

Chapter 22

Copepod Biodiversity in Japan: Recent Advances in Japanese Copepodology

Susumu Ohtsuka and Shuhei Nishida

Abstract Recent advances in our understanding of the biodiversity of copepods in Japanese waters are briefly reviewed. It is noteworthy that the two new species of Platycopioida found in Japan are the first record of this order from the Indo-Pacific. Taxonomic revisions of calanoids in Japanese waters have continued based on both morphological and molecular data. Molecular analyses have revealed the presence of cryptic/sibling species in a common species and of intraspecific variations. Complete mitochondrial DNA sequences from copepods have been analyzed for *Tigriopus japonicus*, which suggest that copepods are genetically ‘eccentric.’ Molecular tools have helped to clarify the phylogenetic relationships of highly modified symbiotic copepods. Population dynamics, life cycles, and distributions of planktonic copepods have been thoroughly investigated in coastal and oceanic waters. These studies highlighted the influence of the Oyashio/Kuroshio currents on the coast, the high mortality of eggs from predation, adaptive responses to phytoplankton blooms, and niche partitioning by habitat and food. Deep-sea calanoids are highly diverse and specialized for detritivory and carnivory. East Asian planktonic copepods have been introduced to America and Europe via ballast water, although Japan not yet received any alien planktonic copepods. In contrast, parasitic copepods have been introduced to Japan via aquaculture. The life cycle of commercially important sea lice was clarified. Because copepods are one of the most abundant metazoans on Earth, more biological but also biomimetic information should be accumulated.

Keywords Alien • Copepod • Indo-West Pacific • Partition • Relict • Zoogeography

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22.1 Introduction

The subclass Copepoda currently includes about 13,000 species of small planktonic, benthic, and symbiotic crustaceans (Huys and Boxshall 1991; Boxshall and Halsey 2004; Boxshall and Defaye 2008). However, this species richness represents a fraction of the real diversity because of the low taxonomic resolution, especially in symbiotic taxa. For example, only 1.3 % of invertebrates and 16.0 % of fish have been reported to harbor symbiotic copepods (Ho 2001). Deep-sea hyperbenthic copepods require specially designed gear such as baited traps and plankton nets fished from deep-sea vessels (e.g., Grice and Hulsemann 1970; Fleminger 1983; Nishida et al. 1999; Bradford-Grieve 2002, 2004; Ivanenko et al. 2007; Markhaseva and Schulz 2008). Because small-sized crustaceans are not directly related to human society as commodities, taxonomic information is largely restricted to two groups: planktonic copepods that are main prey items of commercially important fish, and parasitic copepods which are pests in aquaculture.

Free-living copepods are a key link between primary producers and higher trophic levels in aquatic ecosystems and are considered to be one of the most numerous organisms on Earth (Huys and Boxshall 1991). Taxonomic and ecological research has been focused mainly on planktonic copepods since the first scientific description of a copepod, *Calanus finmarchicus*, by Johan Gunnerus in 1770. Parasitic copepods, such as sea lice (Caligidae and related taxa), have caused serious economic losses in aquaculture, estimated at more than 100 million US\$ (Ho and Lin 2004). More attention is being paid to sea lice and other parasites consequent to the expansion of aquaculture.

In Japan, Mr. Takamochi Mori (1902–1945) and Dr. Otohiko Tanaka (1902–1990), and Dr. Tatsunori Itô (1945–1990) made great contributions to the taxonomic knowledge of marine planktonic and benthic copepods, respectively (Kikuchi 1991; Omori 2002; Ohtsuka et al. 2015). Drs. Satyu Yamaguchi (1894–1976) and Suetoshi Shiino (1908–1978) provided the taxonomic benchmarks for symbiotic copepods (Oishi 1979). Succeeding generations of Japanese copepodologists have built on these pioneering studies.

Since the Showa Era, marine zooplanktology in Japan, including copepodology, has been at the forefront of global research, mainly because of the excellence of the plankton laboratories in Hokkaido University and the University of Tokyo (Omori 2002). Japanese copepodologists have specialized in robust taxonomic and functional morphological work; extensive ecological studies on the distribution, life cycle, and population dynamics; and detailed molecular analyses. In contrast, Japanese parasitology involved with symbiotic copepods has been impacted by the lack of an integrated educational system.

New and amazing discoveries concerning the taxonomy, phylogeny, evolution, zoogeography, and ecology of free-living and parasitic copepods have been made by Japanese copepodologists, contributing much to our understanding of biodiversity, some of which are summarized herein. Mauchline (1998) published a comprehensive monograph on the biology of calanoid copepods; therefore, our focus is

on subsequent studies on free-living copepods and the recent advances in research on symbiotic taxa.

22.2 Taxonomy

22.2.1 *Order Platycopioida: Importance of Near-Bottom and Cave Faunas*

The order Platycopioida comprises the infraclass Progymnoplea established by Huys and Boxshall (1991) and retains primitive features in comparison with other orders. Its distribution is restricted to hyperbenthic layers and caves (Fosshagen and Iliff 1985, 1988; Arbizu 1997; Boxshall and Halsey 2004). Two species of platycopioids occur in shallow near-bottom waters off the Nansei Islands, southern Japan, and are the only records of the order in the Indo-Pacific: *Platycopia orientalis* and *P. compacta* (Fig. 22.1a) (Ohtsuka and Boxshall 1994; Ohtsuka et al. 1998). Based on their circumglobal distribution, Ohtsuka et al. (1998) suggested that platycopioids exhibit a Tethyan track.

No cavernicolous platycopioids are known from Japan, but there are many marine limestone caves in the Ryukyu Islands (Kase and Hayami 1992), so cavernicolous taxa such as *Antrisocopia* and *Nanocopia* (Fosshagen and Iliff 1985, 1988) might be found there. The highly specialized cave-living crustacean class Remipedia is restricted to the East and West Atlantic and South Pacific (Yager and Humphreys 1996; Neibar et al. 2011). Our present awareness of cave-living crustaceans in the North Pacific is low. The discovery of a new thermosbaenacean from an anchialine cave in the Nansei Islands (Shimomura and Fujita 2009) suggests that a comprehensive survey of marine cave-living animals in Japan is necessary.

22.2.2 *Order Calanoida: Revisions of Common Species and Discovery of New Hyperbenthic Taxa*

The taxonomy of brackish and coastal calanoids, the best-studied group in Japanese copepodology, has been revised by integrative molecular and morphological analyses. Such studies revealed the presence of many cryptic or sibling species among common species; for example, *Acartia pacifica* is a common, warm-water species on the coast of Japan, but a closely related species *A. ohtsukai* was recognized from the Ariake Sea and is regarded as a continental relict (Ueda and Bucklin 2006; Sakaguchi et al. 2011). *Pseudodiaptomus inopinus* dominates brackish waters of Japan, but its populations in the Nansei Islands, southernmost Japan, proved to represent a distinct sibling species, *P. nansei* (Sakaguchi and Ueda, 2010). Recently, new species of abundant genera were found: *Centropages maigo* from

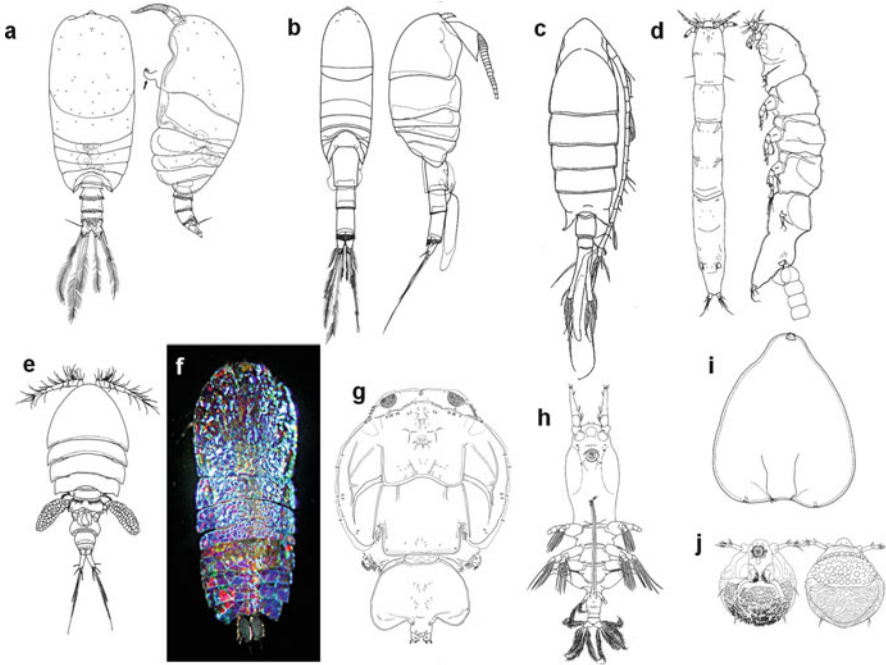


Fig. 22.1 Copepods newly described or previously recorded from Japan. (a) Basal copepod *Platycopia compacta*, female, dorsal (left) and lateral view, ventral hook arrowed (body length = ~0.8 mm). (b) Near-bottom calanoid *Placocalanus inermis*, female, dorsal (left) and lateral (right) view (0.45 mm). (c) Calanoid *Tortanus (Eutortanus) komachi* endemic to Japan, female, dorsal view (~3.0 mm). (d) Poecilostomatoid *Umazuracola elongata* parasitic on skins of black scraper, female, dorsal (left) and lateral (right) view (~1.0 mm). (e) “Poecilostomatoid” *Hemicyclops gomoensis*, female, dorsal view (~1.6 mm). (f) “Poecilostomatoid” *Sapphirina metallina*, male, dorsal view (~2.1 mm). (g) Siphonostomatoid *Caligus sclerotinosus*, female, dorsal view (~3.0 mm). (h) Monstrilloid *Maemonstrilla turgida*, female, ventral view (~1.6 mm). (i) Siphonostomatoid *Neomysidion rahotsu*, female, dorsal view (~0.8 mm). (j) *Neomysidion rahotsu*, dwarf male, ventral (left) and dorsal (right) view (~0.1 mm) (After: (a) Ohtsuka et al. 1998; (b) Ohtsuka et al. 1996b; (c) Itoh et al. 2001; (d) Ho et al. 2006; (e) Itoh and Nishida 2007; (f) original, through the courtesy of Prof. Jun Nishikawa; (g) Ho et al. 2004; (h) Grygier and Ohtsuka 2008; (i, j) Ohtsuka et al. 2005a; with permission from the Zoological Society of Japan (a, d), Taylor & Francis (b), the Plankton Society of Japan (c, e), Springer-Verlag (g, i, j), and John Wiley (h))

