SYMBIOSIS OF PLANKTONIC COPEPODS AND MYSIDS WITH EPIBIONTS AND PARASITES IN THE NORTH PACIFIC: DIVERSITY AND INTERACTIONS

BY

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ABSTRACT

Planktonic crustaceans such as copepods and mysids are two of the most abundant components of the marine zooplankton community and, although they harbor a diversity of symbionts, their real interactions have been poorly understood. We have been investigating planktonic symbiosis and briefly review the biology of symbionts on planktonic crustaceans based mainly on our research conducted in the North Pacific.

Symbiotic histophagous apostome ciliates probably have a significant negative impact on their coastal copepod hosts in view of their high prevalence and their worldwide distributions in the coastal ecosystems. Such symbionts are also likely to impact the populations of the copepod's predators such as chaetognaths. In contrast, symbiosis between copepods and epibionts such as diatoms and suctorian ciliates may be more or less harmless to the host.

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Various endoparasitic alveolates have been discovered infecting from copepods, some of which could have evolved as parasitoids.

Epibiont peritrichians found on the body of gastrosaccid mysids are generally regarded as a commensal, and showed a remarkably high host-specificity to intertidal species as well as a distinct geographic cline with a preference for boreal waters. The sand-burrowing behavior of the mysids, coupled with the diversity and abundance of their preys possibly contributes substantially to the establishment of the symbiotic association with epibionts. A dajid isopod and a nicothoid copepod compete for the space and possibly, food within the marsupium of the mysid host *Siriella okadai*. The annual egg production of the host *S. okadai* seems to be significantly suppressed by these two parasites. Prior to the appearance of mature adults of each of these parasites within the host marsupium, immature individuals occupy particular microhabitats within the host dependent upon the state of maturity of the host. It is important to pay more attention to parasitoid protists on zooplankters in order to better understand the aquatic ecosystem.

INTRODUCTION

The study of marine plankton has paid more attention to prey-predator relationships than to symbiosis, in part because the impact of the latter had been improperly underestimated so that symbiosis was considered to play only a minor role in the ecological interactions structuring pelagic communities (Ohtsuka et al., 2007). Recent investigations have, however, clearly revealed that symbionts have more complex and significant impacts on the population dynamics of their host zooplankters. For example, alveolate parasitoids sometimes lead to mass mortalities of host zooplankters including tintinnids, copepods, and euphausiids (Cachon & Cachon, 1987; Coats & Heisler, 1989; Kimmerer & McKinnon, 1990; Capriulo et al., 1991; Gómez-Gutiérrez et al., 2003, 2006, 2009; Ohtsuka et al., 2004, 2007; Skovgaard & Saiz, 2006). Their interactions broadly range from phoresy, to mutualism through to commensalism and parasitism to parasitoidism (Bush et al., 2001; Rhode, 2005).

The present paper briefly reviews the symbiotic relationship of copepods and mysids with a variety of microscopic symbionts based mainly on our recent investigations carried out in Japanese waters. Symbiosis is generally defined as an association between two different organisms living together, and usually with a gradient of beneficial or deleterious consequences for at least one of them (Bush et al., 2001). However, we redefine this term considering the interspecific relationships in which usually large-sized “hosts” are infested or infected by symbionts.

COPEPOD HOSTS

Apostome ciliates

Apostomes are symbiotic ciliates that mainly infest planktonic and benthic crustaceans at least during one phase of their complex life cycles, which typically include four functionally different morphs: resting phoront, feeding trophont, divisional tomont, and infective tomite stages (Chatton & Lwoff, 1935).

Vampyrophrya pelagica Chatton & Lwoff, 1930 is well investigated in terms of its morphology, cytology and ecology, and most likely plays a pivotal role in the brackish to coastal pelagic ecosystems in the world oceans due to its high prevalence and harmful impact both directly on planktonic copepods and indirectly on their invertebrate predators such as chaetognaths (Chatton & Lwoff, 1935; Grimes & Bradbury, 1992; Ohtsuka et al., 2004). Zooplanktonic invertebrate predators that prey upon parasitized copepods obtain fewer nutrients from their preys, because infected copepods are at least partly consumed by the histophagous apostome. The ciliates can increase mortality in the copepod population, if the copepod is injured by any other means, thus reducing the prey availability in the pelagic ecosystem. Thus, the trophic behavior of the histophagous apostome ciliates could have two adverse affects on higher trophic levels in the zooplankton food web: increasing copepod mortality and depleting the resources available to carnivorous zooplanktonic predators.

