

Review

Symbionts of marine medusae and ctenophores

SUSUMU OHTSUKA^{1*}, KAZUHIKO KOIKE², DHUGAL LINDSAY³, JUN NISHIKAWA⁴, HIROSHI MIYAKE⁵, MASATO KAWAHARA², MULYADI⁶, NOVA MUJIONO⁶, JURO HIROMI⁷ & HIRONORI KOMATSU⁸

¹ Takehara Marine Science Station, Setouchi Field Science Center, Graduate School of Biosphere Science, Hiroshima University, 5–8–1 Minato-machi, Takehara, Hiroshima 725–0024, Japan

² Graduate School of Biosphere Science, Hiroshima University, 1–4–4 Kagamiyama, Higashi-Hiroshima, Hiroshima 739–8528, Japan

³ Japan Agency for Marine–Earth–Science and Technology, 2–15 Natsushima-cho, Yokosuka, Kanagawa 237–0661, Japan

⁴ Ocean Research Institute, The University of Tokyo, 1–15–1 Minamidai, Nakano, Tokyo 164–8639, Japan

⁵ School of Marine Biosciences, Kitasato University, 160–4 Azaudou, Okirai, Sanriku-cho, Ohunato, Iwate 022–0101, Japan

⁶ Division of Zoology, Research Center for Biology, LIPI, Gedung Widayatswaloka, Jl Raya, Jakarta-Bogor Km 46, Cibinong, 16911, Indonesia

⁷ College of Bioresource Sciences, Nihon University, 1866 Kameino, Fujisawa, Kanagawa 252–8510, Japan

⁸ Department of Zoology, National Museum of Nature and Science, 3–23–1 Hyakunin-cho, Shinjuku, Tokyo 169–0073, Japan

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Abstract: Since marine medusae and ctenophores harbor a wide variety of symbionts, from protists to fish, they constitute a unique community in pelagic ecosystems. Their symbiotic relationships broadly range from simple, facultative phoresy through parasitism to complex mutualism, although it is sometimes difficult to define these associations strictly. Phoresy and/or commensalism are found in symbionts such as pycnogonids, decapod larvae and fish juveniles. Parasitism and/or parasitoidism are common in the following symbionts: dinoflagellates, ciliates, anthozoan larvae, pedunculate barnacles, anuropid isopods, and hyperiid amphipods. Mutualism is established between ctenophores and gymnamoebae, and between rhizostome medusae and endosymbiotic dinoflagellates. More information on symbiotic apostome ciliates, anthozoan larvae and hyperiid amphipods is definitely needed for further studies in consideration of their high prevalence and serious damage they can inflict on their hosts. The present paper briefly reviews previously published data on symbionts on these gelatinous predators and introduces new information in the form of our unpublished data.

Key words: ctenophore, host, medusa, mutualism, parasite, parasitoid, phoresy, symbiont

Introduction

Several species of marine medusae and ctenophores have been intensively investigated in recent times, partly because these gelatinous zooplankters have been increasing in line with drastic environmental changes caused by anthropological activities such as species introductions, eutrophication and global warming (cf. Arai 2001, Mills 2001, Uye et al. 2003, Uye 2008). Predation by piscivorous medusae such as the hydromedusa *Aequorea victoria* (Murbach & Shearer) on fish eggs and larvae greatly influences the prey population; it has been calculated to decrease the popula-

tion of herring larvae by up to 73% d⁻¹ off British Columbia (Purcell & Arai 2001). In the Black Sea, an introduced ctenophore *Mnemiopsis leidyi* Agassiz has devastated anchovy fisheries (cf. Shiganova 1998, Kidsey 2002). In the Japan Sea blooming of the giant medusa *Nemopilema nomurai* Kishinouye causes breakage of set nets, decrease of fish catches, and painful stings for fishermen (cf. Kawahara et al. 2006). On the other hand, rhizostome medusae such as *Rhopilema* spp. are important foods for Chinese cooking, and the average annual catches of these edible jellyfish between 1988 and 1999 in southeastern Asia and around the world were 169,000 and 321,000 metric tons, respectively (cf. Omori & Nakano 2001, Nishikawa et al. 2008). Therefore the life cycles, horizontal and vertical distributions, seasonal occurrences and physiological features have

* Corresponding author: Susumu Ohtsuka; E-mail, ohtsuka@hiroshima-u.ac.jp

been intensively studied for these species.

In contrast symbiosis between these predators and other organisms is poorly understood, although some symbionts have been suggested to influence their population dynamics (cf. Bumman & Puls 1996, Moss et al. 2001, Torchin et al. 2002, Ohtsuka et al. 2004). Many species of pelagic fish and arthropods utilize these jellies as food and refuge (cf. Arai 1988, Purcell & Arai 2001). Medusivorous fish such as the butter fish *Pseneopsis anomala* (Temminck & Schlegel) have been supposed to increase in association with proliferation of prey jellyfish (Uye & Ueta 2004). Some apistome ciliates are suggested to utilize jellyfish as a secondary host (Grimes & Bradbury 1992, Ohtsuka et al. 2004). Trophonts of the apistome *Vampyrophrya pelagica* Chatton & Lwoff hatch from phoronts on the body surface of planktonic copepods immediately after predation and ingestion by medusae and ctenophores on infected copepods, and they then consume tissues of the prey more quickly than do the predators (Ohtsuka et al. 2004). Since the prevalence of phoronts on some copepods has been reported to be constantly high (100% in *Paracalanus* sp.) during warm seasons in Japanese coastal waters, some kinds of negative impacts on the population dynamics of these

predators are inferred (Ohtsuka et al. 2004). Mutualism is also found between some scyphozoan medusae and the endosymbiont dinoflagellate *Symbiodinium* (Trench 1987). Symbiotic relationships between these two groups broadly range from simple phoresy to complex mutualism.

The present paper briefly reviews diversified symbiotic relationships between these gelatinous predators and their eukaryotic symbionts in order to comprehend their ecological roles in ecosystems. Although symbionts have been reviewed by Lauckner (1980a, b), Théodoridès (1989), Ohtsuka et al. (2000), and Kitamura (2004), we pay more attention to some special groups of symbionts with reference to their life cycles. Symbiotic terminology follows Bush et al. (2001).