Hokkaido, Honshu, and Shikoku Islands (Ohtsuka et al. 2005c); *Labidocera churaumi* from Okinawa (Hirabayashi and Ohtsuka 2014); and *Tortanus komachi* (Fig. 22.1c) from the coast of the Japan Sea (Itoh et al. 2001).

The taxonomy of the Paracalanidae has been confused at family, generic, and species levels (Hiromi 1981, 1987; Boxshall and Halsey 2004; Cornils and Blanco-Bercial 2013). The Calocalanidae and Mecynoceridae are synonymous with the Paracalanidae on the basis of morphological and molecular data, although two of these families were previously separated (Boxshall and Halsey 2004; Cornils and Blanco-Bercial 2013). According to the molecular analysis by Cornils and

Table 22.1 Common planktonic copepods in the brackish and coastal waters of Japan

Location	Common species	References
Akkeshi Bay, Lake Akkeshi	<i>Acartia hudsonica</i> , <i>A. longiremis</i> , <i>Centropages abdominalis</i> , <i>Eurytemora herdmani</i> , <i>E. pacifica</i> , <i>Paracalanus parvus</i> s.l., <i>Pseudocalanus newmani</i> , <i>Oithona similis</i> *	Ueda (2001)
Ishikari Bay, Hokkaido	<i>Clausocalanus pargens</i> , <i>Mesocalanus tenuicornis</i> , <i>Metridia pacifica</i> , <i>Neocalanus flemingeri</i> , <i>N. plumcрус</i> , <i>Pseudocalanus newmani</i> , <i>Oithona</i> spp.*	Asami et al. (2010)
Funka Bay, Hokkaido	<i>Acartia</i> spp., <i>Calanus pacificus</i> , <i>Clausocalanus</i> spp., <i>Paracalanus</i> sp., <i>Metridia pacifica</i> , <i>Pseudocalanus newmani</i>	Ban et al. (1998)
Onagawa Bay, Honshu	<i>Acartia omorii</i> (as <i>A. clausi</i>), <i>Calanus pacificus</i> , <i>Eurytemora pacifica</i> , <i>Paracalanus parvus</i> s.l., <i>Pseudocalanus minutus</i> , <i>Oithona similis</i> *	Uye (1982)
Okkirai Bay, Honshu	<i>Acartia hudsonica</i> , <i>A. longiremis</i> , <i>A. omorii</i> , <i>A. steueri</i> (<i>Acartia</i> only)	Yamada et al. (2012)
Toyama Bay, Honshu	<i>Ctenocalanus vanus</i> , <i>Mesocalanus tenuicornis</i> , <i>Metridia pacifica</i> , <i>Paracalanus</i> sp., <i>Paraeuchaeta elongata</i> (as <i>E. japonica</i>), <i>Pseudocalanus minutus</i> , <i>Scolecithricella dentata</i> , <i>Oithona atlantica</i> *	Hirakawa et al. (1992)
Tokyo Bay	<i>Acartia omorii</i> , <i>A. sinjiensis</i> , <i>Calanus sinicus</i> , <i>Labidocera rotunda</i> , <i>Paracalanus parvus</i> s.l., <i>Pseudodiaptomus marinus</i> , <i>Oithona davisae</i> *, <i>Hemicyclops japonicus</i> **	Itoh et al. (2011)
Maizuru Bay, Honshu	<i>Acartia erythraea</i> , <i>A. hudsonica</i> , <i>A. omorii</i> , <i>A. sinjiensis</i> , <i>Centropages abdominalis</i> , <i>Paracalanus parvus</i> s.l., <i>Parvocalanus crassirostris</i> , <i>Oithona davisae</i> *, <i>O. nana</i> *, <i>O. similis</i> *, <i>Euterpina acutifrons</i> **, <i>Microsetella norvegica</i> **	Ueda (1991)
Sagami Bay, Honshu	<i>Acartia</i> spp., <i>Calanus sinicus</i> , <i>Clausocalanus</i> spp., <i>Ctenocalanus vanus</i> , <i>Lucicutia flavicornis</i> , <i>Paracalanus parvus</i> s.l., <i>Temora turbinata</i> (Calanoida only)	Shimode et al. (2006)
Suruga Bay, Honshu	<i>Acartia danae</i> , <i>A. omorii</i> , <i>Calanus sinicus</i> , <i>Canthocalanus pauper</i> , <i>Centropages tenuiremis</i> , <i>Clausocalanus furcatus</i> , <i>C. minor</i> , <i>Ctenocalanus vanus</i> , <i>Labidocera japonica</i> , <i>Paracalanus aculeatus</i> , <i>P. parvus</i> s.l., <i>Temora turbinata</i> , <i>Undinula vulgaris</i> (Calanoida only)	Itoh et al. (2005)
Seto Inland Sea, Honshu	<i>Acartia erythraea</i> , <i>A. omorii</i> , <i>A. pacifica</i> , <i>Acrocalanus gibber</i> , <i>A. gracilis</i> , <i>Calanopia thompsoni</i> , <i>Calanus sinicus</i> , <i>Centropages abdominalis</i> , <i>C. tenuiremis</i> , <i>Labidocera rotunda</i> , <i>Paracalanus parvus</i> s.l., <i>Parvocalanus crassirostris</i> , <i>Pontellopsis</i>	Hirota (1962, 1979) and Ohtsuka et al. (2004c)

(continued)

Table 22.1 (continued)

Location	Common species	References
	<i>tenuicauda</i> , <i>Pseudodiaptomus marinus</i> , <i>Tortanus forcipatus</i> , <i>T. gracilis</i> , <i>Oithona similis</i> *, <i>O. davisae</i> *, <i>Euterpina acutifrons</i> ***, <i>Microsetella norvegica</i> ***, <i>Corycaeus affinis</i> ***, <i>Oncaea venusta</i> ***	
Lake Nakaumi, Honshu	<i>Acartia hudsonica</i> , <i>A. sinjiensis</i> , <i>Eurytemora pacifica</i> , <i>Sinocalanus tenellus</i> , <i>Oithona davisae</i> *	Ohtsuka et al. (1999)
Gokasho Bay, Honshu	<i>Acartia omorii</i> , <i>Parvocalanus crassirostris</i> , <i>Oithona davisae</i> *	Hirakawa et al. (2006)
Shijiki Bay, Kyushu	<i>Acartia omorii</i> (as <i>A. clausi</i>), <i>A. steueri</i> , <i>Parvocalanus crassirostris</i> , <i>P. parvus</i> s.l., <i>Oithona brevicornis</i> *, <i>O. nana</i> *, <i>O. oculata</i> *, <i>O. similis</i> *, <i>O. simplex</i> *, <i>Euterpina acutifrons</i> ***, <i>Microsetella norvegica</i> **	Ueda (1980, 1982)
Omura Bay	<i>Acartia omorii</i> ? (as <i>A. clausi</i>), <i>Centropages abdominalis</i> , <i>Paracalanus parvus</i> s.l., <i>Parvocalanus crassirostris</i> , <i>Pseudodiaptomus marinus</i> , <i>Oithona davisae</i> *, <i>Microsetella norvegica</i> **	Itoh and Iizuka (1979)
Yatsushiro Bay, Kyushu	<i>Acartia omorii</i> , <i>Paracalanus parvus</i> s.l., <i>Parvocalanus crassirostris</i> , <i>Oithona davisae</i> * (as <i>O. nana</i>), <i>O. similis</i> *, <i>Microsetella norvegica</i> ***, <i>Corycaeus</i> spp.***	Hirota (1975)
Ariake Sea, Kyushu	<i>Acartia erythroa</i> , <i>A. hudsonica</i> , <i>A. omorii</i> , <i>A. pacifica</i> , <i>Acrocalanus gibber</i> , <i>A. gracilis</i> , <i>Calanus sinicus</i> , <i>Paracalanus parvus</i> s.l., <i>Parvocalanus crassirostris</i> , <i>Pseudodiaptomus marinus</i> , <i>Temora turbinata</i> , <i>Tortanus forcipatus</i> , <i>Oithona attenuata</i> *, <i>O. brevicornis</i> *, <i>O. davisae</i> *, <i>O. similis</i> *, <i>O. simplex</i> *, <i>Euterpina acutifrons</i> ***, <i>Microsetella norvegica</i> ***, <i>Corycaeus affinis</i> ***, <i>Oncaea clevei</i> ***, <i>O. media</i> ***, <i>Hemicyclops</i> sp.***	Beltrão et al. (2011)
River estuaries in western Japan	<i>Acartia ohtsukai</i> , <i>A. sinjiensis</i> , <i>A. tsuensis</i> , <i>Pseudodiaptomus inopinus</i> , <i>Sinocalanus tenellus</i> , <i>Oithona davisae</i> *	Sakaguchi et al. (2011)
Sumiyo Bay, Amamioshima Island, Kyushu	<i>Acartia tsuensis</i> , <i>Pseudodiaptomus ishigakiensis</i> , <i>P. nansei</i> (as <i>P. inopinus</i>),	Oka and Saisho (1994)
Lagoons of Okinawa Island, Okinawa	<i>Acartia fossae</i> , <i>A. sinjiensis</i> , <i>Bestiolina similis</i> , <i>Oithona aruensis</i> *, <i>O. attenuata</i> (stocky form)*, <i>O. dissimilis</i> *, <i>O. oculata</i> *, <i>O. simplex</i> *	Ueda (2001)