The life cycle of *V. pelagica* is briefly summarized below based on Ohtsuka et al. (2004), and on our unpublished data from studies carried out in the Seto Inland Sea, Japan. An oval, encysted phoront, within which one cell is enclosed, is typically attached to the ventral side of the prosome and/or to the prosomal appendages of copepods (fig. 1A, B). Host-specificity was expressed: calanoid and "poecilostomatoid" copepods (see Boxshall & Halsey, 2004), were preferred hosts in comparison of other copepod taxonomic groups, irrespective of body sizes and/or behavior, while some species of the cyclopoid *Oithona* were not selected. The infective tomite of *Vampyrophrya* was observed swimming rapidly around the body of *Oithona*, but finally moving away without successful settlement, from which we inferred some kind of physio-chemical interaction between the tomite and host body surface. High incidence of this apostome was observed between August and January, especially in later summer and fall, when prevalence was nearly 100% in the numerically dominant calanoid *Paracalanus parvus* (Claus, 1863) s.l. Its intensity could exceed 40 cells per host. This stage was characterized by a

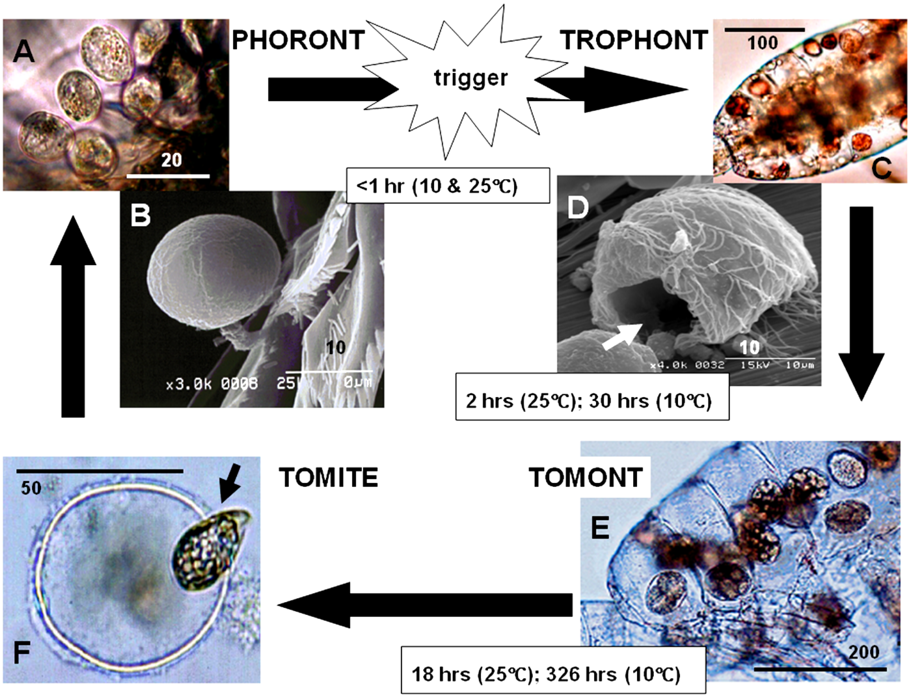

Fig. 1. Life cycle of the apostome ciliate *Vampyrophrya pelagica* infecting planktonic copepods. A, B, phoronts; C, D, trophonts (cytostome indicated by white arrow in D); E, tomonts; F, tomite (arrowed) releasing from tomont cyst. The phoront excyst having a metamorphosis to trophont stage in about 1 hr after the copepods were crashed by needles (trigger stimulus). Approximate stage durations of trophonts and tomonts at 10 and 25°C are indicated in D and E panels, respectively. Scales are in μm. (After Ohtsuka et al., 2004 with permission from Inter-Research.)

specialized intracellular structure, numerous lamellae of ca. 0.04 μm thick, which was identified as a precursor of the food vacuole membrane of the trophont.