Protists

Marine medusae and ctenophores play a role as one of the secondary hosts for the apistome ciliate *Vampyrophrya pelagica*, in which the whole life cycle has almost been revealed (Fig. 1) (Chatton & Lwoff 1935, Grime & Bradbury 1992, Ohtsuka et al. 2004). Soon after planktonic copepods (the first host) infected by the quiescent stage phoront of *V. pelagica* are ingested by these predators, it quickly meta-

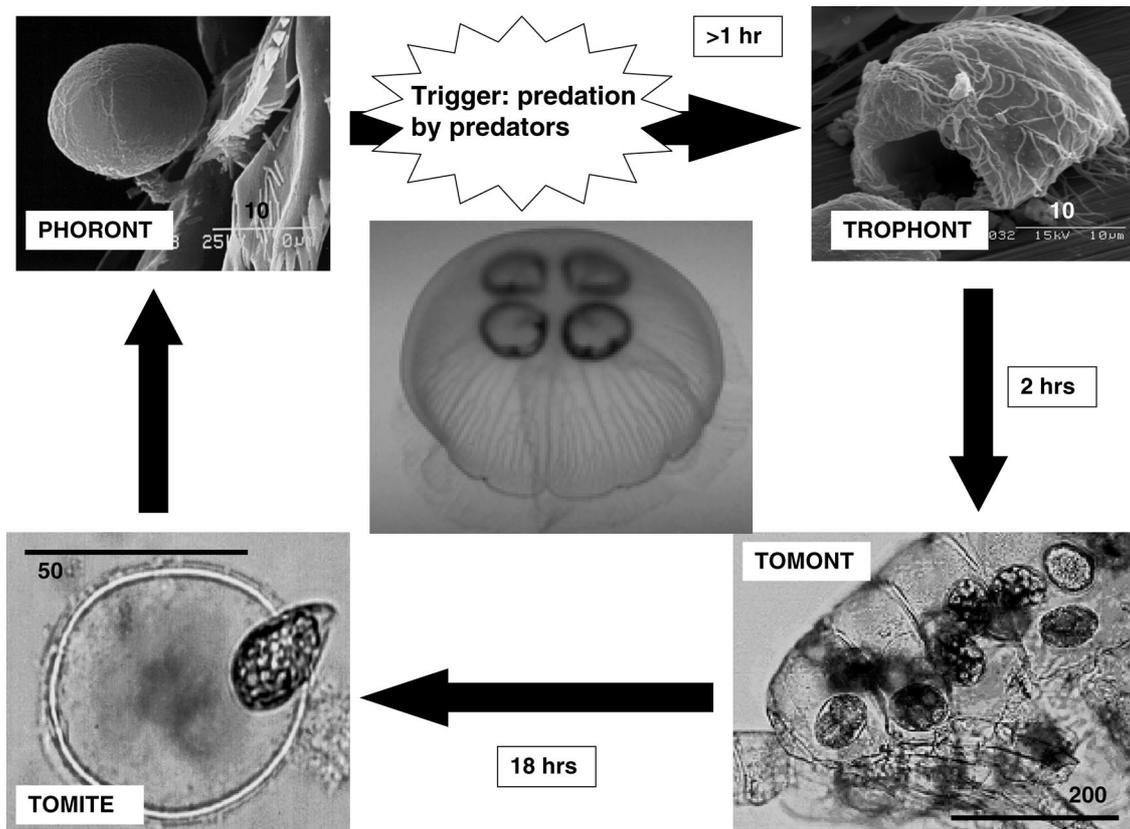


Fig. 1. Life cycle of the apistome ciliate *Vampyrophrya pelagica* after Grime & Bradbury (1992) and Ohtsuka et al. (2004). Metamorphosis from the quiescent stage phoront to the feeding stage trophont is triggered by feeding of predators such as medusae and ctenophores on copepods infected by the ciliates. Tomonts and tomites are division and infective stages, respectively. Duration of each stage at a temperature of 25°C is indicated in hr. Scales in μm. (photos of phoront, tomont and tomite cited from Ohtsuka et al. (2004) with permission from Inter-Research

morphoses into the feeding-stage trophont within the predators' digestive organs, and then consumes the prey tissues more quickly than do the predators. For the predators this implies a loss of energy during capture of prey copepods and no consequent gain of nutrients from them. Since the prevalence of *V. pelagica* on most planktonic copepods is high, up to 100% along the coasts of western Japan during warm seasons (Ohtsuka et al. 2004), it is likely that growth and reproduction of predators on these copepods are greatly inhibited during the high prevalence season. It is also suggested in the Seto Inland Sea of Japan that the population dynamics of the second host, the chaetognath *Sagitta crassa* Tokioka, are affected by the life cycle and prevalence of *V. pelagica* on prey copepods (Ohtsuka et al. 2004). Aposomes are found on a variety of shallow- and deep-water copepods (Sewell 1951, Ohtsuka et al. 2003, 2005), and might also influence their predators. However the aposomes await more detailed surveys throughout the world's oceans.

Moss et al. (2001) investigated epibiont protists on coastal ctenophores, and distinguished two kinds of symbionts: (1) inhabitants on the surface of comb plates (mobile peritrich *Trichodina ctenophorii* (Estes et al.); *Flabellula*-like gymnamoebae); (2) those on the ectoderm (*Vexillifera*-like gymnamoebae; *Protoodinium*-like dinoflagellates). Presumed interactions vary among these symbionts, mutualism for vexilliferids, commensalism for trichodinids, and parasitism for flabellulids and protoodinids on a histological basis. The parasites clearly caused damage to host tissues, probably leading to a severe detrimental effect on the predatory and escape abilities of the hosts, while no damage on the cilia of the host ctenophores was observed due to the peritrichs. A high density of flabellulids was recorded on the comb plates, up to 5,000 cells mm⁻² (average 2,726 mm⁻²). Possible mutualism between the ctenophore and the vexilliferid was inferred through the observation that the host ectoderm was remarkably clean of bacteria or other eukaryotic epibionts, presumably due to the phagocytotic feeding behavior of the vexilliferids.

Parasitic dinoflagellates on medusae are well reviewed by Lauckner (1980a) and Cachon & Cachon (1987). No additional taxonomic or ecological studies have been conducted on species associated with jellyfish since then, although further surveys are still needed. Recently much attention has been paid to the classification of parasitic dinoflagellates, using molecular techniques. Some are assigned to alveolate groups other than dinoflagellates *sensu stricto*, and their dinospores are suggested to be abundant in the water column (Harada et al. 2007). The life cycle and importance of parasitic dinoflagellates on medusae may also be clarified using molecular techniques.

Actual relationships between medusae/ctenophores and protists have been poorly understood, as suggested by Moss et al. (2001), partly because of the small sizes of the symbiotic protists and partly because of the necessity of detailed observations of their pathological impact on the hosts with

electronmicroscopy. However, considering the high prevalences and intensities of some symbiotic protists, more intensive studies are definitely necessary.

Symbiodinium (*Mutualistic dinoflagellates*)

Although a symbiont harbored within some jellyfishes is a protistian alga (a dinoflagellate frequently referred to as "zooxanthella"), it should be independently noted for its unique relationship to specific jellyfishes. The genus *Symbiodinium*, is rather well known due to its mutualistic relationship with other cnidarian animals including corals and sea-anemones, but also due to its symbioses with upside-down jellyfish (*Cassiopeia xamachana* Bigelow, *Cassiopeia andromeda* (Eschschloz)), Papuan jellyfish (*Mastigias papua* (Lesson)) and thimble jellyfish (*Linuche unguiculata* (Swartz)).

Generally, in any mutualistic relationship with zooxanthellae, organic compounds produced by photosynthesis by the symbiont are passed on to the host, mainly as glycerol but also as glucose and amino acids. In return, metabolic wastes produced by the host provide the symbiont with nitrogen and phosphorus. Nevertheless, knowledge is still scanty about nutritional fluxes between the host and the symbiont. In the thimble jellyfish *L. unguiculata*, photosynthetically fixed carbon was estimated as exceeding 10% of the medusa body carbon per day, well in excess of the respiratory demand (Kremer et al. 1990), while heterotrophic zooplankton feeding was estimated to be a major source of nitrogen and phosphorus (Kremer 2005).