(continued)

Table 22.1 (continued)

Location	Common species	References
Kabira Bay, Ishigakijima Island, Okinawa	<i>Acartia erythraea</i> , <i>A. fossae</i> , <i>A. steueri</i> , <i>Parvocalanus crassirostris</i> , <i>Oithina aruensis</i> *, <i>O. dissimilis</i> *, <i>O. oculata</i> *, <i>O. simplex</i> *	Nishida (1985)

No asterisk, Calanoida

*Cyclopoida

**Harpacticoida

***"Poecilostomatoida"

Blanco-Bercial (2013), the genera *Paracalanus* and *Parvocalanus* are paraphyletic and *Acrocalanus* is monophyletic. One of the dominant calanoids in coastal waters, *Paracalanus parvus* s.l., has been taxonomically confused since the beginning of Japanese planktology (see Table 22.1), and resembles *P. parvus*, *P. indicus*, and *P. quasimodo* (Hiromi, 1987). In Korean waters both *P. parvus* and *P. indicus* have been recorded (Kang 1996), but the former is suggested to have a restricted, high-latitude distribution in the North Atlantic (Hiromi 1987). Diagnostic features such as the morphology of the cephalosome and the presence/absence of a spinular row along the outer margin of the third exopodal segments of legs are highly variable even within a local population (Hiromi 1987), so a taxonomic revision of *Paracalanus*, including *P. parvus* s.l., is a high priority on a global scale.

The taxonomy of the coastal/oceanic family Calanidae was also confused, partly the result of low sexual dimorphism. The family was taxonomically revised by Russian copepodologists such as V.A. Jashnov and K.A. Brodsky, and more recently by Miller (1988) and Hulsemann (1994). The following species of *Calanus* and *Neocalanus* have been identified from Japanese waters: *C. pacificus*, *C. glacialis*, *C. sinicus*, *C. jashanovi*, *N. cristatus*, *N. gracilis*, *N. robustior*, *N. plumchrus*, and *N. flemingeri*. In Sagami Bay on the Pacific Coast of Honshu, the vertical distributions of copepodid stages of co-occurring *C. sinicus* and *C. jashanovi* were identified using genetic markers, revealing the presence of large populations of fifth copepodids of *C. sinicus* in the mesopelagic layer (Nonomura et al. 2008). Two sibling species, *N. plumchrus* and *N. flemingeri*, exhibit different annual life cycles in the North Pacific (Tsuda et al. 1999) and the Sea of Japan (Miller and Terazaki 1989) (see Fig. 22.6).

The taxonomy of the coastal/oceanic family Eucalanidae is also very difficult (Fleminger 1973). Geotze (2003) and Geotze and Ohman (2010) studied the molecular phylogeny and zoogeography of Eucalanidae and revealed that intraspecific genetic variation is found even in oceanic taxa, raising interesting questions concerning the nature of any biological barriers to gene flow in oceanic waters. Because calanids and eucalanids are considered not to have complex mating patterns (Tsuda and Miller 1998; Ohtsuka and Huys 2001), it is likely that sexual dimorphic features are less well developed.

As are marine taxa, freshwater taxa are more genetically differentiated than expected. Based on analyses using mitochondrial (mt) COI and nuclear internal transcribed spacers (ITS), Makino and Tanabe (2009) revealed that

Acanthodiptomus pacificus on Japan's main islands consists of a cryptic species complex. They found genetic differentiation at a level of 15–22 % in mtCOI, among lineages corresponding to interspecific variation. Because freshwater habitats, in particular, subterranean waters, are generally more isolated from one another (Karanovic et al. 2013), such endemism as reported by Makino and Tanabe (2009) could be common.

Attention has been paid to the taxonomy and zoogeography of hyperbenthic calanoids, because they form a unique and diverse community just above the shallow- and deep-sea bed. This community contains both primitive and advanced taxa, suggesting complex colonization routes in the course of the calanoid evolutionary history (Ohtsuka 1999; Bradford-Grieve 2002, 2004). Shallow-water genera known from Japanese waters include *Metacalanus* and *Paramisophria* (Arietellidae); *Placocalanus* (Fig. 22.1b), *Pseudocyclops*, and *Ridgewayia* (Pseudocyclopiidae); *Thompsonopia* (described as *Pseudocyclopia muranoi*) (Pseudocyclopiidae); and *Stephos* (Stephidae) (Tanaka, 1966; Ohtsuka, 1984, 1985, 1992, unpublished data; Ohtsuka and Hiromi 1987; Barr and Ohtsuka 1989; Ohtsuka et al. 1991, 1996b; Barthélemy et al. 1998). Deep-sea genera include *Bradyetes*, *Lutamator*, and *Paracommaneta* (Aetideidae); *Sarsarietellus* and *Scutogerulus* (Arietellidae); *Macandrewella* (Scolecitrichidae); *Xanthocalanus* (Phaennidae); and *Tharybis* and *Neoscolecithrix* (Tharybidae) (Tanaka, 1960; Nishida et al. 1999; Ohtsuka et al., 2002, 2003, 2005b; Ohtsuka and Boxshall, 2004; Ohtsuka, unpublished data). Among them Pseudocyclopiidae and Arietellidae are basal offshoots, whereas Aetideidae, Phaennidae, Scolecitrichidae, and Tharybidae are more terminal taxa (Bradford-Grieve et al. 2010, 2014; Blanco-Bercial et al. 2011).

22.2.3 Orders *Poecilostomatoida* and *Cyclopoida*: *Saphirella* *Problem and Other Issues*

The taxonomic position of the order Cyclopoida is unstable (Boxshall and Halsey 2004; Kim and Kim 2000; Huys et al. 2012; Tung et al. 2014). The order “Poecilostomatoida” was included within the Cyclopoida by Boxshall and Halsey (2004), but molecular analyses have shown that this conclusion is premature. “Poecilostomatoids” seem to be composed of several paraphyletic or polyphyletic groups (Kim and Kim 2000; Huys et al. 2012). In this chapter, we handle these orders separately.

Hemicyclops (Fig. 22.1e) and related genera belong to the family Clausidiidae of “Poecilostomatoida” and are recognized as a group basal to Cyclopoida and other poecilostomatoids (Huys et al. 2012). Small, enigmatic, planktonic poecilostomatoids called “*Saphirella*” have been recorded from brackish to oceanic waters (Itoh and Nishida 1991; Itoh 2006). Itoh and Nishida (1995, 2007, 2008) have elucidated that it includes the first copepodid stage of Clausidiidae, in particular, of *Hemicyclops*. Subsequent stages are loosely associated with benthic

organisms such as crabs and polychaetes (Itoh and Nishida 2007, 2008). High abundance of “*Saphirella*”-like copepods or the first copepodid stage of clausidiids was recorded from Tokyo Bay, reaching about 5000 individuals/m³ (Itoh 2006).

The taxonomy of Oncaeidae, a poecilostomatoid family in the mesopelagic community, has been revised by Böttger-Schnack and coworkers (Böttger-Schnack 2009; Böttger-Schnack and Schnack 2013, and references therein), including integrative molecular and morphological studies (Böttger-Schnack and Machida 2011). New genera, such as *Archioncaea*, *Triconia*, *Monothula*, and *Spinoncaea*, have been established, and the existing genera *Oncaea*, *Conaea*, and *Epicalymma* have been extensively revised. The Oncaeidae now includes 113 species (Razouls et al. 2015). When the oncaeid fauna of Japan was compiled by Itoh (1997) for an illustrated guide, it was based on the taxonomy before these revisions. Ecological studies in Tosa Bay (Nishibe et al. 2009), and the Kuroshio Extension area (Itoh et al. 2014) have recorded 45 and 35 oncaeid species, respectively.

New families and genera of “Poecilostomatoida” have been reported from invertebrate and fish hosts in Japanese waters, including Umazuracolidae (Fig. 22.1d) (Ho et al. 2006), Pseudohatschekiidae (Tang et al. 2010), *Biacanthus* (Tang and Izawa, 2005), and *Ttetaloia* (Uyeno and Nagasawa, 2012), all from fish. *Umazuracola* was originally established as the type of a monotypic family, but it was subsequently synonymized with the Taeniacanthidae (Huys et al. 2012). The enigmatic “poecilostomatoid” genus *Limnoncaea* Kokubo, 1914 found in plankton was recognized as an ergasilid, either *Ergasilus* or *Thersitina* (Ohtsuka et al., 2004a, b) (see Sect. 22.4.5: Life Cycle).

