortality (Ohman, 1986) and the overall effect of predation is often dependent on the type of predator (Steele and



**Figure 12** Size and Reynolds number of multiple trophic levels. The viscous world (Reynolds number  $< 1$ ) and the inertial world (Reynolds number  $> 1$ ) are linked by copepods (Reynolds number  $\approx 1$ ). Reproduced from Naganuma, T., 1996. Calanoid copepods: linking lower-higher trophic levels by linking lower-higher Reynolds numbers. *Marine Ecology Progress Series* 136, 311–313.

Henderson, 1995). Copepod mortality rates are difficult to quantify and many models assume constant rates, though it is widely accepted that mortality rates vary to a large degree (Ohman and Wood, 1995). At certain times, mortality can be the most important factor driving population dynamics (Ohman and Wood, 1996). The difficulty in measuring copepod mortality often leads to this important population parameter being overlooked. Consumers also impact size distributions of copepod communities (Brooks and Dodson, 1965) by changing trophic interactions. Predators may also shift species composition by selectively feeding, thereby impacting community diversity. Finally, predators may drive trophic cascades where predation on zooplankton has indirect effects on lower trophic levels, a phenomenon well documented in freshwater lakes (McQueen et al., 1986, 1989). In this section, I discuss the most important predators of copepods in estuarine and coastal systems: zooplanktivorous fish and fish larvae, jellyfish (cnidarians and ctenophores), and other invertebrates. I will then present a brief discussion of the role of predators in shaping copepod communities.

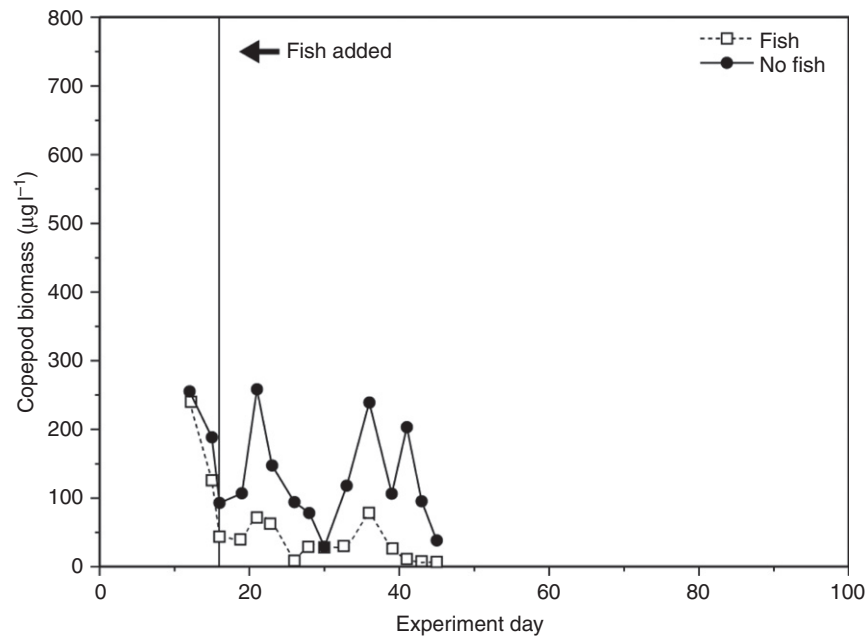
#### 6.05.4.2 Zooplanktivorous Fish and Fish Larvae

Zooplanktivorous fish are found in most of the extant orders of fish and include fish that spend their juvenile and adult lives as planktivores and species that spend only a part of their life as planktivores (Lazzaro, 1987). A complete review of planktivorous fish feeding strategies is beyond the scope of this chapter; instead focus here is on specific examples of copepod interactions with planktivorous fish in experiments and *in situ*. For more information on planktivorous fish feeding, see the review by Lazzaro (1987).

One of the most prominent groups of adult, planktivorous fishes in estuaries are Clupeids, most notably the Engraulidae (anchovies) (Lazzaro, 1987). Bay anchovies (*Anchoa mitchilli*) in experimental mesocosms had a clear top-down effect on copepods and mesocosms without fish had larger size copepods and higher biomass (Figure 13) (Mowitt et al., 2006). In field studies, adult *A. mitchilli* appeared to select zooplankton based on prey size, density, and type, preferring larvae of the fiddler crab (*Uca* spp.) in a tidal creek, North Inlet, USA (Johnson et al., 1990; Allen et al., 1995). Field studies of *A. mitchilli* in Chesapeake Bay, USA show that consumption rates can be high,  $5.29\text{--}12.81\text{ g dry wt } 100\text{ m}^{-3}\text{ d}^{-1}$ , indicating that this species can have a high impact on copepod populations (Wang and Houde, 1995). By contrast, a bioenergetics model for *A. mitchilli* production in Chesapeake Bay, USA found that average bay anchovy production only accounted for a small portion of daily zooplankton production; however, local depletions of zooplankton were possible when *A. mitchilli* consumption rates were high in summer (Luo and Brandt, 1993). Growth rate variation in *A. mitchilli* in Hudson River, USA was likely the result of patches of zooplankton prey and not temperature or salinity variations (Jordan et al., 2000). Post-spawning egg abundance of *A. mitchilli* was determined by pre-spawning copepod prey supply and temperature in the Manatee River, USA (Peebles, 2002). It can be concluded that bay anchovy populations may shape copepod community structure by feeding on larger-sized individuals and depleting copepod populations within patches.