Until the 1970s, *Symbiodinium microadriaticum* Freudenthal was considered as the only species of the genus; however, recent molecular genetic studies have revealed a tremendous level of diversity of the genus, which is apparently beyond the morphological remembrance (reviewed by Coffroth & Santos (2005)). Therefore, the concept of phylotypes is now substitutionally applied for *Symbiodinium* classification, and genetic clades of A through H, based on analyses of ribosomal RNA gene sequences, are well accepted for discussing diversity mapping and eco-physiological characters of *Symbiodinium* (Fig. 2). In particular, with reference to possible specific partnerships with jellyfishes, it seems that the majority of symbiont genetic types associated with *C. xamachana* are clade A (e.g. Savage et al. 2002, Santos et al. 2002) or occasionally clade B (LaJeunesse 2001).

These jellyfishes acquire the symbionts endocytotically through "horizontal transmission (from the environment)", not through "vertical transmission (maternal inheritance)". The process of the acquisition has been well documented in *C. xamachana* as a model animal. The *Symbiodinium* cell was phagocytosed by the endodermal cells and only the cells capturing live *Symbiodinium* were able to escape from digestion by avoiding lysosomal fusion (Fitt & Trench 1983). The detailed mechanisms regarding recognition and selection of *Symbiodinium* are still unknown; it may be plausible to imagine some chemical recognition event, as in

the case of lectin-glycan interaction in soft- and stony-corals (Koike et al. 2004, Wood-Charlson et al. 2006), should also be the case in these jellyfishes.

Hydrozoans

The larvae of two genera of narcomedusae, *Cunina* and *Pegantha*, are known to attach to other medusae, develop into polypoid structures such as stolo-profilers, and these polypoid structures metamorphose into juvenile medusae or to secondary larvae which will transform later on into juvenile medusae (Bouillon 1987), which then go on to feed on other gelatinous zooplankton as their primary diet in the adult stage. These polypoid stages develop almost exclusively within the gastric cavities or on the subumbrella of other medusae but not on the exumbrella. Their reported hosts include Anthomedusae, Leptomedusae, Trachymedusae, other Narcomedusae, and scyphozoans (Bouillon 1987). At present no records exist for ctenophores as hosts. The little information that is available

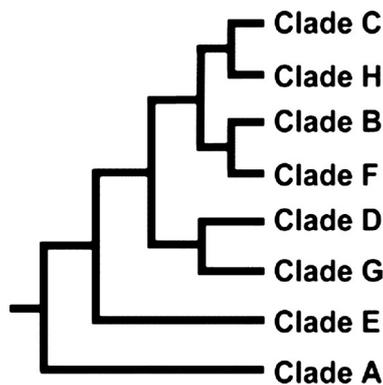


Fig. 2. Cladogram of the dinoflagellate *Symbiodinium*. Clades A–D are predominant in scleractinians, while F–H and E in foraminiferans and sea anemones, respectively. (after Coffroth & Santos (2005) with permission from Elsevier)

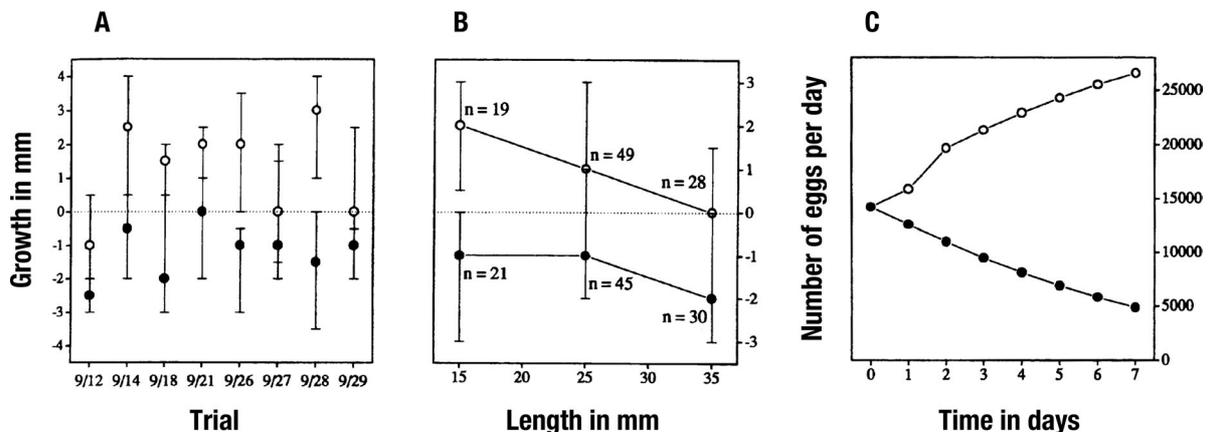


Fig. 3. Negative impacts of parasitic larvae of the anthozoan *Edwardsiella lineata* on the ctenophore host *Mnemiopsis leidyi*. A. Comparison of growth during 20 hours for parasitized (closed circle) and non-parasitized (open circles) host, median and quartiles for 8 trials in September 1995; B. Same, pooled data for all 8 trial divided into 3 classes according to the initial length (<20 mm, 20–29 mm, >30 mm); C. Total egg production of parasitized (closed circles) and non-parasitized (open circles) populations (192 individuals for each). (after Bumann & Puls (1996) with permission from Cambridge University Press).

suggests that none of these associations are species specific but extensive work using molecular markers will be needed to prove this supposition.

Anthozoans

The lined sea anemone *Edwardsiella lineata* (Verill) (the family Edwardsiidae) has a unique life cycle in which the larval phase is highly host-specific to a certain ctenophore as an endoparasite (Reitzel et al. 2006). According to them, planulae of *E. lineata* selectively parasitize *Mnemiopsis leidyi* through the epidermis or the gastrovascular cavity, and finally position themselves along the pharynx or near the esophagus or mouth inside the digestive cavity of the host. They then metamorphose into vermiform parasites with a differentiated mouth, feeding on digested prey material caught by the host through suspension-feeding. After the parasite assumes a spherical, planula-like shape, and exits the host, it reinfects another host or settles as a polyp. The endoparasite absorbs nutrients from the host, leading to its starvation and a reduction in fecundity (Bumann & Puls 1996). Both small- and large-sized parasitized individuals showed significantly lower growth rates than did non-parasitized ones even after only a short period, 20 hours (Fig. 3A, B), and the total number of eggs produced by the former was about one-fifth that of the latter after 7 days of incubation (Fig. 3C). Bumann & Puls (1996) implied that this parasite might be the only parasite affecting the host populations.