Three new species of the cyclopoid *Halicyclops* were described from estuaries of the Ariake Sea: *H. continentalis* as a continental relict and *H. uncus* and *H. ariakensis* as endemics (Ueda and Nagai 2009). New taxa of cyclopoids were found in marine invertebrates: *Chamicola* from bivalves (Ohtsuka et al. 2000a), *Loboixys* from ascidians (Ooishi 2006), and *Parenterognathus* and *Enterognathus* from comatulids (Ohtsuka et al. 2010, 2012). Sixty-one species of the cyclopoid family Cyclopidae, excluding groundwater species, were recognized from Japanese freshwaters by Ishida (2002).

The taxonomy and distribution of Oithonidae, representing the smallest but numerically dominant cyclopoids, in Suruga Bay and the Indo-Pacific oceanic waters were studied by Nishida et al. (1977) and Nishida (1985), respectively. These studies revealed that the species dominating in estuaries and embayment waters of Japan and previously reported as *Oithona nana* (e.g. Yamazi, 1955; Hirota and Hara, 1975) were *O. davisae* (see also Nishida and Ferrari, 1983 for taxonomic confusion among related species).

In Okinawan estuaries *Oithona dissimilis* is abundant, but two different size forms are distinguished (Ueda et al. 2011): the larger form is distributed in the lower estuaries (salinity, 25), and the smaller in the upper estuaries (around 7.5). These forms differ by 1.84–2.21 % in nuclear LSU rRNA and by 20.9–21.3 % in mtCOI, suggesting that *O. dissimilis* constitutes at least two cryptic species.

22.2.4 Other Orders: New Discoveries Continued

Two genera of the order Misophrioida are known from Japan: the deep-sea *Benthomisophria* and the hyperbenthic *Misophriopsis* (Tanaka, 1966; Ohtsuka et al., 1992). Misophrioids are not rare in the shallow and deep hyperbenthic communities (Ohtsuka, unpublished data), so undescribed taxa are likely to be discovered. Similar to Platycopioidea and Calanoida, two new families, and many genera and species of misophrioids, have been discovered from marine caves worldwide (cf. Boxshall and Jaume 2000b).

Some new families and genera of the order Siphonostomatoida have been reported from invertebrate and fish hosts in Japanese waters: *Archidactylina* from hagfish (Izawa 1996), *Neomysidion* (Fig. 22.1i, j) from mysids (Ohtsuka et al. 2005a), and *Dangoka* from elasmobranchs (Izawa 2011). Molecular data (Freeman et al. 2013) support the proposal (Dojiri and Ho 2013) that *Pseudocaligus* is a junior synonym of *Caligus* (Fig. 22.1g).

A new genus of Monstrilloidea, *Maemonstrilla* (Fig. 22.1h), was described from the Ryukyu Islands (Grygier and Ohtsuka 2008). *Maemonstrilla* (Japanese “mae” meaning anterior) bears anteriorly directed genital spines on the genital compound somite of the female, which are posteriorly directed in other monstrilloids. Because egg masses attached to the spines are positioned in a space surrounded by the right and left legs, Grygier and Ohtsuka (2008) regarded it as a kind of brood chamber. According to Huys et al. (2007), the Monstrilloidea should be relegated to a family within the order Siphonostomatoida.

Taxonomy of benthic harpacticoids was led by Dr. T. Itô, who passed away in 1990. Since then, progress in harpacticoid taxonomy has been focused on freshwater (Ishida and Kikuchi 2000 and references therein) and phytal species (Takemori and Iwasaki 2009; Harris and Iwasaki 2009, and references therein). The biodiversity and community structure of deep-sea harpacticoids in Japanese waters have been extensively studied (Shimanaga et al. 2004, 2008; Kitahashi et al. 2013, 2014a, b).

22.3 Phylogeny and Zoogeography

22.3.1 Phylogeny of Copepods

Genetic analyses of copepods have generated insight into their origin, evolution, and zoogeography. Copepods are ‘eccentric’ in the organization of mitochondrial genes, and show low sequence similarity to those of other arthropods (55.1–57.5%) (Machida et al. 2002). Although such information has been utilized to estimate phylogenetic relationships among higher taxa of Arthropoda (Boore et al. 1995), it appears inapplicable to copepods. In addition, deletion of a mitochondrial gene (ND6 protein-coding gene) can occur even within the calanoid genus *Neocalanus*

(Machida et al., 2006). The functional significance of such genetic abnormality is unknown.

The phylogeny of copepod orders is still under debate. The first offshoot, the order Platycopioida, is supported by morphology (Andronov 1974; Ho 1990, 1994a; Huys and Boxshall 1991). A genetic analysis of *Platycopia orientalis* is now in progress, which should allow the phylogenetic position of Platycopioida to be estimated more precisely (Tanaka et al., unpublished data).

Genetic analyses of the calanoid superfamilies support the morphology-based phylogeny of Andronov (1974) (Blanco-Bercial et al. 2011; Figueroa 2011; Bradford-Grieve et al. 2010, 2014). The molecular data indicate early divergence of the basal superfamilies Pseudocyclopoidea (including synonymized Epacteriscoidea), Diaptomoidea, and Arietelloidea from other superfamilies. The Pseudocyclopoidea is restricted to benthic layers, and is defined as a plesiomorphic taxon with an “underlying pattern of full development of arthrodistal membranes between body somites and limb segments” (Bradford-Grieve et al. 2014).

A phylogeny of *Neocalanus* spp. by Machida et al. (2006) illustrates evolutionary processes in oceanic copepods (Ohtsuka et al. 2009b). The North Pacific lineage *Neocalanus flemingeri*–*N. plumchrus*–*N. cristatus* and the Antarctic circumpolar *N. tonsus* show a typical antitropical distributions; *N. gracilis* and *N. robustior* have a wide circumtropical distribution (Fig. 22.2a). The divergence and colonization of *Neocalanus* are deduced in accord with Cenozoic events (Machida et al. 2006; Ohtsuka et al. 2009b). The taxa showing antitropical distributions are characterized by adaptation to seasonal phytoplankton blooms and by ontogenetic vertical migration, consistent with their origin in the Oligocene. In addition, the existence of three Northern Hemisphere species suggests that speciation could have occurred in marginal seas after the Miocene.

Molecular phylogenetic analyses are informative for inferring relationships of highly modified parasitic copepods. Adult females of *Pectenophilus ornatus* infect the gills of the Japanese scallop as an endoparasite (Nagasawa et al. 1988) and resemble rhizocephalan barnacles. Molecular analysis by Huys et al. (2006), using nuclear 18S rDNA, revealed that it represents a highly transformed member of Mytilicolide of “Poecilostomatoida”.

22.3.2 Zoogeography of East Asian Copepods

A comprehensive speciation pattern was proposed for the Indo-West Pacific coastal *Labidocera pectinata* species complex, based on vicariant events in accord with eustatic changes in sea level during the Pleistocene (Fleminger 1986). Such a vicariant mechanism is applicable to other Indo-West Pacific species groups, such as *Tortanus* (*Atortus*) species complexes, *Centropages alcocki* species group, *Labidocera detruncata* species complex, and *Pseudodiaptomus poppei* species subgroup (Ohtsuka and Kimoto 1989; Walter et al. 2002; Ohtsuka et al. 2005c, 2007b; Srinui et al. 2013; Hirabayashi and Ohtsuka 2014).

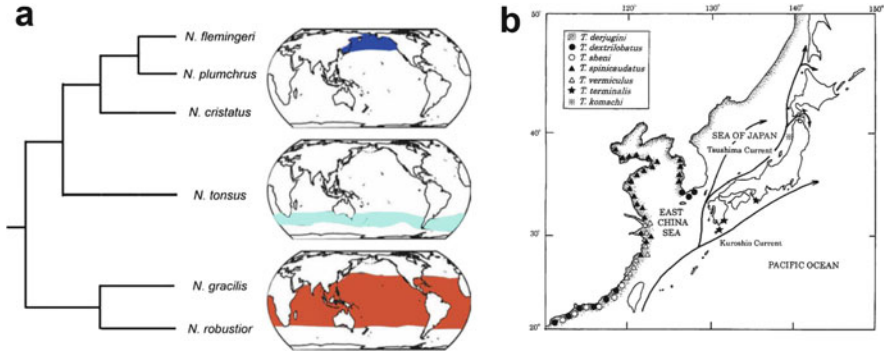


Fig. 22.2 Horizontal distributions of two groups of calanoid copepods. (a) Molecular phylogeny (right) and horizontal distributions (left) of the oceanic calanoid genus *Neocalanus* spp. (b) Distribution of seven species of the brackish/coastal calanoid subgenus *Tortanus* (*Eutortanus*) in East Asia. Note the distribution of *T. (E.) terminalis* along the Pacific coast of Japan (After Machida et al. 2006 (a); Itoh et al. 2001 (b); with permission from: Springer-Verlag (a); the Plankton Society of Japan (b))

The ancient East China Sea during the Pleistocene was considered as an enormous gulf of low-salinity water in glacial periods, and as a historic center of speciation for present-day brackish taxa (Nishimura 1981). All members of the subgenus *Tortanus* (*Eutortanus*) (Fig. 22.1c) originated from this gulf and were adapted to brackish water. The only exception, *T. (E.) terminalis*, is adapted to high-salinity water, and seems to have expanded its distribution eastward along the coast of Honshu Island (Fig. 22.2b), possibly because it had originated in high salinity near the mouth of the gulf (Ohtsuka and Reid 1998).