A trophont (fig. 1C, D) excysts from a phoront when the parasitized copepods are: (1) fed upon by invertebrate predators such as chaetognaths or medusae, that break the copepod body allowing the ciliates to excyst, (2) physically damaged, and presumably, (3) unsuccessful in molting (Grimes & Bradbury, 1992; Ohtsuka et al., 2004). In any case, body fluids leaking from the copepod or physically damaged copepods trigger the ciliate metamorphosis. Feeding of fish larvae of fish such as *Plecoglossus altivelis altivelis* (Temminck & Schlegel, 1846) on parasitized copepods didn’t result in hatching of phoronts in the laboratory. Trophonts enter via fissures in the copepod exoskeleton, and commence to consume copepod tissues by a large cytostome (fig. 1D). The cell volume eventually increases to about 30 times that of the initial trophont cell. This increase in trophont size is enabled by the intracellular precursor material of the phoront. Fully-grown trophonts metamorphose into encysted tomonts inside the empty body of the consumed copepod (fig. 1E). Up to 20 tomites cells are released from a tomont. These infective cells search for a new copepod host (fig. 1F) and then metamorphose into phoronts again.

In the cold-water season they almost completely disappeare from the hosts except in large-sized species such as *Calanus sinicus* Brodsky, 1965 (∼3 mm long) with sufficient long longevity to harbor phoronts, which seem to attach just before the phase of intensive production of tomites finished. This phenomenon can be explained by the relationship between seasonal fluctuation in water temperature and duration of development of apostome life stages. In the laboratory low temperature clearly causes delay in developmental duration of each stage, in particular, of the tomont stages. Completion of the divisional stage took about 330 h for 50% cells at 10°C, about 20 times longer than at 25°C. Production of the infesting tomites appears to be suppressed by low temperature.

Suctorian and peritrich ciliates

Symbiotic relationships between suctorian ciliates and pelagic copepods have been intensively investigated in the subarctic waters of the North Pacific (Yamaguchi, 2006, unpubl.). The attachment of four epibiont suctorian genera, *Paracineta*, *Pelagacineta*, *Tokophrya* and *Trophogemma* on copepods was observed exclusively on the urosome of 10 relatively large-sized, mesopelagic species of six calanoid copepod genera. *Tokophrya* and *Trophogemma* exhibited high host-specificity on *Paraeuchaeta birostrata* Brodsky, 1950 and *P. elongata* (Esterly, 1913), respectively. The attachment of suctorians to copepods seems to be species- and stage-specific. Carnivorous hosts and adult females had higher infestation rates, suggesting higher host-specificity on hosts of larger size, greater longevity, and/or higher escape ability from predators. This means that suctorians are less impacted by being eaten by predators of the copepod hosts.

Paracineta (fig. 2F, G) and *Pelagacineta* suctorian ciliates exclusively infest adult females of the particle-feeding calanoid *Metridia pacifica* Brodsky, 1950. Prevalence was relatively higher in the Bering Sea and at higher latitudes in the North Pacific in summer and fall with an average of 9.4% (range 0-70%) (table I). A geographical gradient was also observed, with higher attachment in cold waters (<10°C) (table I).