Reitzel et al. (2007) have intensively investigated the infection of the parasitic stage of *E. lineata* on three species of ctenophores off Wood Hole on the coast of the northern Atlantic during summer and early winter. The host-specificity was very strict in the following order: *Beroe ovata* Bruguière (highest prevalence 100%) > *M. leidyi* (60%) > *Pleurobrachia pileus* (Müller) (0%). However the highest incidence in *B. ovata* was indirectly caused by pre-

dation by *B. ovata* on *M. leidyi*. This is also supported by the fact that the intensity was much higher in *B. ovata* (range 1–64; average 13.9) than in *M. leidyi* (1–9; 1.97), and that the incidence was positively correlated with the host size. No infection in *P. pileus* would be due to the difference in its feeding mode in which tentacles are used for the collection of small zooplankters and the mouth is open only briefly to ingest them. In contrast *M. leidyi* employs a ramming-type feeding mechanism in which its mouth is open during swimming. This behavior guarantees an opportunity for *E. lineata* to enter the mouth of the host.

In addition to *E. lineata* larvae of two species of the genus *Peachia* (the family Haloclavidae) infect hydro- and scyphomedusae (Spaulding 1972, McDermott et al. 1982). Spaulding (1972) made a thorough investigation on the life cycle of *Peachia quinquecapitata* McMurrich infecting the hydromedusa *Clytia gregaria* (Agassiz) (as *Phialidium gregarium*) on the Pacific coast of North America. The life cycle differs from that of *E. lineata*, and is composed of two phases, the endoparasitic and ectoparasitic phases. Planulae parasitize the stomach or radial canals of the host through the mouth, and then remain in the gastrovascular cavity for an average of 11 days after infection during the endoparasitic phase. After that, the larvae move out of the mouth or burrow through the radial canal tissue to reach a gonad. The ectoparasitic larvae attach to the host by means of nematocysts, and then metamorphose into juveniles with tentacles, a siphonoglyph and a pharynx, feeding on the go-

nads of the host. After an average of 31 days the anemones are released from the host, and fall to the bottom. Juveniles of another species of *Peachia*, *P. parasitica* (Agassiz) were observed to infect the scyphomedusae *Cyanea capillata* (Linnaeus) in Chesapeake Bay (McDermott et al. 1982); juveniles with 12 tentacles attached to the subumbrella of the host by means of an expanded mouth, or were embedded in the tissues.

Trematodes, cestodes and nematodes

Lauckner (1980a, b) compiled descriptions of the relationships between parasitic helminthes/nematodes and medusae/ctenophores and information on their life cycles. Recently Marcogliese (1995, 2002) has summarized knowledge on the transmission of parasitic helminthes, acanthocephalans and nematodes through intermediate zooplankter hosts to definitive fish hosts. Generally these are considered to be generalists lacking distinct host-specificity. Trematodes such as *Derogenes*, *Lecithocladium*, *Neopechona* and *Opechona* and nematodes such as *Hysterothylacium* utilize gelatinous zooplankters as (the second) intermediate and/or paratenic hosts (Fig. 4). The majority of these parasites seem to prefer copepods, chaetognaths and euphausiids as intermediate hosts rather than medusae or ctenophores, because this may reflect the relatively higher abundance of these prey zooplankters than the gelatinous predators. Actually incidences are extremely low in the former groups, ranging from less than 0.01% to at most 1.0%, while they

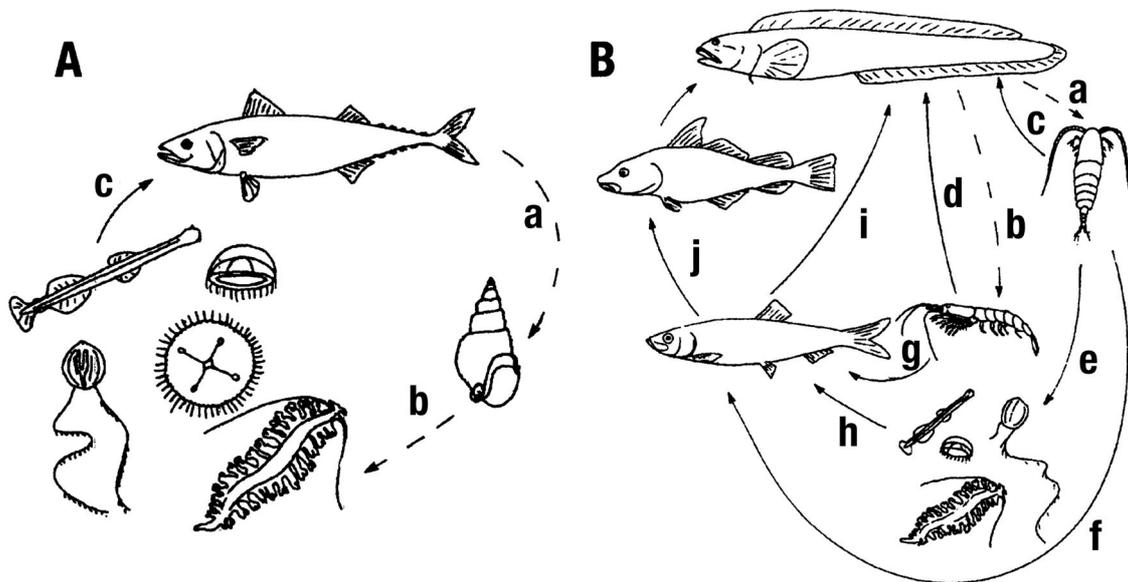


Fig. 4. Presumed life cycles of the trematode *Opechona bacillaris* (A) and the nematode *Hysterothylacium aduncum* (B). Dotted lines indicate free-living stages of the parasites. A: a. Eggs are ingested by the first intermediate gastropod host *Nassarius pygmaeus*; b. Free-living cercariae penetrate the second intermediate zooplankters such as ctenophores, medusae, polychaetes and chaetognaths; c. Infected zooplankters are ingested by the definitive host *Scomber scombrus*. B: a, b. Eggs are ingested by copepods or other crustaceans; c, d. Infected crustaceans may be ingested by definitive fish host; e. Infected crustaceans may be ingested by non-crustacean predatory zooplankters; f–h. Zooplankters may be fed upon by the intermediate or paratenic fish host; i. Infected intermediate or paratenic fish host may be consumed by the definitive host; j. Infected fish may be ingested through another paratenic host by the definitive host. (after Marcogliese (1995) with permission from Springer).

are much higher in the latter (Marcogliese 1995). Martorelli (2001) has investigated the prevalence and intensity of metacercariae of digeneans, the definitive hosts of which are fish, in two hydromedusae (*Phialidium* sp. and *Liriope tetraphylla* Chammiso & Eyesenhardt) and one ctenophore (*Mnemiopsis mccradyi* Mayer) in the Argentine Sea. The highest prevalence and intensity (30% and 2–20) were observed in *M. mccradyi* for *Opechona* sp. that infects all of the above three species as intermediate hosts and *Scomber japonicus* Houttuyn as a definitive host. These data fall within the values reported previously by Marcogliese (1995). Large invertebrate predators such as medusae and ctenophores tend to be involved in transmission of assemblages of parasites (Marcogliese 2002). One to six unidentified cestodes were reported to parasitize the infundibulum, the pharynx or the tentacle sheaths of the ctenophore *Pleurobrachia pileus* in the Georges Basin (Pagès et al. 2007b).