The Ariake Sea, western Kyushu, is known for its many benthic, nektonic, and planktonic continental relicts (Sato 2000). Planktonic relicts have been studied since the first report of *Sinocalanus sinensis* by Hiromi and Ueda (1987), followed by *Tortanus derjugini*, *Acartia ohtsukai*, and *Halicyclops continentalis*, the last two of which were described as new species (Ohtsuka et al. 1995; Itoh et al. 2001; Ueda and Bucklin 2006; Ueda and Nagai 2009).

Japanese freshwaters lie within the Palaearctic region that accommodates 134 genera and 1204 species of copepods, the most speciose freshwater region in the world (Boxshall and Defaye 2008). This area is characterized by a wide species diversity of Cyclopidae (29%), Canthocamptidae (27%), and Diaptomidae (12%), and by the greatest species and family richness of fish parasites.

Freshwaters have been repeatedly colonized by copepods since the Paleozoic (Ho 1994b; Boxshall and Jaume 2000a). Wyngaard et al. (2010) studied the phylogeny and zoogeography of *Mesocyclops* from the Old and New Worlds to infer possible colonization routes. The monophyly of Old World taxa and the paraphyly of New World taxa are clear in their analysis. Three hypotheses are proposed for the origin and dispersal of *Mesocyclops* since the Cretaceous: New World origin, Laurasian origin, and West Gondwana origin. Surprisingly, even in a single species, *Eurytemora affinis*, rapid and repeated colonization from marine to

freshwater habitats has occurred (Lee 1999). Makino and Tanabe (2009) found that Japanese populations of the freshwater *Acanthodiptomus pacificus* are genetically differentiated, comprising three lineages and showing a parapatric distribution. Such divergence can be related to marine transgression and regression events, and to introgressive hybridization during the Miocene.

22.4 Ecology

22.4.1 Population Dynamics

Population dynamics of numerically important species of freshwater and marine planktonic copepods have been intensively studied. In the Seto Inland Sea, population dynamics of coastal species of calanoids, cyclopoids, and harpacticoids have been investigated by Uye and colleagues (Uye and Sano 1995, 1998; Lian and Uye 1996a, b; Lian et al. 1996; Uye et al. 2002). These studies revealed high mortality in calanoid populations during the egg stage or early stages by predation or cannibalism. In the northwestern Pacific, the ontogenetic migration and life cycles of large-sized particle-feeders such as *Neocalanus* spp. and *Eucalanus bungii* have been surveyed by Miller and Terazaki (1989), Kobari and Ikeda (2001), and Tsuda et al. (2004). These copepods are adapted to phytoplankton blooms and diapause in deep layers during non-bloom seasons (see Fig. 22.6). *Eucalanus bungii* and *Neocalanus flemingeri* exhibit biennial life cycles in the Oyashio region (Kobari and Ikeda 2001; Tsuda et al. 2004).

Life cycles of some numerically important, freshwater calanoid and cyclopoid copepods have been investigated, and special attention was paid to dormancy of eggs and copepodids (Ban 1992, 1998; Ban and Minoda 1994; Kobari and Ban 1998).

Life histories of two clausidiid copepods, *Hemicyclops gomsoensis* and *H. spinulosus* associated with invertebrate burrows, were studied in the Tama River estuary, demonstrating the significance of burrow association in generating and maintaining species diversity in mudflats (Itoh and Nishida 2007, 2008).

Recent studies have pointed out that the population dynamics of copepods are strongly influenced not only by their predators but also by parasites and parasitoids (Ianora et al. 1987; Kimmerer and McKinnon 1990; Ho and Perkins 1985; Ohtsuka et al. 2000c, 2004c, 2007a, 2011a).

22.4.2 *Distribution of Marine and Brackish Planktonic Copepods in Japan*

The current systems in the seas around Japan are complex and influence the horizontal and vertical distributions of free-living and symbiotic copepods. The cold Oyashio and the warm Kuroshio/Tsushima Currents (see Fig. 22.2b) are each well characterized by planktonic indicators (Ohtsuka and Ueda 1999). A unique phenomenon is the submergence of the Oyashio Current in Sagami Bay, where the Kuroshio is prevalent in the upper layer, and is characterized by the occurrence of deep populations of the cold-water species *Neocalanus cristatus* (Omori, 1967; Oh et al., 1991). The composition and abundance of copepods in a warm core originating from the Kuroshio were compared with those in adjacent waters of the Oyashio off northeastern Japan (Hattori 1991). The warm core strongly influenced the distributional patterns of copepods, and cold-water species such as *N. cristatus* and *Eucalanus bungii* avoided the core (Hattori 1991).

The book *An Illustrated Guide to Marine Plankton in Japan* (Chihara and Murano 1997), containing illustrated keys to species of copepods occurring in Japanese and adjacent waters, contributed much to the enhancement of ecological research in the region.

Seasonal changes in species composition and abundance of planktonic copepods in Japanese coastal waters have been intensively studied (Table 22.1). Coasts influenced by Oyashio waters are characterized by cold-water species such as *Acartia longiremis*, *A. omorii*, *A. steueri*, *Eurytemora pacifica*, *Pseudocalanus newmani*, and *Oithona similis*. Coasts adjacent to the Kuroshio Current are distinguished by warm-water species such as *Calanus sinicus*, *Parvocalanus crassirostris*, *Paracalanus parvus* s.l., *Temora turbinata*, *Labidocera japonica*, *Corycaeus affinis*, and *Microsetella norvegica*. Inlet and brackish waters in the main islands of Japan are dominated by *Acartia sinjiensis*, *A. hudsonica*, *A. erythraea*, *A. tsuensis*, *Parvocalanus crassirostris*, *Sinocalanus tenellus*, *Pseudodiaptomus inopinus*, *P. marinus*, *Oithona davisae*, and *Euterpina acutifrons*. In the Nansei Islands, brackish areas are characterized by *Acartia tsuensis*, *Pseudodiaptomus ishigakiensis*, *P. nansei*, and *Oithona dissimilis*. The horizontal zonation of planktonic copepods (Fig. 22.3) is determined by combinations of water temperature, salinity, food concentration, and predation pressure (Ueda 1991, 2001).

Extremely high abundances of *O. davisae* were recorded in the Ariake Sea (Hirota 1990), Lake Nakaumi (Ohtsuka et al. 1999), and Tokyo Bay (Itoh et al. 2011; Itoh and Nishida 2015), reaching about 1 million individuals/m³. Some coastal calanoids such as *Acartia*, *Labidocera*, *Pontella*, and *Tortanus* (*Atortus*), and cyclopoids such as *O. oculata* form dense swarms or schools during the daytime and disperse at night (Ueda et al. 1983; Kimoto et al. 1988; Ohtsuka et al. 2000b).

In subarctic to subtropical coastal waters of Japan, seasonal succession in planktonic copepod communities is remarkable, and it reflects combinations of

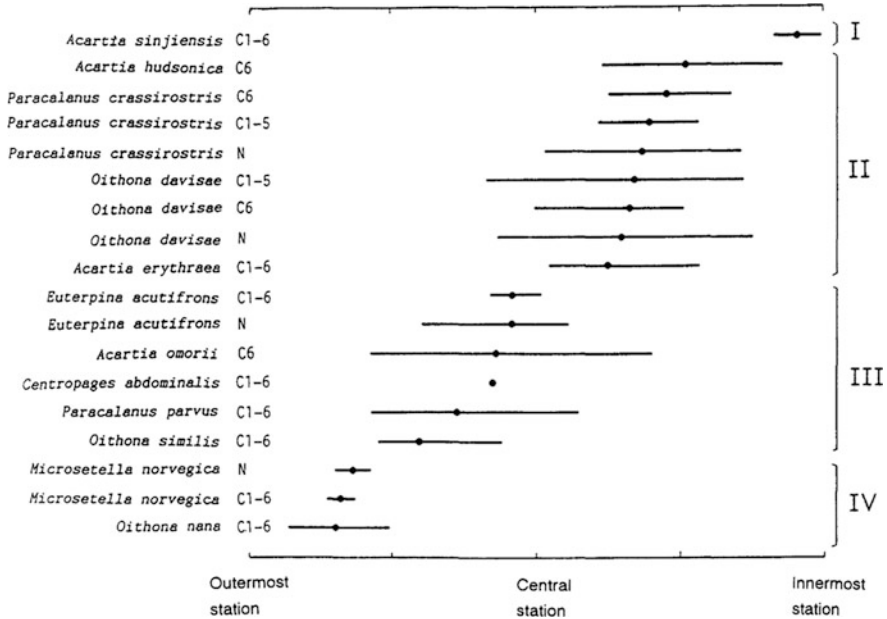


Fig. 22.3 Distribution ranges of abundant planktonic copepods in Maizuru Bay, western Japan. Horizontal lines and circles represent distribution ranges in the bay during the period of high abundance and their mean points, respectively. C1–C6 first to sixth copepodid stages, N naupliar stages, I–IV coepod communities represented by indicator(s) (After Ohtsuka and Ueda 1999, with permission from the Plankton Society of Japan)

seasonal changes in water temperature, salinity, inflow of currents, foods, and other environmental factors. Some brackish and coastal diaptomoidean taxa such as *Acartia*, *Centropages*, *Labidocera*, and *Tortanus* produce resting eggs at the beginning of a period unfavorable for planktonic adults, which diapause in sediments (Uye 1985; Ban 1998).