The effect of planktivorous fish assemblages on copepod populations has also been examined. The presence of zooplanktivorous fish (*Retropinna semoni* and *Hypseleotris* spp.) in experimental billabongs (River Murray, Australia) appeared to reduce the number of larger-sized zooplankton, but had only a small influence on the overall zooplankton assemblage (Nielsen et al., 2000). A zooplanktivorous assemblage of reef fish was studied at the Poor Knights Islands, 20 km off the east coast of New Zealand. Zooplanktivorous fish in this location substantially reduced zooplankton populations in localized patches (Kingsford and Macdiarmid, 1988). On broader spatial and temporal scales, it was concluded that fish would not substantially impact zooplankton populations, but localized production of planktivorous fish would be affected (Kingsford and Macdiarmid, 1988). An assemblage of zooplanktivorous fish that included *A. mitchilli* did not significantly affect copepod population dynamics in nearshore areas of the northern Gulf of Mexico, USA, indicating that larval fish competition for food is unlikely to contribute to mortality (Dagg and Govoni, 1996). It appears from this limited sample of papers that zooplanktivores appear to have similar effects as bay anchovy: the ability to structure the size distribution of





**Figure 13** Copepod biomass in mesocosms (volume = 1 m<sup>3</sup>; diameter = 1.13 m; depth = 1.0 m) with no fish and fish added (4 fish m<sup>-3</sup>). Reproduced from Mowitt, W.P., Houde, E.D., Hinkle, D.C., Sanford, A., 2006. Growth of planktivorous bay anchovy *Anchoa mitchilli*, top-down control, and scale-dependence in estuarine mesocosms. *Marine Ecology Progress Series* 308, 255–269.

zooplankton and cause localized depletions of zooplankton, but an inability to affect overall zooplankton production on broader, system-wide scales.

Fish larvae and juvenile feeding on zooplankton has received considerable attention. This is because zooplankton are thought to affect recruitment by contributing to larval and juvenile fish survival during the 'critical period' when fish experience high mortality (Hjort, 1914). A substantial number of studies have investigated the interaction between zooplankton and larval fish in the sea in an attempt to corroborate Cushing's match-mismatch hypothesis (Cushing, 1974, 1975, 1990). Estuarine and coastal ecosystems have higher rates of fisheries production compared to open ocean systems – a fact attributed to higher rates of primary production (Ryther, 1969; Nixon, 1988). Of equal importance may be the role of estuarine and coastal systems as nurseries for larval fish (Beck et al., 2001, 2003). While the nursery concept as outlined by Beck et al. (Beck et al., 2001, 2003) primarily refers to habitat areas, such as seagrass beds and wetlands, other areas of estuarine and coastal systems may be just as important when their populations of zooplankton are considered.

Cushing (1983) suggested that fish larval density of 1 m<sup>-3</sup> was too dilute to impact a zooplankton density of 100–1000 m<sup>-3</sup>. Cushing (1983) concluded that larval haddock, plaice, and other oceanic fish larvae were too dilute during their early stages, but this reverses as they reach larger sizes. Estuaries and coastal systems have higher zooplankton abundances than the oceanic systems referred to by Cushing (1983); therefore, the question may be revisited in these systems. Do fish larvae and juveniles have adequate zooplankton prey in estuarine/coastal systems and do fish larvae and juveniles affect zooplankton populations *in situ*? These questions have been studied extensively in coastal areas. According to a bioenergetics model, larval and juvenile sprat (*Sprattus sprattus*)

and herring (*Clupea harengus*) in the Baltic Sea accounted for 50% and 45% of total zooplankton consumption, respectively (Arrhenius and Hansson, 1993). Larval Pacific herring (*Clupea harengus pallasii*) and Pacific whiting (*Merluccius productus*) in Dabob Bay, USA were found to significantly impact prey populations in a species-specific manner (Bollens, 1988). Slower growing populations of *Pseudocalanus* spp. were always impacted by fish predation, whereas the more rapidly growing populations of *Calanus pacificus* were not impacted (Bollens, 1988). At a front separating shallow, coastal waters from deeper, offshore water in the North Sea, neritic copepods (*Acartia* spp.) were preyed upon by whiting (*Merlangius merlangus*) (Nielsen and Munk, 1998). The impact of predation by the whiting was low (<10% of copepod production d<sup>-1</sup>), indicating that copepod biomass would increase in coastal waters landward of the front (Nielsen and Munk, 1998). Cod larvae (*Gadus morhua*) off the western Irish Sea were found to feed almost exclusively on copepods and observed abundances were sufficient to meet energetic demands of cod larvae (Thompson and Harrop, 1991). When additional larval fish species are considered, competition for larval prey may intensify and larger cod larvae require higher densities of copepodites (Thompson and Harrop, 1991). Pepin and Penney (2000) concluded that larval fish are unlikely to exert significant predation pressure on zooplankton (<0.1% of zooplankton prey consumed d<sup>-1</sup>). Thus, density-dependent growth was unlikely in Conception Bay, Canada larval fish populations (Pepin and Penney, 2000).

Estuaries provide important nursery areas for many species of fish, particularly anadromous species whose larvae are reared within the estuary and shelf-spawning fish that return to the estuary as juveniles. The larvae of these species typically feed on copepods and other zooplankton prior to switching to more varied adult diets. Estuaries are thought to be good habitat for fish larvae for several reasons: (1) high abundances of

zooplankton; (2) abundant habitat for predator avoidance, such as seagrass beds (Beck et al., 2001) and/or high turbidity areas that reduce susceptibility to visual predation; and (3) multiple hydrographic features that increase encounter rates with zooplankton prey, such as tidal fronts, turbidity maxima, and wind-driven fronts (Rothschild and Osborn, 1988; Mackenzie and Leggett, 1991). Estuaries often have prolonged periods of high zooplankton production that confer a higher probability of larval survival and recruitment to the adult population, that is, the 'match-mismatch' hypothesis of Cushing (Cushing, 1974, 1975, 1990). Thus, fish that spawn in these areas have experienced differential survival and have evolved to return to estuarine spawning areas each year. Others have indicated that the more variable environments of some estuaries lead to less predictable peaks in zooplankton production, suggesting that match-mismatch may be less relevant in some estuarine environments (Newton, 1996).