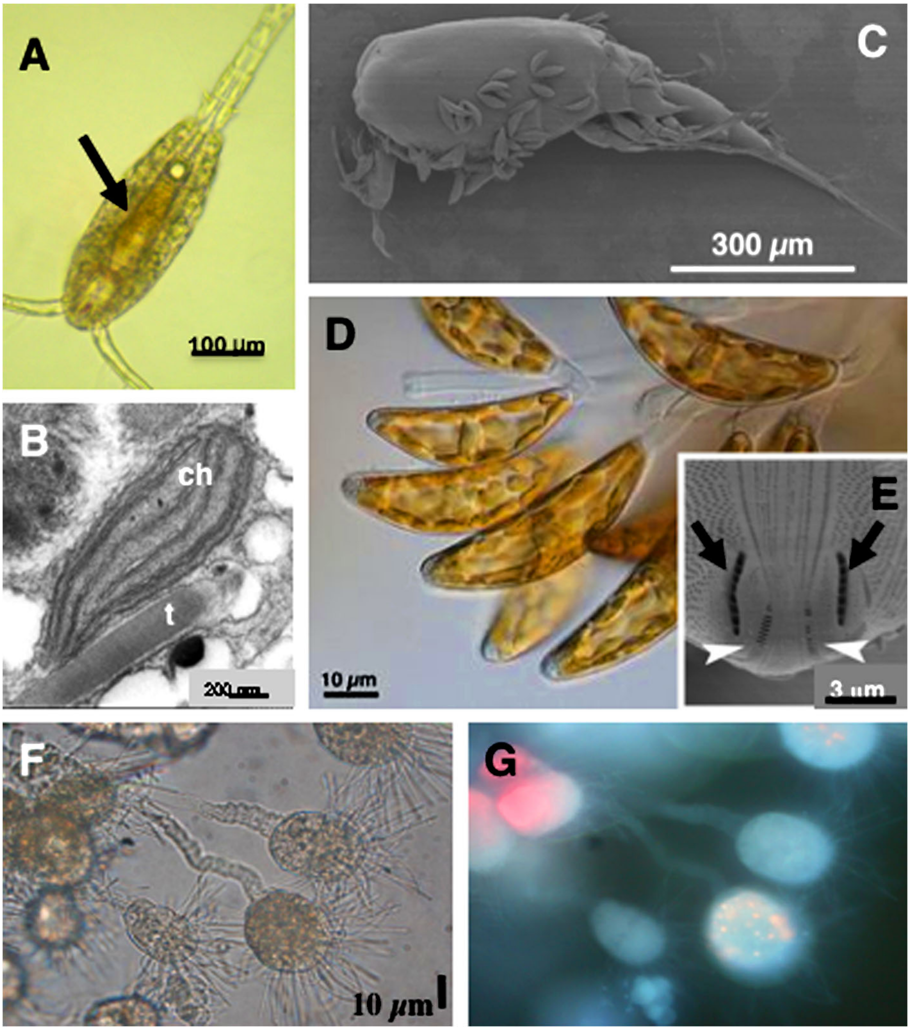

Fig. 2. A, *Blastodinium oviforme* in gut of *Oithona* sp. (arrowed); B, TEM microphoto of trophont cell of *B. oviforme*, ch = chloroplast, t = trichocyst; C, *Corycaeus affinis* infected by the diatom *Pseudohimantidium pacificum*; D, in-situ *P. pacificum* with stalks; E, two pairs of pores (attachment secretory pores indicated white arrowhead; stalk-substance releasing pores by black arrows); F, G, *Paracineta* sp., epibiont on urosome of adult female of *Metridia pacifica* (G in blue excitation with fluorescent microscope).

Adult females of *M. pacifica* infested by the suctorian ciliates contained 2.0-5.4 times higher concentration of fluorescent pigment than uninfested copepods, suggesting that the epibionts are also particle feeders (fig. 2G). Thus, copepods infested with suctorians are nutritionally more enriched for

TABLE I

Latitudinal changes in prevalence of suctorian ciliates of adult females of *Meteridia pacifica* collected during June to August 2004 in the North Pacific (after Yamaguchi, 2006)

Location	Temperature (°C)	Density (indiv. m^{-3})	Prevalence (%)
Bering Sea (177°W)			
53°30′N	8.1	63.0	67.6
Northeast Pacific (165°W)			
50°00′N	7.9	33.1	48.1
49°00′N	8.2	108.4	23.3
48°00′N	8.0	4.0	4.0
47°00′N	9.2	5.9	4.8
45°30′N	10.4	9.2	0.0
44°00′N	10.8	19.7	0.0
42°30′N	11.0	1.7	0.0
41°00′N	13.8	0.5	0.0

the copepod predators of copepods. The abundance and biomass of suctorians on copepods were estimated at 1.7×10^5 cells m^{-2} and 816 μg C m^{-2}, corresponding about 0.1-0.3% and 0.3-0.4% of those of free-living ciliates, respectively.