Recently we have found a remarkably high prevalence (100%) and intensity (over 90 per host) of metacercariae of digeneans, possibly assignable to *Neopechona* sp. (Fig. 5A) (T Shimazu pers comm), in *Aurelia aurita* s.l. (N=20, 7–25 cm in umbrella diameter) in the Seto Inland Sea, western Japan on 16 June 2008 (Ohtsuka et al. unpubl). A single individual of *Chrysaora melanaster* Brandt collected simultaneously was also infected by the metacercariae. These were exclusively found within the mesogloea of the umbrella margins and oral arms that may be bitten more readily during predation by fish that are the definitive hosts. The following fish are known to prey upon the medusae, and are regarded as candidates for their definitive hosts: *Scomber japonicus japonicus* Houttuyn; *Acanthopagurus schlegeli* (Bleeker); *Psenopsis anomala* (Temminck & Schlegel); *Stenphanolepis cirrhifer* (Temminck & Schlegel); *Thamnaconus modestus* (Günther) (Namikawa & Soyama 2000, Yasuda 2003). As already pointed out by Lauckner (1980a), the medusa-associated family Carangidae may be infected by the adults of trematodes through intermediate host medusae. In addition many dead metacercariae were found in the mesogloea, suggesting that there may be a critical duration for their transmission to definitive hosts. In the same locality in August 2008 no host was infected by the metacercariae (N=49, 6–14 cm in umbrella diameter), suggesting that their seasonal occurrence in the jellyfish is distinct.

Molluscans

Some planktonic nudibranchs belonging to the families Phylliroidea, Glaucidae and Fionidae may be regarded as symbionts on medusae, but are probably better classed as carnivorous specialists (Lalli & Gilmer 1989). All members except for the Fionidae, accommodating a single species *Fiona pinnata* (Eschscholtz), are highly specific to hydromedusae or siphonophores. For example, juveniles of *Phylliroe bucephala* Péron & Lesueur were found living on the subumbrella of the anthomedusa *Zanclaea costata* Gegenbaur, and rapidly grew while consuming it, while *Cephalopyge trematoides* (Chun) is highly specific to the

siphonophore *Nanomia* (Lalli & Gilmer 1989). The pleustonic *Glaucus* preys upon neustonic siphonophores and chondrophores such as *Physalia*, *Velevella* and *Porpita* (Lalli & Gilmer 1989). An association between the cephalopod *Argonauta argo* Linnaeus (female) and the rhizostome *Phyllorhiza punctata* von Lendenfeld was observed *in-situ* off Bohol Island, the Philippines (Heeger et al. 1992). The cephalopod grasped the exumbrella of the jellyfish with its suckers, and fed on zooplankton captured by the jellyfish through a hole in the exumbrella made by the cephalopod's biting. In addition they presumed that the cephalopod could utilize the jellyfish as protection or camouflage. Another example of an association between cephalopods and medusae is unique. Males and immature females of the planktonic, blanket octopus *Tremoctopus violaceus* Chiaie use stinging tentacles of the Portuguese Man-of-War *Physalia* spp., holding them in the suckers of two pairs of upper arms for defense against predators (Jones 1963).

Pycnogonids

Juveniles and adults of the deep-sea pycnogonid *Pallenopsis scoparia* Fage were observed to attach to the subumbrella of the scyphozoan *Periphylla periphylla* (Peron & Lesueur), feeding on its tentacles and other tissue (Child & Harbison 1986). Recently Pagès et al. (2007a) have observed juveniles and an adult male of the pallenopsid pycnogonid *Pallenopsis tritonis* Hoek piggybacking on the exumbrella of the mesopelagic anthomedusan *Pandea rubra* Bigelow, using an ROV at depths of 792–913 m off Japan. In the latter case no sign of predation was observed. Nine species of pycnogonids have so far been reported to infect hydrozoan and scyphozoan medusae with or without polyp stages (Pagès et al. 2007a).

Copepods

Humes (1969, 1970, 1985) reviewed associations between copepods and medusae. One species of Harpacticoida and six species of Cyclopoida (as Poecilostomatoida) have so far been found from scyphozoans: *Nitocra medusaea* Humes on *Aurelia* sp. (locality: New Hampshire); *Paramacrochiron ennorensis* Reddiah on unidentified medusae (India); *P. sewelli* Reddiah on *Lychnorhiza malayensis* Stiasny (India); *P. rhizostomae* Reddiah on *Rhizostoma* sp. (India); *P. japonicum* Humes on *Thysanostoma thysanura* Haeckel (Japan); *Pseudomacrochiron stocki* Reddiah on *Dactylometra quinquicirrhia* Agassiz (India); *Sewelochiron fidens* on *Cassiopea xamachana* (Puerto Rico). Regarding hydromedusae an association between deep-living copepod *Pseudolubbockia dilatata* Sars and the narcomedusa *Aegina citrea* Eschscholtz has recently been reported at depths of 606–1098 m off Monterey, California, using an ROV (Gasca et al 2006). Since not only adults but also early to late copepodid stages of the copepod were found on the subumbrella cavity of the medusae, it was supposed that the copepods utilize the host as sites for mating and molting. Humes (1985) suggested that these cope-

Pods feed on mucus secreted from the host. These cyclopoid (as poecilostomatoid) copepods were formerly assigned to the family Lichomogidae, but now belong to an independent family Macrochironidae (cf. Boxshall & Halsey 2004).

The cyclopoid family Sapphirinidae was reported to be associated with salps (Heron 1973), although it is likely to be distributed in the epipelagic zone also as free-living forms (Chae & Nishida 1995). Recently *Sapphirina nigromaculata* Claus has been observed attached to the hydromedusa *Aequorea coerulescens* (Brandt) in the shallow water of the Gulf of California, although Gasca & Haddock (2004) provided no detailed comments on the interaction.

Thecostracans

Pedunculate barnacles such as *Dosima*, *Conchoderma*, *Alepas*, *Anatifa* and *Anelasma* have been reported to attach themselves to the subumbrella, exumbrella and oral arms of scyphomedusae (*Cephea*, *Cyanea*, *Pelagia*, *Rhopilema*) or rarely, to the chitinous floats of neustonic anthomedusae such as *Velevella* and *Porpita* (cf. Pagès 2000). Most cases were relationships between *Alepas* and scyphomedusae such as *Pelagia* and *Cyanea*.

According to Pagès (2000), *Alepas pacifica* Pilsbury prefers the subumbrella, gonadal area and areas of the umbrella of scyphomedusae where few or no cnidocysts exist, and attaches itself to the host with a sucker-like peduncle rather than cement glands. Its host-specificity on *Diplumaris malayensis* Stiasny was distinct, since it has never been found on the related species *Aurelia aurita*. However the prevalence was low, at around 5%. It is likely that the barnacle not only takes particles from the ambient waters but also feeds directly on the host gonads. Therefore this is interpreted as true parasitism rather than phoresy. The attachment was recognized on the umbrella of *Cyanea nozakii* Kishinouye in the Seto Inland Sea, Japan on 27 September 2008 (Kawahara unpubl).