Larval anadromous fish have been investigated for their importance to commercial harvests and sport fishing. Two major anadromous species of interest are striped bass (*Morone saxatilis*) and white perch (*M. americana*). The year class success of striped bass is often determined by the success of first feeding larvae in the San Francisco Estuary, USA (Meng and Orsi, 1991). In Chesapeake Bay, the larval diets of each species are dominated by the copepod *E. affinis* and the cladoceran *Bosmina longirostris* (Setzler-Hamilton, 1991; Setzler-Hamilton and Hall, 1991). High abundances of *E. affinis* are associated with increased freshwater input and expansion of the ETM zone (Kimmel and Roman, 2004). North and Houde (2003) found that a significant amount of variability in feeding larvae of striped bass and white perch were explained by zooplankton abundance. Furthermore, high abundances of zooplankton and fish larvae were concentrated by the ETM, resulting in significant trophic transfer (Shoji et al., 2005). Freshwater input into the estuary can serve as a proxy for the strength and persistence of the ETM region with more freshwater input causing expansion of the ETM region (Schubel, 1968). Freshwater input explained recruitment variability better than spawning stock biomass models (North and Houde, 2003), suggesting that larval survival was more important to these populations than spawning stock biomass. In the Hudson River, USA, the occurrence of larval striped bass and white perch with high zooplankton 'blooms' was investigated. Based on an energetic analysis, it was concluded that fish larval success was strongly connected to the zooplankton 'bloom' that occurred as temperatures rose in the spring (Limburg et al., 1997).

Other anadromous fish species are also linked to copepod populations in the upper reaches of estuaries. In the St. Lawrence River ETM, the primary food for larval Atlantic tomcod (*Microgadus tomcod*) and rainbow smelt (*Osmerus mordax*) was the copepod *E. affinis* (Winkler et al., 2003). However, these species were not suspected to have an impact on *E. affinis* standing stocks as most of the predation was by two species of mysids (Winkler et al., 2003). Larval Japanese temperate bass (*Lateolabrax japonicus*) in the Chikugo River, Japan fed on copepods *Cyclops vicinus* and *Sinocalanus sinensis* (Hibino et al., 1999). Japanese temperate bass appeared to migrate to areas of high *S. sinensis* abundance, suggesting that this copepod was critical to larval survival in this system (Hibino et al., 1999). Freshwater flow also impacted this migration by increasing

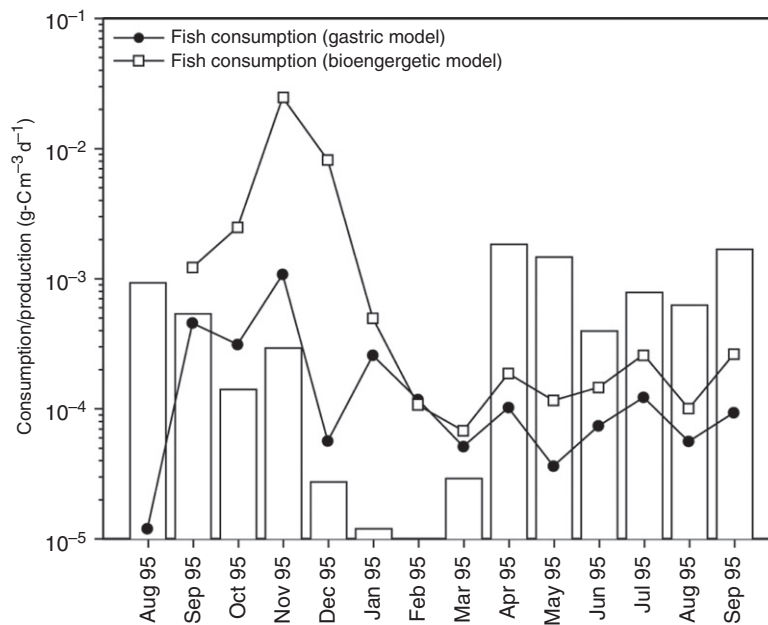
larval seaward dispersion and decreasing zooplankton abundance (Shoji et al., 2006).

Larval stages of Atlantic menhaden (*Brevoortia tyrannus*) feed on zooplankton prior to switching to phytoplankton diets as adults (Stoecker and Govoni, 1984). Atlantic menhaden guts contained up to 99–100% of copepodites and adult copepods in the Newport River Estuary, USA (Kjelson et al., 1975). Atlantic menhaden produced a negative instantaneous growth rate in zooplankton in Narragansett Bay, USA, primarily due to the fact that Atlantic menhaden are schooling fish and can deplete local patches of zooplankton (Durbin and Durbin, 1998). Juvenile herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) consume estuarine copepods during their period of residency in the Schelde Estuary, Belgium (Maes et al., 2005). The effect of these predators on copepod populations varied seasonally due to fish migration in and out of the system. This effect suggested that larvae can exert top-down control on the local copepod population (Figure 14) (Maes et al., 2005). Larval Atlantic mackerel (*Scomber scombrus*) in Long Island Sound, USA fed on several species of copepods (*A. hudsonica*, *T. longicornis*, and *Pseudocalanus* spp.) as they increased in size (Peterson and Ausubel, 1984). Atlantic mackerel fed selectively on *T. longicornis* and *Pseudocalanus* nauplii and were able to consume large numbers, but were not sufficiently abundant to impact copepod population dynamics in this system (Peterson and Ausubel, 1984).