Dinoflagellates and their closely related alveolates

Symbiotic dinoflagellates sensu lato comprise a phylogenetically miscellaneous assemblage, according to recent genetic analyses (López-Garcia et al., 2001; Silberman et al., 2004; Skovgaard et al., 2005; Dolvin et al., 2007; Harada et al., 2007). Several dinoflagellates are extracellular parasites, while others are intracellular. Their effects on hosts vary from almost harmless (*Blastodinium*) to fatal (*Atelodinium*, *Syndinium*, etc.) (Ianora et al., 1987; Kimmerer & McKinnon, 1990; Shields, 1994; Horiguchi et al., 2006; Skovgaard & Saiz, 2006).

Blastodinium is an endoparasitic dinoflagellate found in the gut of a variety of copepods (fig. 2A). *Blastodinium* infection causes reduced survival of starved adults and sterility of infected females of the poecilostomatoid *Oncaea*, although it is almost harmless to other copepods (Skovgaard, 2005). Our observations of the ultrastructure of the trophont of *Blastodinium oviforme* Chatton, 1912 that infects *Oithona* sp. revealed the presence of chloroplasts and trichocysts in the cell (see fig. 2B), implying photosynthetic activity within the copepod gut (Pasternak et al., 1984; Ianora et al., 1987; Skovgaard, 2005). Skovgaard & Saiz (2006) reported the remarkable annual variation in occurrence of *Blastodinium* spp. parasitizing planktonic copepods in the northwestern Mediterranean Sea. They found that the highest incidence coincided with the greatest abundance of the hosts. They estimated that sterility was in the range of 0.05 to 0.16 d^{-1} for *Oncaea scottodicarloi* Heron & Bradford-Grieve, 1995. Skovgaard & Saiz (2006) also estimated that mortality rate caused by infection by *Syndinium turbo* Chatton, 1910 ranged from 0.08 to 0.15 d^{-1} for *Paracalanus parvus* females. Other endoparasites belonging to *Atelodinium* can be fatal and have been reported to cause mass mortalities of copepods in the Mediterranean Sea (Ianora et al., 1987) and Australia (Kimmerer & McKinnon, 1990). *Atelodinium* sp. parasitic on *Paracalanus indicus* Wolfenden, 1905 is reported to kill the females at the maximum rate of 41% per day (Kimmerer & McKinnon, 1990).

Diatoms

A variety of pennate diatoms (fig. 2C-E) are associated with planktonic copepods as epibionts and they show high host-specificity (Hiromi et al., 1985). Symbiosis between the diatom *Pseudohimantidium pacificum* Hustedt & Krasske, 1941 and the members of the poecilostomatoid family Corycaeidae has been investigated (Russel & Norris, 1971; Hanaoka et al., unpubl.). During the copepod mating, the diatoms can move from one to another host, using viscous secretion released from tips of the cells (white arrowheads in fig. 2E) and this transfer takes about 10 minutes. After settlement, stalk substance is released from another pair of pores on both sides of the tip (black arrows in fig. 2E). The diatoms can proliferate asexually on the body surface of the host, although the life cycle is not as yet elucidated.

Generally, these epibiont diatoms might be able to derive the following benefits from the symbiotic association (cf. Hiromi et al., 1985): (1) enhanced photosynthesis due to the near-surface distribution of copepods during the daytime; (2) replenishment of nutrient supply due to the host movement during its diel vertical migration; (3) avoidance of particle-feeders; (4) utilization of nutrients released from host bodies and/or from captured prey animals. In contrast, copepods may suffer from negative impacts due to the diatom attachment: (1) loss of energy due to increased drag in swimming and feeding; (2) greater susceptibility to visual predators due to increasing apparent volume; (3) interference with host mating.

Some ecological characteristics of copepods are related to the attachment of epibiont diatoms. Carnivorous copepods such the calanoid families Candaciidae and Pontellidae are preferred by some epibiont diatoms as hosts. However, *Sceptronema orientale* Takano, 1983 exhibits an extremely high host-specificity to the harpacticoid *Euterpina acutifrons* (Dana, 1848) which is possibly a particle-feeder (Skovgaard & Saiz, 2006; Hanaoka et al., unpubl.).