Isopods

The deep-sea giant isopod *Anuropus* was reported to parasitize large-sized scyphozoans (Barham & Pickwell 1969, Saito et al. 2002). Barham & Pickwell (1969) first observed *Anuropus bathypelagicus* Menzies & Dow (8 cm in body length) riding under the umbrella of the scyphozoan *Deepstaria enigmata* Russell at a depth of 723 m in the San Diego Trough, using a submersible, and thought that its host-specificity might be high. A pair of *Anuropus* have also been observed attached to *Deepstaria enigmatica* at 929 m in Sagami Bay (Lindsay et al. 2001) and at 669 m depth off the east of the main island of Japan (41°00'N, 144°41'E) using an ROV (Lindsay et al. 2004).

Saito et al. (2002) collected a juvenile (22.3 mm long) and two immature females (35.5, 76.2 mm long) of *Anuropus pacificus* Lincoln & Jones together with a giant scyphomedusa (*Stygiomedusa* sp.?) of over 1 m in diameter at depths of 500–600 m off the western part of the mainland

of Japan. These blind giant isopods can be regarded as a true parasite, utilizing scyphozoans as food and as a vehicle for transportation.

Amphipods

Harbison et al. (1977) and Laval (1980) reviewed symbiotic relationships between hyperiid amphipods and cnidarians/ctenophores. These are important to compile previous data on the comprehensive biology of hyperiids. The families Lanceolidae and Lycaeidae are associated with scypho- and hydromedusae, while the Paraphronimidae, Lycaeopsidae, Pronoidae, Platyscelidae, Parascelidae and some species of the Phronimidae exclusively prefer siphonophores; the family Oxycephalidae is highly host-specific to ctenophores but can occasionally be found on hydromedusae and it seems specificity is high within different geographical areas but that the preferred host can vary between geographic areas (Lindsay unpubl); the families Hyperiididae and Dairellidae parasitize various medusae and/or ctenophores. Their degree of dependence on hosts varies according to species. Some are essentially parasitoids, and totally depend on the host for the entire life cycle (Laval 1980). In contrast *Parathemisto gaudichaudii* (Guerin) and *Hyperia* spp. (Hyperiididae) are loosely associated with salps or medusae during the juvenile stages only (Harbison et al. 1977, Laval 1980, Dittrich 1988). Associations also seem to be sex-dependent. In some species males tend to spend more time in free-living mode swimming in the water than females, and this can also be speculated in species where no direct observations have been made due to morphological features such as a more developed urosome with larger pleopods and a more produced rostrum in the former than in the latter.

The life cycles of hyperiids are also diversified. Eggs are laid in the female marsupium or directly onto the host. The latter case can be seen in *Bougisia ornata* Laval (Hyperiididae) in which eggs are laid deep in the mesogloea of the umbrella of the leptomedusa *Phialidium* by the female (Laval 1980). The number of eggs of hyperiids is relatively high in comparison with that of benthic gammarid amphipods, ranging from 10 to less than 600 per brood (Laval 1980). Generally hyperiids hatch directly as manca stages, in which two “larval” stages, i.e., pantchelid stage with an undifferentiated abdomen and a subsequent protoplean stage with a segmented abdomen but without fully developed pleopods and uropods, can be distinguished before the “juvenile” stages with an almost fully developed abdomen (see Laval 1980); a number of hyperiids hatch at the protoplean stages. After demarsupiation (transfer of the young from the marsupium to the host), the juveniles start feeding on host tissues, prey captured by the host, or both. In some species of the Hyperiididae on medusae, juveniles grow on the hosts, feeding on prey captured by the medusae and/or body fluids from the radial canals of the hosts, while in *Brachyscelus* (Lycaeidae) on medusae individuals seem to consume host tissues directly (Harbison et al. 1977, Laval

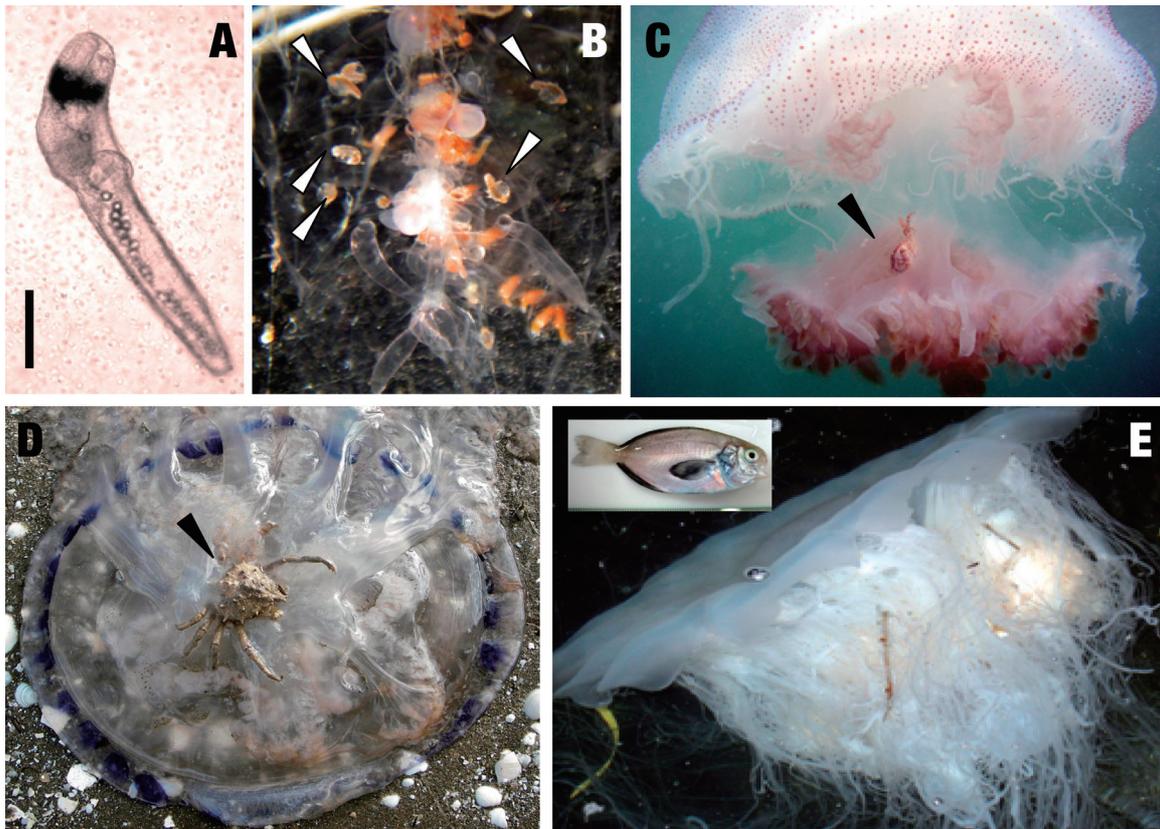


Fig. 5. Symbionts of medusae found in the present study. A. Metacercaria larva of a tentatively identified digenean *Neopechona* sp. found in the mesoglea of the scyphozoan *Aurelia aurita* s.l. collected in the Seto Inland Sea, Japan (16 June 2008), scale bar=0.1 mm; B. Juveniles of the hyperiid family Pronoidae (arrowed) in the bracts of the physonectid siphonophore *Agalma okenii* collected from the Nansei Islands, Japan (22 May 2008); C. Portunid crab *Charybdis feriata* (arrowed) riding on the oral arms of the rhizostome scyphozoan *Rhopilema hispidum* found off Thanh Hoa, Viet Nam (21 April 2007); D. Spider crab *Libinia ferreirae* (arrowed) riding near the mouth of the rhizostome scyphozoan *Lychonorrhiza lucerna* captured off San Clemente, Argentina (21 March 2006); E. The scyphozoan *Cyanea nozakii* collected in the Seto Inland Sea, Japan (5 August 2008), with which young individuals of butterflyfish *Psenopsis anomala* were associated (inserted).