It is clear that copepods play an important role in larval fish diets. However, this convention may not be applicable for all fish species. Many fish diet studies are based on gut content analysis, a technique that can overlook certain types of prey that do not preserve well in guts. An alternative technique that is increasingly used to analyze fish guts is stable isotope analysis. A stable isotope study on coastal larval fish shed further light on the role of zooplankton in the diets of these fish. Pepin and Dower (2007) studied the diets of six species of larval fish: capelin (*Mallotus villosus*), cunner (*Tautoglabrus adspersus*), radiated shanny (*Ulvaria subbifurcata*), witch flounder (*Glyptocephalus cynoglossus*), American plaice (*Hippoglossoides platessoides*), and yellowtail flounder (*Limanda ferruginea*) in Conception Bay, Canada. Four species (American plaice, yellowtail flounder, cunner, and radiated shanny) fed primarily on copepods, as expected; however, larval witch flounder and capelin fed on phytoplankton and heterotrophic protists, a finding not supported by stomach contents, which consisted of copepods (Pepin and Dower, 2007). This study highlights the fact that copepods and other zooplankton may not always be the primary food source of larval fish.

#### 6.05.4.3 Gelatinous Zooplankton

Gelatinous zooplankton (pelagic cnidarian medusae and ctenophores; also called jellyfish) are crucial members of food webs (Mills, 1995; Purcell and Arai, 2001; Purcell, 2009; Richardson et al., 2009). In estuarine and coastal systems, they represent an intermediate to top trophic level that preys upon zooplankton (Baird and Ulanowicz, 1989; Purcell, 1992; Purcell et al., 1994), other jellyfish (Purcell and Cowan, 1995; Purcell, 2005), and fish eggs and larvae (Purcell and Arai, 2001). Jellyfish can be voracious predators, particularly on zooplankton. Jellyfish have often been labeled a 'trophic dead end' given their unappealing nature to humans (Richardson et al., 2009) and for diverting carbon



**Figure 14** Copepod production as a function of fish consumption. Fish consumption was estimated using a gastric evacuation model and a bioenergetic model. Reproduced from Maes, J., Tackx, M., Soetaert, K., 2005. The predation impact of juvenile herring *Clupea harengus* and sprat *Sprattus sprattus* on estuarine zooplankton. *Hydrobiologia* 540, 225–235.

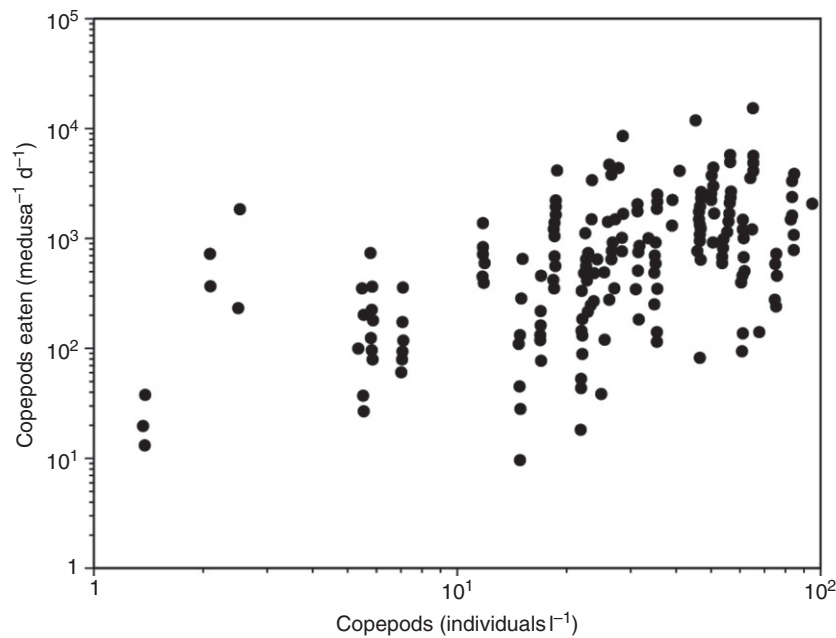
away from fish. Despite their acknowledged importance, jellyfish are understudied in aquatic systems worldwide and, in particular, in estuaries and other coastal systems.

A variety of pelagic cnidarian species feed on zooplankton in estuarine and coastal systems. The two species that have received the most attention are the scyphozoans *Aurelia aurita* and *Chrysaora quinquecirrha*, though other species have been investigated, such as *Pseudorhiza haekeli* (Fancett and Jenkins, 1988; Purcell and Sturdevant, 2001; Barz and Hirche, 2005), *Cyanea capillata* (Fancett and Jenkins, 1988; Purcell and Sturdevant, 2001; Barz and Hirche, 2005), and *Phyllorhiza punctata* (Garcia and Durbin, 1993). In the western Baltic Sea (Kiel Bight) Germany, Behrends and Schneider (1995) reported that *A. aurita* medusae controls overall zooplankton abundance. *Aurelia aurita* appeared to feed selectively, preferring *Pseudocalanus* spp., *Paracalanus* spp., and *Oithona similis* to *Centropages hamatus* and *A. tonsa* (Behrends and Schneider, 1995). Mass occurrences of *A. aurita* medusae in this system can result in zooplankton depletions and therefore food limitation (Schneider and Behrends, 1998). A pair of other studies suggests that the impact of *A. aurita* on copepod communities is negligible. When mean abundance of *A. aurita* was highest in the central Baltic Sea (Bornholm Basin), only 0.1% of copepod standing stock per day was consumed by this species (Barz and Hirche, 2005). A similar result was reported in Limfjorden, Denmark where *A. aurita* exhibited low clearance rates on copepodites and nauplii (Hansson et al., 2005). This may be due to the depletion of larger prey as *A. aurita* feeds on copepods in a size selective manner, ingesting larger copepodites and adults at higher rates (Suchman and Sullivan, 2000).