MYSID HOSTS

Ciliates

Approximately ten or more ciliate species belonging to subclasses Chonotrichia, Suctoria, and Peritrichia are known to be epibionts of mysids (Hanamura & Nagasaki, 1996; Fernandez-Leborans & Tato-Porta, 2000a, b; Fernandez-Leborans, 2001; Hanamura, 2000, 2004; Ohtsuka et al., 2006). Some species are inferred to have negative impacts on their hosts due to interference with visual perception, swimming and respiration, and to competition for food particles, while others show no discernible effects on them (Hanamura, 2000; Ohtsuka et al., 2006).

Epibiont peritrich ciliates belonging to the Vorticellidae and Epistylididae exhibit high host-specificity and show a distinct geographical cline in prevalence on the genus *Archaeomysis*, a sand-burrowing member of the Gastrosaccinae (Hanamura & Nagasaki, 1996, Hanamura, 2000; Ohtsuka et al., 2006). The ciliate infestation is restricted to intertidal boreal species, but never occur on the southern temperate inhabitants or infralittoral species or non-sand-burrowing mysids (Hanamura & Nagasaki, 1996; Ohtsuka et al., 2006). These regional infection patterns seem to be due partly to remarkable behavior of intertidal *Archaeomysis*, which swims in the water in high tide and burrows into sediments as soon as the water recedes. It is possible that high food availability may contribute to high incidence of the ciliates in northern waters. In Ishikari Bay, northern Japan, the prevalence of the peritrich ciliates on *Archaeomysis articulata* Hanamura, 1997 annually reached on average 92%, suggesting that the ciliates are capable of colonizing the new integument of the host shortly after molting takes place (Hanamura, 2000). Suctorian ciliates on the oceanic calanoid copepods show similar geographical clines, reflecting higher prevalence in cold waters (see table I).

Copepods and isopods

Dajid isopods and nicothoid copepods are common ectoparasites on the body surface or within the marsupium of mysids (Hansen, 1897; Mauchline, 1980; Rhode, 2005; Ohtsuka et al., 2005, 2006, 2007). Recently we have found

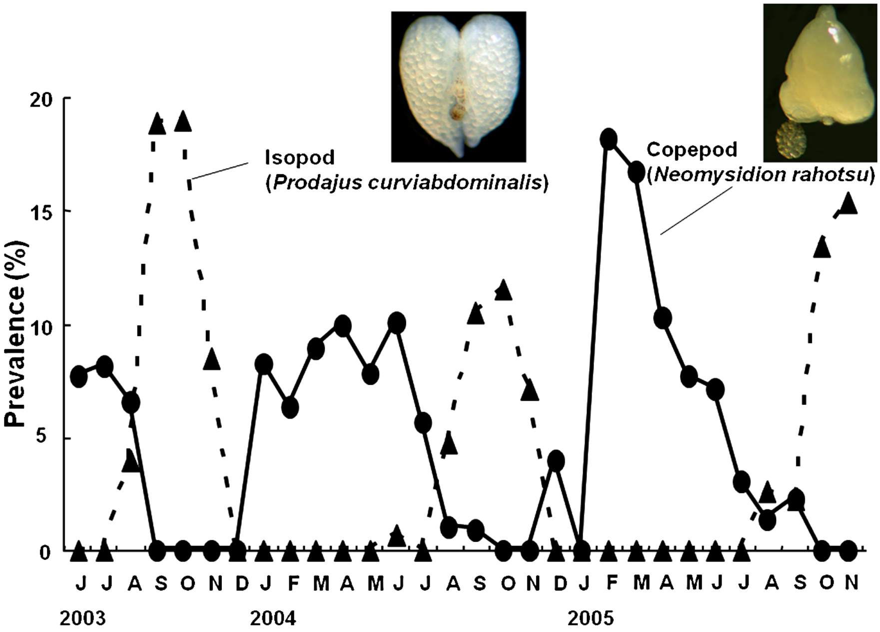

Fig. 3. Seasonal segregation of two crustacean parasites (dajid isopod *Prodajus curviabdominalis* and nicothoid copepod *Neomysidion rahotsu*) parasitizing within marsupium of the mysid *Siriella okadai*. (After Ohtsuka et al., 2007 with permission from Inter-Research.)