In Lakes Nakaumi and Shinjiko, *Sinocalanus tenellus* aggregates just above the pycnocline (Harada et al. 1985). The mechanism by which positioning of planktonic copepods is maintained during flooding in estuaries was clarified by Ueda et al. (2004). Two brackish species, *Sinocalanus sinensis* and *Pseudodiaptomus inopinus*, aggregated just above the bottom in submerged channels outside the mouth during heavy flooding. Losses from the populations, in particular of immature copepodids, were compensated by reproduction after the flood.

In oceanic calanoids and oncaeid copepods, niche partitioning by vertical habitat or food is conspicuous irrespective of feeding habits (Yamaguchi et al. 2002; Kuriyama and Nishida 2006; Nishibe et al. 2009; Matsuura et al. 2010; Sano et al. 2013, 2015; Itoh et al. 2014). Each species of the detritivorous family Scolecitrichidae (Nishida and Ohtsuka 1997) showed a specific combination of body size, vertical distribution, and diel migration pattern in the epipelagic and mesopelagic zones of Sagami Bay (Kuriyama and Nishida 2006) (Fig. 22.4,

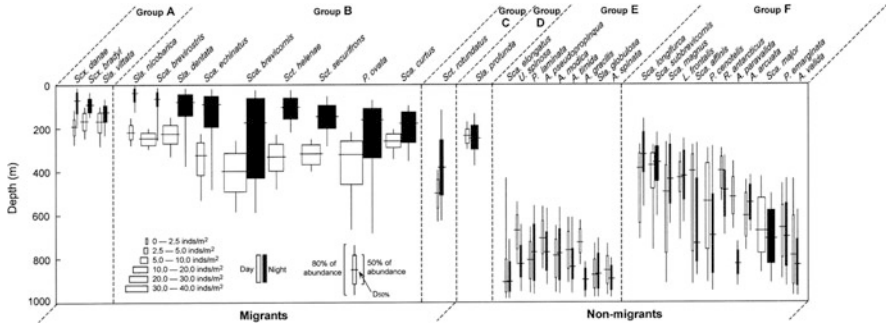


Fig. 22.4 Vertical distributions and abundance of the family Scolecitrichidae in Suruga Bay, middle Japan. The width of the box denotes the density of 50% of the population between 25 and 75% distributional depth. Abbreviated generic names: *A* *Amallothrix*, *L* *Lophothrix*, *R* *Racovitzanus*, *Sca* *Scaphocalanus*, *Sla* *Scolecithricella*, *Sct* *Scolecithrix*, *U* *Undinothrix*. See Table 22.2 for grouping. (After Kuriyama and Nishida 2006, with permission from Koninklijke Brill NV)

Table 22.2). These scolecitrichids co-exist by segregation in spatiotemporal distributions, antipredation behaviors, and diet. Carnivorous species of *Euaugaptilus* in the Sulu Sea and Celebes Sea similarly showed segregation in vertical distribution and food niche (Matsuura et al. 2010). *Oncaea* also exhibited body size-dependent niche separation in the upper 200 m in the Kuroshio Extension region, and the population size was correlated with appendicularian abundance (Itoh et al. 2014); this is explained by the feeding of oncaeids on phyto- and zooplankers retained on discarded appendicularian houses (Alldredge 1972; Ohtsuka and Kubo 1991; Ohtsuka et al. 1993, 1996a; Nishibe et al. 2015).

Molecular techniques can be applied in the analysis of copepod community structure. Hirai et al. (2013) recommended ITS2 and 28S rDNA as molecular markers for calanoids and detected high intraspecific variability in subtropical waters. Hirai et al. (2015) estimated species richness and abundance of planktonic copepods using a metagenomic approach. Such innovative techniques can be highly effective in understanding community structure.

22.4.3 Feeding: Highly Complex Feeding Habits in Oceanic Regions

High-speed cinematographic studies have revealed that particle-feeding calanoids employ suspension-feeding rather than filter-feeding (Koehl and Strickler 1981; Paffenhöfer et al. 1982). In addition, carnivory and detritivory have also been revealed in a wide variety of planktonic copepods (Nishida et al. 1991; Ohtsuka and Kubo 1991; Ohtsuka et al. 1993, 1997; Nishida and Ohtsuka 1996, 1997; Nishida et al. 2002; Sano et al. 2013). Feeding of planktonic copepods has been

Table 22.2 Groups of the Scolecitrichidae in Suruga Bay, central Japan, based on vertical distribution and diel migration pattern

Group	Ecological definition
A	Epipelagic migrants: migrant with major population in the upper 200 m both day and night
B	Interzonal migrants: migrant with major population in the upper 200 m at night and below 200 m in the daytime
C	Upper mesopelagic migrants: migrant with major population in the upper mesopelagic zone (200–400 m) both day and night
D	Upper mesopelagic non-migrants: non-migrant with major population in the upper mesopelagic zone (200–400 m)
E	Lower mesopelagic species: species with major population below 700 m
F	Mesopelagic species: species with a broad range below the 200-m layer

From Kuriyama and Nishida (2006)

intensively investigated by Japanese copepodologists since Anraku and Omori (1963) and Itoh (1970). The amazing feeding habits of oceanic calanoids have been revealed by Japanese researchers (Ohtsuka and Onbé 1989; Nishida et al. 1991, 2002; Ohtsuka and Kubo 1991; Nishida and Ohtsuka 1996, 1997; Ohtsuka and Nishida 1997; Ohtsuka et al. 1997; Matsuura and Nishida 2000; Sano et al. 2013). Specialized carnivory and detritivory are found mainly in oceanic waters.

Heterorhabdus (Fig. 22.5a) and related genera have a pair of fangs on the mandibular gnathobases (Nishida and Ohtsuka 1996). Venom or anesthetic is released from two glandular cells via paired pores on the posterior surface of the labrum (Fig. 22.5b). These glands may be modified salivary glands homologous with those of particle-feeding heterorhabdids such as *Disseta* and *Mesorhabdus* (Ohtsuka et al., 1997). Some augaptilid genera have specialized ‘button setae’ on the maxillae and maxillipeds, which may function as shock absorbers during prey capture (Matsuura and Nishida 2000). Candaciids carry heavily chitinized, sword-like elements on the maxillae, which are remarkably different from those of carnivores such as Euchaetidae, Pontellidae, and Tortanidae (Ohtsuka et al. 1987; Ohtsuka and Onbé 1991). *Candacia* is specialized for predation on gelatinous zooplankters such as appendicularians (Ohtsuka and Onbé 1989; Ohtsuka and Kubo 1991).

Detritivory is known in the so-called Bradfordian families such as Phaennidae, Scolecitrichidae, and Tharybidae (Nishida and Ohtsuka 1997; Nishida et al. 2002). The maxillae, maxillipeds, and rarely, maxillules bear special chemosensory elements to detect detrital material. Essentially two types of chemosensors are recognized: worm-like and brush-like setae (Nishida and Ohtsuka 1997). Based on ultrastructure, the former may be a general sensor and the latter a specific one. In addition to mouthpart chemosensors, the phaennid *Cephalophanes* has highly developed naupliar eyes (Fig. 22.5c) that may be used to detect crustacean detrital material via associated bioluminescent bacteria (Nishida et al. 2002).

Non-calanoids, such as *Oithona* and *Oncaea*, have been shown to exhibit different feeding habits by Japanese copepodologists. *Oithona davisae* prefers

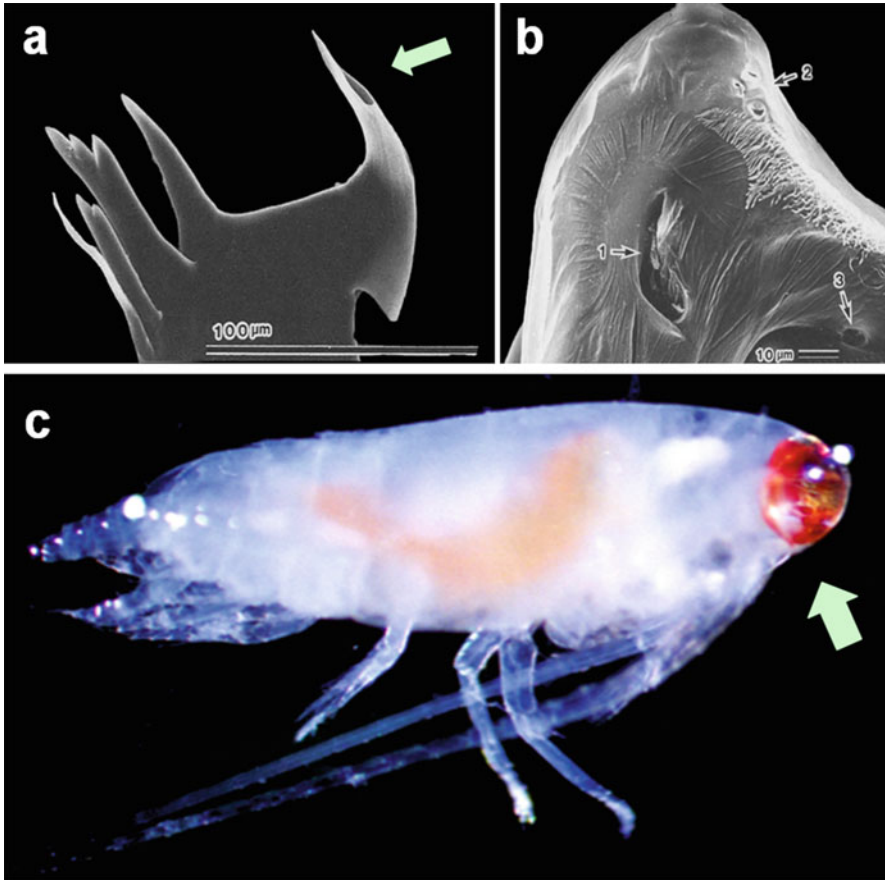


Fig. 22.5 Specialized feeding strategies of deep-sea calanoids. (a) Mandibular cutting edge of specialized carnivorous genus *Heterorhabdus*, hypodermic needle-like structure (arrowed). (b) Openings of the venom gland (1) and other secretory glands (2, 3) on posterior surface of the labrum of *Heterorhabdus*. (c) Specialized detritivore *Cephalophanes*, lateral view, large reddish naupliar eye (arrowed) (After Nishida and Ohtsuka, 1996 (a, b): with permission from Springer-Verlag)

dinoflagellates to diatoms (Uchima 1988). *Oncaea* and related genera are associated with discarded appendicularian houses, feeding on plankters retained on the appendicularian feeding nets (Ohtsuka and Kubo 1991; Ohtsuka et al. 1993, 1996a).