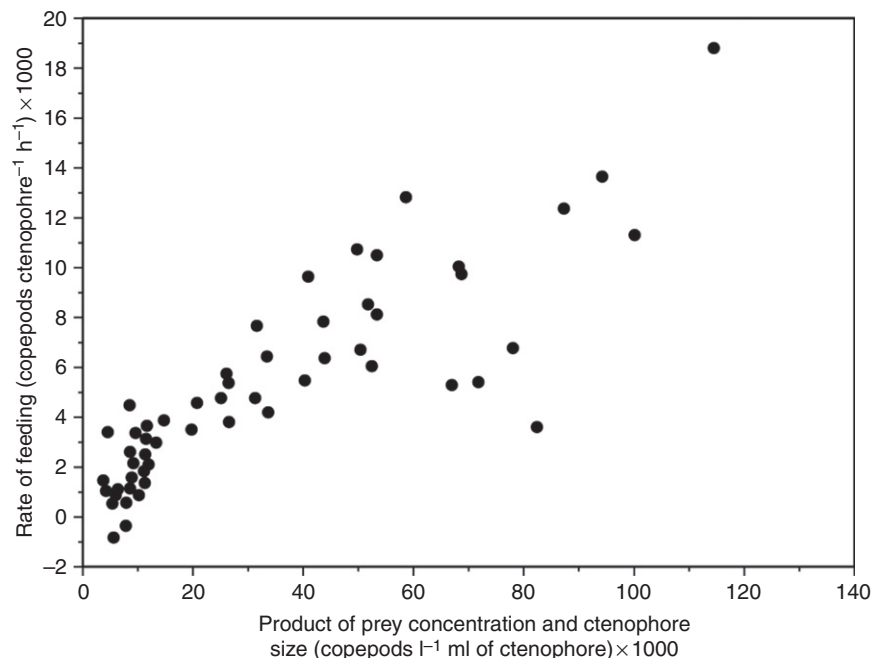
The sea nettle, *Chrysaora quinquecirrha*, is a common scyphozoan in temperate estuarine and neritic systems. The guts of *C. quinquecirrha* consisted of 55–71% *A. tonsa* in Chesapeake Bay, USA during summer (Purcell, 1992) and *C. quinquecirrha*

ingestion rates on copepods increased linearly with copepod abundance (Figure 15). *Chrysaora quinquecirrha* feeds selectively on larger sized *A. tonsa*, suggesting that small size is an effective refuge from sea nettle predation (Suchman and Sullivan, 1998). Purcell (1992) suggested that *C. quinquecirrha* may cause localized declines of copepods in the summer; however, sea nettles play a more important role in controlling another zooplankton predator, the ctenophore *Mnemiopsis leidyi*. A study in the lower Chesapeake Bay, USA showed that zooplankton populations declined significantly during the first appearance of *M. leidyi*, but rebounded as *C. quinquecirrha* populations increased (Feigenbaum and Kelly, 1984).

The most influential species affecting zooplankton populations within estuaries is the ctenophore *M. leidyi*. *Mnemiopsis leidyi* can reach high biomass in warm, temperate waters with high zooplankton abundance, typically *A. tonsa* (Kremer, 1994). This ctenophore feeds on phytoplankton and micro-zooplankton as larvae and zooplankton as juveniles and adults (Purcell et al., 2001; Sullivan and Gifford, 2004). Feeding rates of *M. leidyi* do not appear to decrease as copepod abundance increases (Figure 16) (Bishop, 1967). High feeding rates of *M. leidyi* that were independent of zooplankton abundance were also reported in Narragansett Bay, USA (Kremer, 1979). This corresponds with a drop in assimilation efficiency at high food abundance (Reeve et al., 1989). A later study in Narragansett Bay found *M. leidyi* abundances to be 20–100 ctenophores  $m^{-3}$  that resulted in 20% of zooplankton standing stock being removed per day (Deason, 1982). Mountford (1980) found similar abundances (up to 58  $m^{-3}$ ) in Barnegat Bay, USA and an almost complete removal of the copepod population when *M. leidyi* abundances were high. *Mnemiopsis leidyi* is perhaps best known for its dramatic effects as an introduced species, particularly in the Black Sea (Purcell et al., 2001). After *M. leidyi* was introduced to the Black Sea in the



**Figure 15** Feeding rates of *Chrysaora quinquecirrha* as a function of copepod abundance in Chesapeake Bay, USA. Reproduced from Purcell, J.E., 1992. Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay, USA. Marine Ecology Progress Series 87, 65–76.



**Figure 16** Feeding rates of *Mnemiopsis leidyi* as a function of the product of copepod abundance and *M. leidyi* biovolume. Reproduced from Bishop, J.W., 1967. Feeding rates of the ctenophore, *Mnemiopsis leidyi*. Chesapeake Science 8, 259–264.

early 1980s, zooplankton populations decreased substantially as *M. leidyi* populations exploded (Shushkina and Vinogradov, 1991; Shiganova, 1998). *Mnemiopsis leidyi* has since invaded the Caspian Sea (Bilio and Niermann, 2004) and the northern Mediterranean Sea (Purcell et al., 2001).

Research into gelatinous predators should continue to increase in importance. Many authors have been suggesting

that jellyfish populations have been on the rise (Mills, 2001; Hay, 2006; Attrill et al., 2007; Richardson and Gibbons, 2008; Richardson et al., 2009). These authors point to numerous factors that are the direct result of human activity that may lead to aquatic systems that are dominated by jellyfish in the future. These factors include (1) overfishing resulting in reduced competition and predation on jellyfish; (2) habitat

modification that creates more polyp/juvenile habitat; (3) climate change causing waters to warm and stratify; and (4) eutrophication leading to hypoxia, which jellyfish can tolerate more readily than fish (summarized in Richardson et al., their figure 2). However, other researchers have pointed out that little is known about bloom formation in jellyfish populations (Mills, 2001) and jellyfish often exhibit bloom-behavior to take advantage of system variability (Boero et al., 2008) or show variability that is best linked to climate cycles (Purcell et al., 2007). If gelatinous zooplankton populations continue to rise, studies investigating predation on zooplankton populations will be needed to assess the interaction between fish and gelatinous zooplankton for a shared resource: zooplankton.