1980). Juveniles of *Eupronoe* sp. (Pronoidae) are encysted in the mesogloea of nectophores and bracts of physonectid siphonophores (Fig. 5B), and are suggested to feed on pre-digested food from the radial canals of the host (Harbison et al. 1977). Adult females tend to continue to stay with the host for continuous oviposition and/or maternal care, while males are free-swimming predators (Harbison et al. 1977, Laval 1980).

The life cycle of the cosmopolitan hyperiid *Hyperia galba* (Montagu) was investigated in the North Sea by Ditttrich (1988) in detail. Its hosts were scyphomedusae such as *Aurelia aurita* (24.3%), *Chrysaora hyoscella* (Linnaeus) (63.2%), *Rhizostoma pulmo* (Macri) (7.6%) and *Cyanea capillata* and *C. lamarckii* (Linnaeus) (4.7% in combination): 99.8% of all hyperiids were associated with these scyphomedusae, while only 0.2% occurred free in the water column. The seasonal occurrence of the hyperiid was correlated with that of scyphomedusae in the water column. In May or June associations between small medusae and the hyperiids first appeared, while no ephyrae were parasitized

by the amphipods in early spring. Prevalence and intensity increased with season, finally reaching more than 80 to 100% and about 10 to over 80, respectively, in fall. The highest number of hyperiids per host (486) was found on *C. hyoscella*. At the end of October or in early November both the host and the parasite disappeared from the water column. During the period of non-occurrence of the hyperiids in the water column the parasites are suggested to hibernate on benthic polyps. Breeding was restricted to August–October for adult females of 7.0 to 13.6 mm body length, in which the fecundity ranged from 61 to 456 eggs per female. Two generations were annually assumed. Durations for embryonic development and intermolt at 10 and 15°C, which approximately corresponds to the minimum and maximum water temperatures during the occurrence period of the parasites, were 19.0 and 31.5 and 12.5 and 19.1 days, respectively. Consequently it took about 9 months to grow up to an adult of 9 mm long at 15°C. Ditttrich (1988) suggested that since *H. galba* feeds mainly on plankters captured by the host and occasionally on the host

tissues (Laval 1980), the high prevalence and intensity of the hyperiid on scyphomedusae directly caused a breakdown of the hosts. The species was also reported to prey upon the tissue of the ctenophore *Beroe* sp. in the Gulf of Maine and adjacent waters (Pagès et al. 2007b).

New findings concerning associations between hyperiids and gelatinous zooplankters have been accumulating, using SCUBA and ROV (Gasca & Haddock 2004, Gasca et al. 2006, Lindsay et al. 2008). Recently maternal care has been discovered in a species of the family Oxycephalidae, *Oxycephalus clausi* Bovallius, parasitic on the ctenophore *Ocyropsis crystallina* (Rang) in the Gulf of California (Gasca & Haddock 2004), in addition to the well-known hyperiid family Phronimidae (Harbison et al. 1977, Laval 1980). Many new combinations of associations between hyperiids and medusae were also revealed in the surface and deep-waters off California with an ROV and SCUBA (Gasca et al. 2006).

Some species of gammarid and caprellid amphipods are also associated with hydro- and scyphomedusae (Vader 1972), most of which can be regarded as commensalism (as inquilinism) (Théodoridès 1989). The mesopelagic gammarid *Parandania boeckii* (Stebbing) prey upon scyphomedusae such as *Atolla* spp. (Moore & Rainbow 1989).

Decapods

Caridean shrimps can be associated with large-sized scyphozoans (Bruce 1972). The rhizostome *Mastigias papua* collected from the Pacific coast of middle Japan harbors three species of carideans on the oral arms: one pandalid *Chlorotocella gracilis* Balss and two hippolytids, *Latreutes anoplonyx* Kemp and *L. mucronatus* (Stimpson) (Hayashi & Miyake 1968). Of these *L. anoplonyx* seems to be more closely associated with medusae (Hayashi & Miyake 1968), and has also been found attached to *Nemopilema nomurai*, *Rhopilema esculentum* Kishinoue, *Rhizostoma* sp. and *Acromitus flagellatus* (Häckel) (Hayashi et al. 2004). Copulation and breeding of *L. anoplonyx* seem to occur on the host medusae (Hayashi et al. 2004). In contrast the other two species have been frequently found as plankton, suggesting that they are more loosely associated with medusae (Hayashi & Miyake 1968).

Marliave & Mills (1993) have found interesting relationships between larvae of the facultative-symbiont pandalid shrimps and host hydromedusae in the laboratory and field on the Pacific coast of North America. In the field, zoeal stages of six pandalid species were observed piggyback-riding on hydromedusae of nine species, one ctenophore and discarded appendicularian houses. Incidence of larvae of *Pandalus danae* (Stimpson) on *Proboscoidactyla flavicirrata* (Brandt) and other hydromedusae was usually low, but rarely up to about 50%. Their laboratory experiments clearly showed that the piggyback-riding of pandalid shrimp larvae caused negative impacts on the behavior and growth of the host, leading to death, due to an increase in energy load. However the hitchhiker neither damaged nor

fed on the host. This interaction may be regarded as an extreme example of phoresy.

Phyllosoma larvae of scyllarid lobsters have been frequently observed to rest on exumbrellar surfaces of hydromedusae and scyphomedusae or to hold one to three small medusae with the third or fourth pereopods (Shojima 1963, Thomas 1963, Herrnkind et al. 1976). Off the western shore of Bimini, the Bahamas in October 1973, high prevalence, 19.9% (N=402) was recorded between phyllosoma larvae of *Scyllarus* and *Aurelia aurita*. According to Shojima (1963), these associations were observed only at night. Although real interactions between them are still unclear, it is supposed that the riding of phyllosoma on medusae saves swimming energy and helps in avoiding predation (Herrnkind et al. 1976). Recently a scyllarid lobster phyllosoma was reported to swim while dragging a prayid siphonophore behind it, suggesting importance as food and/or defense against predation but refuting the idea of energy-saving due to transportation (Ates et al. 2007). A recent molecular technique with 18SrDNA has been applied to identification of food items of some species of scyllarid and palinurid phyllosoma larvae, and suggested that these feed on appendicularians, salps and cnidarians (Suzuki et al. 2006).