22.4.4 *Reproduction*

The copulatory behavior of coastal, diaptomoidean calanoids such as *Centropages*, *Labidocera*, and *Pseudodiaptomus* has been well studied by western

copepodologists (cf. Blades and Youngbluth 1979). However, those of more derived oceanic taxa (non-diatomoideans) were unknown before Tsuda and Miller (1998) observed mating behavior of *Calanus marshallae*. Diatomoideans have a geniculate right antennule in males and need several tens of minutes to complete the copulatory process (duration from grasping of mate to attachment of spermatophore) (Ohtsuka and Huys 2001). In contrast, advanced calanoids lack geniculate antennules and expend only 0.1 s to a few seconds in copulation (Tsuda and Miller 1998), which is interpreted as an antipredation strategy of the advanced taxa [=Myelinata sensu Lenz (2012)] with myelinated nerve fibers (Tsuda and Miller 1998; Ohtsuka and Huys 2001; Lenz 2012). A mating plug was first observed in a diatomoidean copepod *Tortanus (Atortus)* (Ohtsuka and Huys, 2001; Barthélémy et al., 2003).

Bioluminescence is reported in some oceanic calanoids, harpacticoids, and “poecilostomatoids” (Herring, 1988) and may be involved in mating, antipredation, and warning behaviors (Herring 1988, 2007; Herring et al. 1993; Takenaka et al. 2013). The evolution of genes coding luciferase in the oceanic Arietelloidea and their adaptive significance are explored by Takenaka et al. (2013).

Mating behavior of the planktonic cyclopoid *Oithona davisae* was observed by Uchima and Murano (1988). This behavior differs from that of calanoids in precopulatory spiraling by the male in search of a mate and to diffuse the pheromone released from the female; grasping of specialized setae on female leg 4 by both antennules of the male. The function of the special “cephalosome flap organ” (Nishida 1986) located laterally on the male cephalothorax is not clear but may be involved in perception of hydrodynamic disturbance or sex pheromones during spiraling.

Sea sapphires or males of the “poecilostomatoid” genus *Sapphirina* (Fig. 22.1f) are unique in having beautiful, species-specific iridescence caused by the multiple layers of hexagonal guanine platelets in the epidermal cells (Chae and Nishida 1994). The specific colors of the males may be involved in mating (Chae and Nishida 2004).

Precopulatory mate-guarding was investigated in the shallow-water interstitial harpacticoid *Phyllopodopsyllus* sp. (Shimanaga and Shirayama, 2005): the adult male mainly grasps the fifth and fourth copepodid stages of the female. They noted a significant correlation between the population density and the number of precocious couples.

22.4.5 Life Cycle

Diapause in freshwater and marine planktonic copepods was intensively studied in Japan in the 1970s–1990s. It is classified into three categories: egg, naupliar, and copepodid dormancy (Ban 1998). Egg dormancy is common in freshwater, brackish, and marine calanoids (Uye 1985; Ban 1998; Ohtsuka et al. 1999); copepodid dormancy is found in freshwater cyclopoids (Kobari and Ban 1998) and oceanic

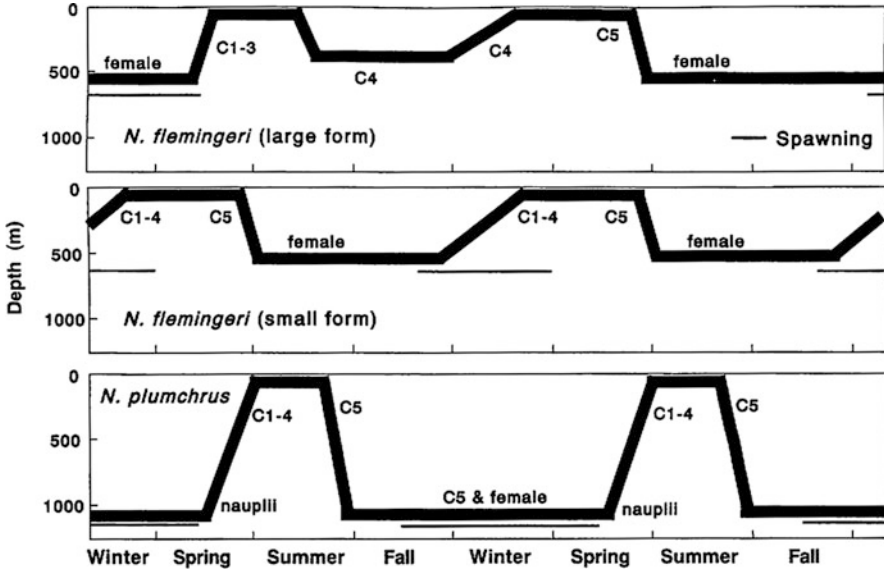


Fig. 22.6 Ontogenetic migration and biennial life cycle of the oceanic calanoids, *Neocalanus flemingeri* (small and large forms) and *N. plumchrus*, in the Oyashio region. Phytoplankton bloom occurred in April and May. C1–C5 first to fifth copepodid stages (After Tsuda et al. 2001, with permission from the Plankton Society of Japan)

calanoids (Miller and Terazaki 1989; Kobari and Ikeda 2001; Tsuda et al. 2004). Naupliar dormancy is known from the Antarctic calanoid *Paralabidocera antarctica* (Tanimura et al., 1996). As *Neocalanus* spp. and *Eucalanus bungii* are pivotal import members of the North Pacific ecosystem, their life cycles have been investigated by Japanese copepodologists (Miller and Terazaki 1989; Tsuda et al. 1999, 2001, 2004; Kobari and Ikeda 2001). They showed that spawning, growth, and diapause occur in concert with phytoplankton blooms, and that spatiotemporal partitioning was apparent among these large-sized particle-feeders (Fig. 22.6).

The life cycle of sea lice (Caligidae) such as *Caligus* and *Lepeophtheirus* has been clarified. This is a vitally important discovery, because the developmental stages of these pathogenic copepods were confused. In *Caligus*, two naupliar, one (infective) copepodid, and four chalimus stages are distinguished before adults, whereas in *Lepeophtheirus*, two naupliar, one copepodid, two chalimus, and two preadult stages are differentiated (Ohtsuka et al. 2009a; Venmathi Maran et al. 2013). Chalimi and preadults are clearly defined as postnaupliar stages between the infective copepodid and adult (Venmathi Maran et al. 2013). The number of postnaupliar (= copepodid) stages of sea lice is identical to that of other copepods (six stages, including adults) (Huys and Boxshall 1991).

In *Caligus fugu*, the site specificity of developmental stages is remarkable: copepodids infect fins of host puffer fish, and then metamorphose to chalimi firmly attached to the fin via a frontal filament, while adults temporarily attach to the host

body surface using paired lunules and the cephalothoracic sucker, and can move freely over the host (Ohtsuka et al. 2009a; Tasumi et al. 2015). The lunules are derived as modifications of the dorsal membrane along the margin of the paired frontal plates (Kaji et al. 2012).

More attention is now paid to pelagic adult sea lice, because some records of their occurrence in plankton seem not to be accidental (Ho and Lin 2004; Venmathi Maran and Ohtsuka 2008; Venmathi Maran et al. 2012b, c). For example, both sexes of *Caligus undulatus* have never been found on any fish host (Ho and Lin 2004; Venmathi Maran and Ohtsuka 2008; Suarez-Morales et al. 2012; Venmathi Maran et al. 2012b, c). There are similarities with the life cycle of some freshwater and brackish Ergasilidae (Ohtsuka et al. 2004a, b) in which adult females frequently detach from the host and swim freely in the water column.

22.4.6 Alien Problem

The introduction of alien copepods has resulted in elimination of native species, economic losses in aquaculture, and devastation of indigenous ecosystems (Fleminger and Kramer 1988; Orsi and Ohtsuka 1999; Ohtsuka et al. 2004d, 2008, 2011b; Ohtsuka and Hiromi 2009; York et al. 2014). Planktonic and benthic copepods have been introduced via ballast water or as contamination in the international trade of aquatic products (Ohtsuka et al. 2004d, 2008, 2011b). Parasitic copepods have been introduced via the international trade of aquatic products or pets (Ohtsuka et al. 2004d). No introductions of alien planktonic and benthic copepods in Japan have as yet been reported, partly because Japan is referred to as an exporter of ballast water based on foreign trade statistics (Ohtsuka et al. 2008; Ohtsuka and Hiromi 2009). Our molecular analysis suggests that the calanoid *Pseudodiaptomus marinus* has most likely been introduced from Japan to San Francisco Bay via ballast water (Ohtsuka et al. 2011b; Shimono et al., unpublished data). East Asian copepods have also been reported from European waters: *Pseudodiaptomus marinus* from the North Sea (Brylinski et al. 2012) and *Oithona davisae* from the Mediterranean (Saiz et al. 2003), the Black Sea (Temnykh and Nishdia 2012), and the North Sea (Cornils and Wend-Heckmann 2015).