#### 6.05.4.4 Other Invertebrates

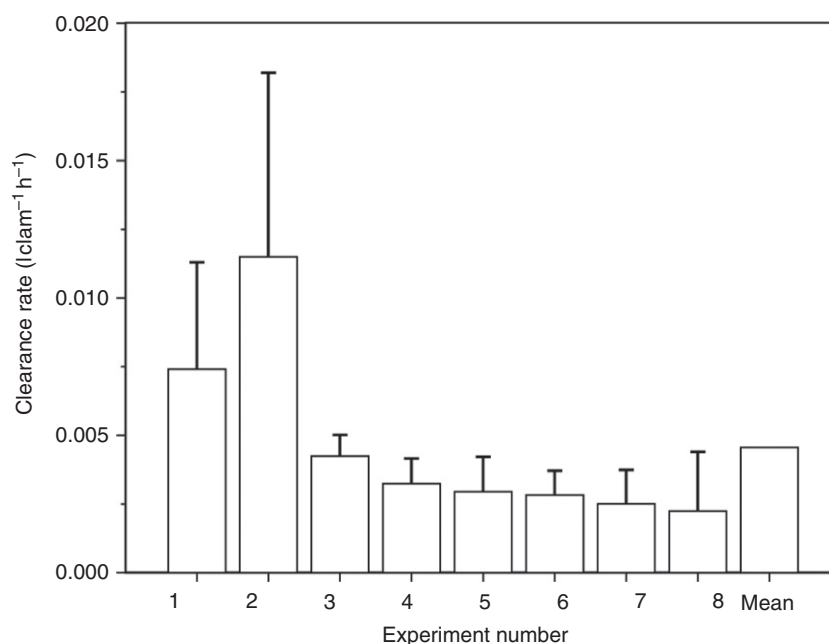
Predators other than fish and gelatinous zooplankton also impact copepod populations. In many estuarine and coastal areas, mysid shrimp are important predators of copepods. Fulton (1982) showed a significant impact on *A. tonsa* populations in enclosures by the mysids *Mysidopsis bigelowi* and *Neomysis americana*. The mysid *Mysis mixta* preyed almost exclusively on copepods (*E. affinis*) in the northern Baltic Sea (Hansson et al., 1990). This study suggested that mysid predation could influence zooplankton populations, but other factors such as food supply were also important (Hansson et al., 1990). *Mysis mixta* appeared to be food limited in the northern Baltic Sea where observed growth rates could not be explained by ambient densities of zooplankton ( $10\text{--}20\text{ l}^{-1}$ ) (Mohammadian et al., 1997). Two species of mysids, *Mesopodopsis wooldridgei* and *Rhopalophthalmus terranatalis*, preyed upon copepodites and nauplii in the Sundays River, South Africa (Jerling and Wooldridge, 1995). The predation rates of these species feeding on copepodites increased linearly

with increasing prey concentrations and did not saturate (Jerling and Wooldridge, 1995). The mysid *Neomysis integer* was found to consume copepods (*E. affinis*) primarily in the ETM zones of the Elbe, Westerschelde, and Gironde (Lehtiniemi et al., 2002). Mysids (*N. Americana* and *Mysis stenolepsis*) are the most important predators of zooplankton in the ETM region of the St. Lawrence Estuary, Canada (Winkler et al., 2003). These two species appear to have undergone niche partitioning where *M. stenolepsis* feeds primary on *E. affinis* nauplii and copepodites and *N. americana* feeds on smaller prey, such as rotifers, nauplii and veligers (Winkler et al., 2007). Mysids appear to be important predators of copepods, but are often overlooked in most estuarine systems.

Bivalves may also prey upon zooplankton in specific situations. Though this phenomenon has been little studied, there are a few examples of direct predation on zooplankton by bivalves in estuarine systems. Within a year of the introduction of the clam *Corbula amurensis* to San Francisco Bay, USA, the abundance of adult copepods for the three most common species had declined 53–91% (Kimmerer et al., 1994). This decline was attributed to an increase in mortality of nauplii, and *C. amurensis* was able to remove 8.2% of *E. affinis* nauplii  $\text{d}^{-1}$ , accounting for the observed declines in adults (Figure 17) (Kimmerer et al., 1994). The hard clam, *Mercenaria mercenaria*, has been shown to prey on early life stages of *A. tonsa* in experimental mesocosms (Lonsdale et al., 2007, 2009). Bivalve predation may be very important in shallow embayments and enclosed systems.

#### 6.05.5 Summary and Future Research Directions

Estuaries and coasts are locations of large human population centers and the result has been significant alterations in the structure and functioning of these ecosystems. Anthropogenic



**Figure 17** Grazing rate of the clam *Corbula amurensis* on *Eurytemora affinis* nauplii in experiments from the San Francisco estuary. Reproduced from Kimmerer, W.J., Gartside, E., Orsi, J.J., 1994. Predation by an introduction clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. Marine Ecology Progress Series 113, 81–93.