Juveniles of the portunid crab *Charybdis* (*Charybdis*) *ferriata* (Linnaeus) (Fig. 5C) were observed to attach to the oral arms of *R. esculentum* caught in Sagami Bay on the Pacific coast of the mainland of Japan (Suzuki 1965), *Rhopilema hispidum* (Vanhöffen) off Thanh Hoa, Viet Nam (21 April 2007: see Nishikawa et al. 2008) and *Mastigias* sp. off Cirebon, Indonesia (10 September 2008: Nishikawa pers obs), respectively. Suzuki (1965) regarded this symbiotic relationship as exploitation, but it may correspond to phoresy defined by Bush et al. (2001), because juveniles and adults of some portunids are occasionally associated with floating algae for dispersal (Suzuki 1965). Recently Nogueira & Haddad (2005) have reported an association between the rhizostome *Lychnorhiza lucerna* Haeckel and the spider crab *Libinia ferreirae* Brito Capello (Fig. 5D) off San Clemente, Argentina, in which prevalence was recorded at only 8%. Considering the attachment of only megalopa larvae and young individuals of the crab, the medusae seem to be utilized solely as a floating nursery before settlement (Nogueira & Haddad 2005).

Ophiuroids

Fujita & Namikawa (2006) summarized associations between six species of rhizostome medusae (*Rhopilema hispidum*, *R. esculentum*, *R. nomadica* Galil, Spanier & Ferguson, *Cephea cephea* (Forskål), *Netrostoma* sp., an unidentified rhizostome) and relatively small individuals (6–12 mm in disc diameter) of the ophiuroid *Ophiocnemis marmorata* (Lamarck) in the Indo-West Pacific. This species is the only ophiuroid associated with medusae, certainly grasping the jellyfish with terminal hooklets of the arms. The association is supposedly formed by the vertical migra-

tion of the rhizosomes: when the medusae descend near or on the sea-bottom, the brittle star hitchhikes on them. The ophiuroid seems to utilize the medusae for dispersal, in some cases, at distances up to 1,000 km.

Fish

Arai (1988, 2005) and Purcell & Arai (2001) comprehensively reviewed interactions between medusae/ctenophores (as coelenterates) and fish, in which five categories were distinguished: (1) predation by fish on coelenterates; (2) predation by coelenterates on fish; (3) competition among fish and coelenterates; (4) coelenterates as intermediate hosts for fish parasites; (5) swimming association between fish and coelenterates. We focus on the last category (mutualism and commensalism) rather than on predation and competition herein. A number of fish, in particular, post-larval fish rather than larvae, are associated with large-sized scyphomedusae, siphonophores and some ctenophores (Arai 1988, Purcell & Arai 2001). The most famous association is between the man-of-war *Physalia physalia* Linnaeus and *Nomeus gronovii* (Gamelin), in which both eat and be eaten (Arai 1988). In the fish, special behavioral and chemical defence mechanisms against the toxic medusae are known (Arai 1988). This may be an instance of commensalism. A different commensal relationship between juveniles of walleye pollock *Theragra chalcogramma* (Pallas) and scyphomedusae (mainly *Chrysaora melanaster* followed by *Cyanea capillata*) was found in the surface waters of the Bering Sea, using an ROV (Brodeur 1998). Their association was restricted mainly during the daytime. At night *C. melanaster* remained around the thermocline at depths of 35–40 m, while juvenile pollock separately aggregated near the surface. Since pollock fed neither on the medusae nor on their parasitoid hyperiids, he concluded that juvenile pollock are considered to be facultative commensal or simply show a thigmotactic response to floating objects such as medusae.

The association between scyphomedusae such as *C. capillata* and *Rhizostoma octopus* (Linnaeus) and juveniles of whiting *Merlangius merlangus* (Linnaeus) may be an example of mutualism, cleaning of parasites on the medusae by the whiting and medusan protection due to their toxins for the whiting (Arai 1988). However, there are controversial observations between them, probably depending on differences in individuals and the age of the fish. Facultative and obligatory associations with medusae exist in the families Gadidae, Carangidae, and Stromateidae plus at least six other families (Purcell & Arai 2001). As symbiotic fish grow, they tend to become predators (Arai 1988, Purcell & Arai 2001). The bythitid fish *Thalassobathia pelagica* Cohen seems to associate with the bathypelagic scyphomedusa *Stygiomedusa gigantea* (Browne) in a species-specific manner (Drzen & Robison 2004). Associations of fish with siphonophores include that of juvenile caristiid fish with the cystonect *Bathyphysa conifera* (Studer) (Janssen 1989) and the calycophoran *Praya* sp. (Lindsay et al. 2001),

where it seems that the fish steals food from and eats pieces of its siphonophore host as well as using it for defence (Janssen 1989). The myctophid fishes *Leuroglossus stilbius* Gilbert and *Stenobranchius leucopsarus* (Eigenmann & Eigenmann) have been observed in situ in association with the physonect siphonophore *Apoemia* sp. (Robison 1983).

Yasuda (2003) reviewed fish associated with *Aurelia aurita* and others that mainly occur in Japanese waters. Larvae of *Psenopsis anomala*, *Decapterus maruadsi* (Temminck & Schlegel) and *Rudarius ercodes* (Jordan & Fowler) are associated with *A. aurita* which they use as a refuge, and only the first doesn't prey upon the host. We also observed at least five young individuals of the butterfish *P. anomala* (Fig. 5E, inserted: standard length of one individual collected with a dip net: 64 mm) associated with *Cyanea nozakii* (Fig. 5E: bell diameter 43 cm) feeding on *A. aurita* s.l. in the middle part of the Seto Inland Sea, western Japan on 5 August 2008; this association was reconfirmed between one individual of *C. nozakii* (bell diameter 39 cm) and one young butterfish (48 mm) on 1 September 2008 (Ohtsuka & Kawahara pers obs). The young fish may feed indirectly on *A. aurita* captured by the jelly-predator rather than directly on it, utilizing it also as a refuge.

As pointed out by Purcell & Arai (2001), these associations may be involved in transmission of parasites such as digeneans, cestodes and nematodes from the intermediate hosts to the final fish hosts.

Summary

Medusae and ctenophores consist of a unique community in pelagic ecosystems, since they harbor a wide variety of symbionts. The associations range from phoresy to parasitoidism or mutualism, although it is sometimes difficult to discriminate among them. These gelatinous predators are simply utilized as a substrate or a refuge in the vast water column by some symbionts, and as food or food suppliers for others. More complicated associations are also known in several symbionts. The symbionts on these animals could be tentatively classified into the following categories, although not only further *in-situ* observations but also laboratory experiments are required to uncover their exact relationships.

Phoresy: lubbockiid copepods; pycnogonids; zoea of pandalid shrimps; juveniles of crabs; ophiuroids; fish

Parasitism: dinoflagellates; larvae of edwardsiid and haloclavid anthozoans; macrochironid and harpacticoid copepods; stalked barnacles; anuropid isopods; phyllosoma larvae of scyllarid lobsters; cephalopods

Parasitoidism: hyperiid amphipods

Commensalism: peritrich ciliates; copepods; zoea of pandalid shrimps; fish

Mutualism: dinoflagellate *Synbiodinium*; vexilliferid gymnameobae

Predation: nudibranchs; cephalopods; fish

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Note in proof

Complicated relationships among a scyphozoan and two ectosymbionts were revealed in the following paper: Towanda T, Thuesen EV (2006) Ectosymbiotic behavior of *Cancer gracilis* and its trophic relationships with its host *Phacellophora camtschatica* and the parasitoid *Hyperia medusarum*. *Mar Ecol Prog Ser* 315: 221–236.