new taxa of these crustaceans within the marsupium of *Siriella okadai* Ii, 1964 in the Seto Inland Sea, Japan: the isopod *Prodajus curviabdominalis* Shinomura, Ohtsuka & Naito, 2005 and the copepod *Neomysidion rahotsu* Ohtsuka, Boxshall & Harada, 2005 (Ohtsuka et al., 2005, 2006, 2007; Shimomura et al., 2005). The adult copepod and, possibly, the isopod feed voraciously on host eggs. The parasites alternatively occupy the marsupium of the host (fig. 3): the presence of the parasitic isopod was restricted to the middle summer through late fall (water temperature marked >20°C), whereas the parasitic copepod was present from the mid winter to summer (<20°C) (Ohtsuka et al., 2007). Their coexistence on the same host individual was extremely rare. The isopod dominance may be caused because the females have larger body size, more motility, and possibly higher feeding rates in comparison with those of the copepod. During the occupation of the host marsupium by the isopod, the copepod may exhibit an unusual behavior that allows it to avoid predation from the isopod. The isopod life cycle probably includes a pelagic phase in which larvae utilize intermediate hosts such as planktonic copepods while adults are absent from the mysids (Ohtsuka et al., 2007).

Interestingly, immature females of these two parasites show a specific behavior to enter the host before they arrive at their final microhabitat, the marsupial lumen. The isopod penetrates the space between the carapace and dorsal tergites, while the copepod embeds itself in the host body tissue. However, the infection pathways from this initial infection site in the host body to the marsupium are still unknown. This unique parasitic behavior is shown only in the mysid females. Presumably, the infective stage of the Dajidae male directly enters the mysid female marsupium where they subsequently metamorphose into dwarf adult. The infection behavior of the Dajidae female allows for temporal coupling until the mysid host becomes mature with a fully developed marsupium, and also lowers the chance of detachment from the host. In contrast, the parasitic copepods seem to grow within the host body tissue, feeding on it.

The prevalence of females of the isopod and the copepod in the marsupium of the host mysid usually averaged 9 and 7%, respectively, with a maximum of about 20% for both parasitic species (Ohtsuka et al., 2007). Adult females of the nicothoid copepods fed on host eggs at a rate of 7 to 10 eggs female^{-1} d^{-1} (Ohtsuka et al., 2007). Considering the high prevalence and intensive feeding on the mysid host eggs, it is likely that these two parasites impact the dynamics of the mysid population. A closely related nicothoid copepod *Hansenulus trebax* Heron & Damkaer, 1986 showed high prevalence, up to 52% within on the marsupium of *Neomysis mercedis* Holmes, 1896 (Daly & Damkaer, 1986). This level of parasitism was suggested as having an adverse influence on higher trophic levels such as fish.

PERSPECTIVES

Marine zooplankters provide a diverse and dynamic substrate in the vast extent of the water column for epibionts, and can serve as food sources for parasites and parasitoids. However, precise interactions between zooplankton hosts and their symbionts are rarely studied and thus little understood. The host specificity and the life cycles of these symbionts, including information on infective stages, deserve further investigations. In particular, symbiotic alveolate protists have significant negative impacts on the population dynamics of their hosts. Therefore symbionts should be regarded as important components of aquatic food webs. We must also pay an attention to relationships between global climate change and symbiosis in the marine ecosystem (cf. Kutz et al., 2005).

ACKNOWLEDGEMENTS

We would like to express our sincere thanks to Drs. Geoffrey A. Boxshall and Rony Huys for reviewing the draft. This study was partly supported by grants from the Japan Society for the Promotion of Sciences (Nos. 20380110 awarded to SO; 21770100 to MS).

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First received 2 November 2009.
Final version accepted 11 January 2010.