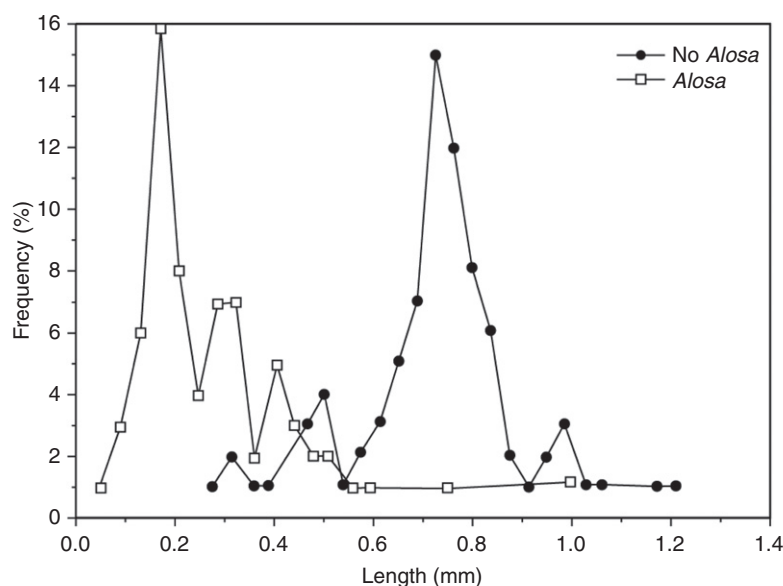


impacts include nutrient over-enrichment (eutrophication) from nonpoint and point sources, invasive species, aquaculture, coastal development, overfishing, habitat alteration, climate change, and water use (Pew, 2003). The consequences of these impacts are well documented for most groups of organisms inhabiting estuarine and coastal systems, in particular phytoplankton, benthos, and fish. For example, cultural eutrophication (Nixon, 1995; Smith et al., 1999; Cloern, 2001) is one of the best-studied human impacts and has been linked to long-term changes in phytoplankton biomass (Harding and Perry, 1997; Smith et al., 1999; Burkholder et al., 2006) and species composition (Gallegos, 1992; Paerl et al., 2003). Excess phytoplankton often goes ungrazed and can lead to the development of hypoxic bottom waters (Diaz and Rosenberg, 1995, 2008) that decimate benthic, sessile populations (Rabalais et al., 2002; Wu, 2002) and demersal fish (Pihl et al., 1991, 1992; Pihl, 1994). Fish have also been studied in relation to eutrophication, with excess nutrients being linked to increased production (Nixon, 1988), but also potential impacts due to hypoxia (Caddy, 1993, 2000) and overfishing (Breitburg et al., 2009). At the fulcrum of this phytoplankton-to-fish energy transfer are zooplankton, critical components of the food web.

Zooplankton are affected by the various human activities listed above, but the exact response of zooplankton as a group to these threats is poorly understood. Eutrophication would be expected to increase zooplankton populations; however, long-term increases in zooplankton populations have not been found in estuaries (Micheli, 1999; Kimmel and Roman, 2004). Severe eutrophication, characterized by large-scale algal blooms, can suppress zooplankton populations particularly if the blooms consist of unpalatable or toxic species (Muller-Navarra et al., 2000; Muller-Solger et al., 2002; Muller-Navarra, 2008). However, under moderate eutrophication, predation may prevent an increase in zooplankton biomass (Micheli, 1999).

It should be clear from the research reviewed in this chapter that copepods play a critical role in functioning of estuarine and coastal systems. Copepods in these ecosystems have evolved feeding strategies to take advantage of a wide variety of available prey and organic material, magnifying the pathways of energy flow to higher trophic levels. A major conclusion of this exercise has been that a more complex, but holistic, view of trophic interactions has replaced the classic food chain of phytoplankton to zooplankton. It should also be apparent that considerable variability in the relationship between food, temperature, body size, growth, and reproduction exist. However, some general patterns appear to emerge. Food limitation is present in coastal and estuarine systems. This can be related to diet diversity and increased autotrophic and heterotrophic resources. Food quality is a critical, parameter that may shed the most light on growth and reproductive patterns in copepods in the future. Trophic interactions between copepods and their prey may be largely based on nutritional requirements (Muller-Navarra, 2008). Further investigation into these interactions may cause the views of copepod feeding again to shift further from the classical food web paradigm of phytoplankton to zooplankton to fish.

Predators can shift copepod size distributions. A classic paper by Brooks and Dodson (1965) showed conclusively that zooplanktivorous fish are directly responsible for shifting size distributions in lakes (Figure 18). Lakes with no alewives (*Alosa aestivalis*) had zooplankton that ranged in size from 0.8–1 mm, whereas lakes with alewives had zooplankton that ranged in size from 0.3 to 0.5 mm (Brooks and Dodson, 1965). This paper has been widely cited in the freshwater literature and lake studies continue to investigate the role of predators in driving size distributions, but this topic has received comparatively little attention in estuarine and coastal systems. Turner (2004) and Hopcroft et al. (2001) pointed out that small copepods (<1 mm length) are the dominant organisms in all systems. Size selective predation does occur as discussed



**Figure 18** Size-frequency distribution of zooplankton in Crystal Lake, USA in 1942 (no planktivorous fish, *Alosa aestivalis*) and in 1964 (after the establishment of *A. aestivalis*). Reproduced from Brooks, J.L., Dodson, S.I., 1965. Predation body size and composition of plankton. *Science* 150, 28–35.