The parasitic copepod *Caligus sclerotinosus* (Fig. 22.1g) has spread over western Japan since Ho et al. (2004) reported it in Oita Prefecture. It was originally described from the gilthead sea bream *Pagrus auratus* in Australia and has likely been introduced to farming areas of red sea bream *P. major* in western Japan through the import of fish seed (Ho et al. 2004; Nagasawa et al. 2010; Ohtsuka 2010). The endoparasitic copepod *Mytilicola orientalis* has been introduced from Japan to Europe and the Pacific Coast of North America via transplantation of the cultured oyster *Crassostrea gigas* and has reinfected commercial and noncommercial native bivalves in Europe (Stock 1993; Steele and Mulcahy 2001).

Ueda and Ishida (1997) surveyed the freshwater copepod fauna in Okinawa from 1984 to 1991, compared with the results of a survey by F. Kiefer more than 50 years

ago. Larger copepods such as *Mesocyclops* had disappeared, but smaller *Thermocyclops crassus* was dominant, which they suggested might have been a result of eutrophication and the introduction of planktivorous African cichlids.

22.5 Fisheries

22.5.1 *Copepods as Prey for Fish*

Relationships between feeding behavior of fish juveniles and the distribution of planktonic copepods have been investigated in the mouth of Chikugo River, Kyushu. Larvae and early juveniles of Japanese temperate bass *Lateolabrax japonicus* migrate to the turbid, low-salinity area of the river, where they prey upon the abundant calanoid *Sinocalanus sinensis* (Hibino et al., 1999; Suzuki et al., 2008). Larvae of two species of tongue sole *Cynoglossus* have different vertical distribution patterns in concert with tides, but both preferably feed on the benthic harpacticoid *Pseudobrydya* sp. (Yagi et al., 2009).

Calanoid and cyclopoid copepods such as *Acartia*, *Tortanus*, and *Oithona* form dense swarms near the bottom exclusively during the daytime (Ueda et al. 1983; Kimoto et al. 1988; Ohtsuka and Kimoto 1989; Ohtsuka et al. 2000b). Swarming is considered to be an anti-predation strategy. However, early juveniles of red sea bream *Pagrus major* and crimson sea bream *Evynnis japonica* feed primarily on planktonic copepods such as *Acartia* from the near-bottom (Kiso 1981, 1982). Anti-predation from gobies by inhabiting burrows has been suggested for the poecilostomatoid *Hemicyclops gomsoensis* by field and experimental observations (Itoh and Nishida 2013).

22.5.2 *Copepods Parasitic on Cultured Fish*

Caligids are well known as fish pests causing economic losses in marine fish farms. Pathogenic species in Japan include *Caligus fugu* on tiger puffer *Takifugu rubripes*; *C. longipes* on striped jack *Pseudocaranx dentex*; *C. orientalis* on rainbow trout *Onchorhynchus mykiss*; *C. sclerotinosus* on red sea bream *Pagrus major*; *C. spinosus* on yellowtail *Seriola quinqueradiata*; *Lepeophtheirus longiventris* on spotted halibut *Verasper variegatus*; and *L. paralichthydis* on olive flounder *Paralichthys olivaceus* (Ogawa, 1996; Nagasawa, 2004; Lester and Hayward, 2006; Ohtsuka et al., 2009b, unpublished data). The pennellid copepod *Peniculus minuticaudae* infects fins of thread filefish *Stephanolepis cirrhifer* and has expanded its distribution in western Japan and Korea (Venmathi Maran et al. 2012a; Ismail et al. 2013). These ectoparasites infect fins and skin of host fishes and cause inflammation, anemia, osmoregulatory failure, and secondary

bacterial infection (Lester and Hayward 2006). The salmon louse *Lepeophtheirus salmonis* causes heavy mortality of cultured Atlantic salmon *Salmo salar* in Europe and North America, but not in Japan (Nagasawa 2004). Coho salmon *O. kisutch* cultured in Japan is immunologically more resistant to the parasitism by caligids (Nagasawa 2004).

In freshwater aquaculture in Japan, the “poecilostomatoid” family Ergasilidae, the “cyclopoid” family Lernaecidae, and the siphonostomatoid family Lernaepodidae are recognized as pests (Johnson et al. 2004; Piasecki et al. 2004; Nagasawa et al. 2007).

22.5.3 Copepods Parasitic on Commercially or Ecologically Important Invertebrates

A highly modified copepod *Pectenophilus ornatus* is endoparasitic on the gills of Japanese scallop *Mizuhopecten yessoensis*. It is pathogenic in culture areas of northern Japan (Nagasawa et al. 1988; Suzuki and Matsutani 2009). Its prevalence on juvenile scallops reached 100 % in Miyagi Prefecture, northern Honshu (Suzuki and Matsutani 2009). In China, mass mortality of the cultured hard clam *Meretrix meretrix* was caused by the “poecilostomatoid” *Ostrincola koe* (Ho and Zhang, 1994), which is widely distributed in East Asia including Japan, and shows a wide host specificity (Kim and Sato 2010).

The life cycle and ecology of the nicothoid copepod *Neomysidion rahotsu* (Fig. 22.1i, j) parasitic on mysids was studied in the Seto Inland Sea (Ohtsuka et al. 2005a, 2007a, 2011a). The infection impacts fertility, because adult females prey upon host eggs in the marsupium. Interestingly, another parasite *Prodajus curviabdominalis* (Dajidae, Isopoda) utilizes the same host and site and possibly shows the same feeding habit. The two parasites alternate in their seasonal occupation of the host’s marsupium and, as a result, the host mysid is constantly infected throughout the year. Another nicothoid copepod *Choniomyzon inflatus* was described from the external egg masses of a commercially important fan lobster *Ibacus novemdentatus*, although its feeding habits are unknown (Wakabayashi et al. 2013).

22.6 Conclusions

Studies on the copepod biodiversity in Japanese waters are summarized as follows.

1. The species diversity of marine and freshwater planktonic copepods has been well resolved in Japanese waters since the pioneering studies of the late Drs. H. Marukawa, T. Sato, and S. Kokubo in the Taisho era (the 1910s), whereas benthic and symbiotic taxa urgently need more intensive survey. Symbionts,

especially on invertebrates, are poorly known in Japan. Cavernicolous and hyperbenthic copepods have been given less attention than in Western countries, although some have shed light on important phylogenetic and zoogeographic events.

2. Seas surrounding Japan are strongly influenced by a combination of the Kuroshio and Oyashio Currents, resulting in high species richness. These waters are zoogeographically complex, composed of a mixture of the Indo-West Pacific and East Asian elements, followed by the Okhotsk–Bering and Arctic–North Atlantic ones, in coastal waters, Tethyan relicts in the subtropical regions, and continental relicts in the Ariake Sea. The East Asian elements have originated from the ancient East China Sea since the Miocene. Freshwater taxa are essentially Palearctic.
3. Molecular studies have revealed the presence of cryptic and sibling species within common species and demonstrated the unique mitochondrial gene arrangements of copepods. Molecular techniques have become a powerful tool for rapidly estimating species composition and biomass of copepod communities.
4. The ecological attributes of copepods in Japanese waters are diverse, in response to the complex environments. Distinct seasonal changes are reflected in the complicated life cycles of marine and freshwater copepods: ontogenetic vertical migration or dormancy at the population level and succession and interspecific interactions at the community level.
5. The biology of deep-sea copepods has been intensively studied in Japanese waters. Special sensory and feeding organs of planktonic detritivores and carnivores have been revealed in taxa inhabiting deep waters off Japan. Habitat and food resource partitioning or niche separation is conspicuous in deep-sea planktonic copepods, irrespective of taxonomic group and feeding habit.
6. Brackish-water copepods, especially those inhabiting river mouths, have special strategies for population maintenance. Some brackish calanoids are very abundant and are important prey items for juveniles of commercially important fish.
7. Aquaculture is intensive in Japan, where serious problems are caused by parasitic copepods such as caligids and pennellids. Alien parasites have been introduced to Japan and are now spreading. Planktonic copepods have also been introduced from Asian countries to other regions via ballast water. Because some of them are regarded as invasive aliens with the capacity to impact indigenous ecosystems drastically, the ballast water management of the International Maritime Organization (IMO) should become effective as soon as possible.

22.7 Perspectives

Molecular techniques have driven rapid advances in copepodology. However, as many copepodologists have already noticed (Mauchline 1998), simple microscopic observations are still necessary. The taxonomic identity of the dominant planktonic species *Paracalanus parvus* s.l. on the Japanese coasts still awaits clarification. Because copepods are one of the most abundant metazoans on Earth, and are directly or indirectly related to human beings, the taxonomy, ecology, and physiology of copepods should be more intensively studied with regard to changes in global environments. In addition, we should better utilize copepods from a biomimetic aspect, as Benuys (1997) insists that biomimetics is essential to create sustainable human societies in the future. In particular, their optical and chemical sensors are so acute and compact that these could be biomimetic applications. In addition, the mystery of the rearrangement of mitochondrial genes in copepods should be solved.

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