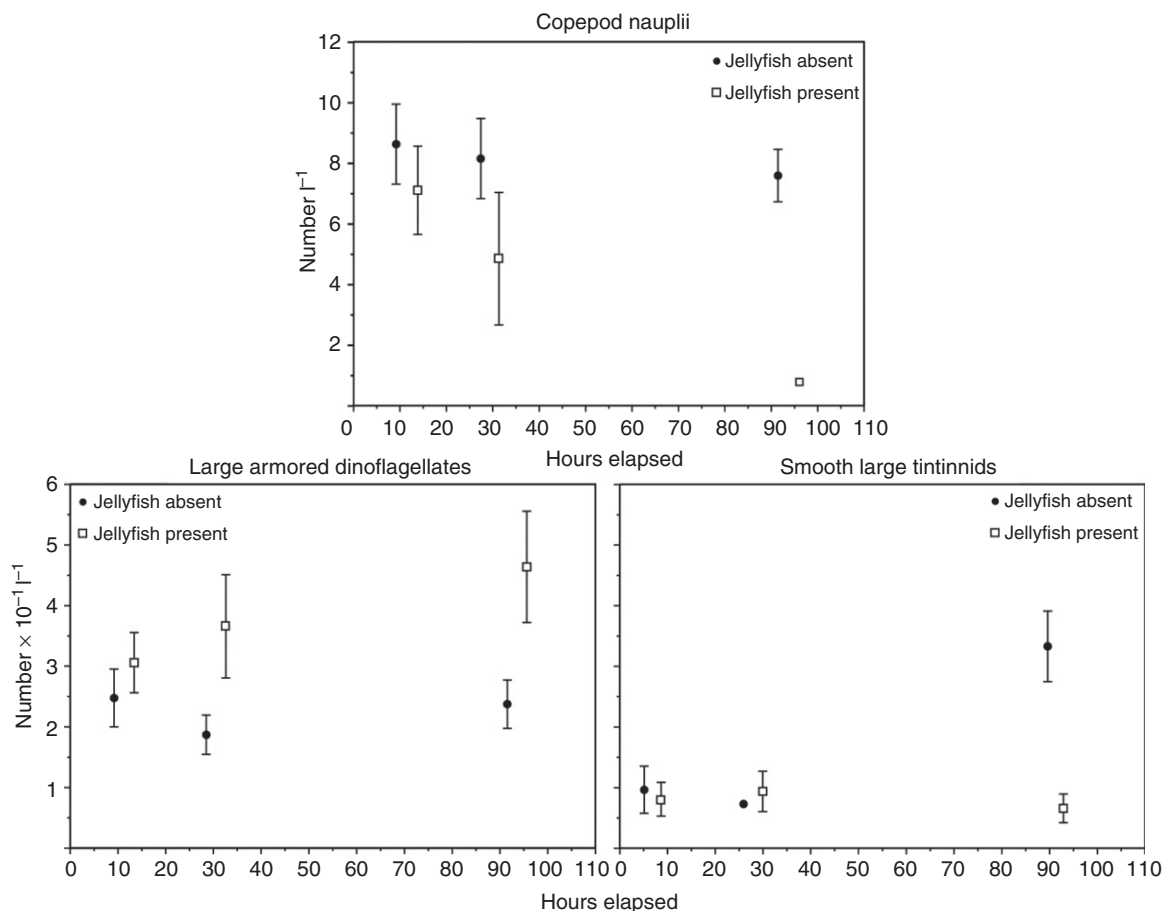


previously, but it is more difficult to attribute all losses of larger copepods to predation in open systems due to the potential role advective loss may play in shaping copepod size distribution. Size is an important parameter and may be used to extrapolate from individuals to community metrics, such as secondary production, through the application of allometric theory (Cyr and Pace, 1993) and size spectrum theory (Zhou and Huntley, 1997; Kerr and Dickie, 2001). Size distributions of copepods with likely receive more attention and be applied more widely to ecological questions in the future.

The phenomenon of trophic cascades has a long history (Hairston et al., 1960). Trophic cascades occur through the exertion of top-down control on a food web by predators. For example, in a simple food chain linking phytoplankton to zooplankton to fish, fish may stimulate the production of phytoplankton biomass indirectly by consuming the zooplankton that graze on the algae. In aquatic systems, trophic cascades have been shown to structure lake communities (McQueen et al., 1986, 1989) and determine lake productivity (Carpenter et al., 1985). This concept works well in closed systems like lakes, but does it operate in more open systems? Mesocosm or *in situ* enclosure studies using estuarine plankton communities suggest that trophic cascades do occur. Graneli and Turner (2002) placed the ctenophore *Pluerobrachia pileus*,

copepods, ciliates, and phytoplankton in experimental mesocosms in the Gulmar Fjord, Sweden. Ctenophore predation on copepods reduced copepod predation on ciliates, therefore increasing grazing of phytoplankton by small ciliates (Graneli and Turner, 2002). The addition of jellyfish (*Catostylus mosaicus*) had a similar effect on copepods and microzooplankton in Lake Illawarra, Australia, a coastal lagoon. Jellyfish drove a trophic cascade in mesocosms by reducing copepod nauplii abundance, thereby reducing predation on dinoflagellates and tintinnids (Figure 19). Jellyfish preyed heavily on mesozooplankton allowing the red tide forming dinoflagellate *Noctiluca scintillans* to bloom under nutrient-rich conditions (Pitt et al., 2007). The formation of dinoflagellate blooms was also suggested to be related to the release of microzooplankton grazing pressure due to copepod grazing of microzooplankton in the Choptank River, USA (Stoecker et al., 2008). Trophic cascades such as this are probably operating in a variety of systems at various times and may be critical in controlling phytoplankton bloom dynamics and transfer of primary production to higher trophic levels.

Copepods will continue to be a focus of research in coastal and estuarine systems in the future. Data from studies exploring copepod population shifts due to food limitation or predation will be needed for dynamic models that trace



**Figure 19** Variation in the mean abundance of copepod nauplii, large armored dinoflagellates, and smooth large tintinnids over a mesocosm experiment with and without jellyfish (*Catostylus mosaicus*). Reproduced from Pitt, K.A., Kingsford, M.J., Rissik, D., Koop, K., 2007. Jellyfish modify the response of planktonic assemblages to nutrient pulses. *Marine Ecology Progress Series* 351, 1–13.

ecosystem energy flow in ecosystems. These models are becoming increasingly important as uncertainty in how estuarine and coastal ecosystems will respond to human-induced climate change continues to be an issue (Hays et al., 2005). Fisheries will continue to be heavily exploited in direct proportion to human population growth. Studies of copepod trophic ecology will be vital as management agencies move away from tradition fisheries management toward ecosystem-based approaches (Pikitch et al., 2004). Only with increased knowledge of the trophic role of copepods in estuarine and coastal systems can the dream of ecosystem-based management be realized.

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