

Planktonic Phases in Symbiotic Copepods: a Review

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Abstract.—In symbiotic copepods, most naupliar stages are typically planktonic, playing a primary role in dispersal, while the first copepodid usually represents the infective stage. Later copepodid stages, including adults, are associated with host organisms. Many symbiotic copepods have abbreviated life cycles, with a reduced number of naupliar stages and two different feeding habits. These patterns are presumably related to distinct life cycle strategies. Exceptional cases are exemplified by members of the Monstrillidae and Thaumatopsyllidae, both of which are protelean parasites, with infective nauplii and non-feeding planktonic adults. In the Caligidae, the life cycle follows a generalized pattern, but adults of many species like *Caligus undulatus* seem to exhibit a dual mode of life involving host switching. Adults leaving the first host become temporarily planktonic before attaching to the final host. This dual mode of life is also found in adults of the Ergasilidae. Abbreviation of the planktonic phase is characteristic for some symbiotic taxa, thus suggesting that they have evolved to become highly efficient in locating and infecting new hosts without needing long-distance larval dispersal. The life cycle of copepods associated with zooplankters is also briefly reviewed. Zooplankters are clearly less used as hosts by copepods than benthic invertebrates. It is likely that symbiotic copepods dynamically utilize planktonic phases in their life cycle, thus maintaining the balance between dispersal, host location, reproduction, and predator-avoidance strategies.

Symbiotic copepods have one or more planktonic phases for dispersal, infection, host-switching, mating, and presumably, predator-avoidance (Kearn 2004; Huys 2014; Venmathi Maran et al. 2016). Usually, the primarily planktonic naupliar stages play a key role in dispersal. The first copepodid stage is infective, and the subsequent stages, including adults, then typically establish a symbiotic association with a host organism. In some taxa, adults are also a swimming stage for dispersal, mating, host-switching, and presumably predator-avoidance. In the Ergasilidae, adult females of some taxa seem to show a dual mode of life

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Taxon	NI	NII	NIII	NIV	NV	NVI	CI	CII	CIII	CIV	CV	Adult
<i>Hemicyclops spinulosus</i> Itoh and Nishida, 1998 (Clausididae)	○	○	○	○	○	○	○	○	○	○	○	○
Ergasilidae spp. (♀)	○	○	○	○	○	○	○	○	○	○	○	○
<i>Ergasilus genuinus</i> (Kokubo, 1914) (♀)* (Ergasilidae)	○	○	○	○	○	○	○	○	○	○	○	○
<i>Cancerilla tubulata</i> Dalyell, 1851 (Cancerillidae)							○	○	○	○	○	○
<i>Scottomyzon gibberum</i> (T. and A. Scott, 1894) (Scottomyzontidae)							○	○	○	○	○	○
<i>Lernaea cyprinacea</i> Linnaeus, 1758 (♀) (Lernaeidae)							○	○	○	○	○	○
Thaumatopsyllidae		○	○									
Caligidae spp.								○	○	○	○	○
<i>Caligus undulatus</i> Shen and Li, 1959* (Caligidae)								○	○	○	○	○
<i>Lernaeocera branchialis</i> (Linnaeus, 1767) (♀) (Pennellidae)								○	○	○	○	○
Monstrillidae		?					?	?	○	○	○	○
<i>Choniomyzon inflatus</i> Wakabayashi, Otake, Tanaka and Nagasawa, 2013 (Nicothoidea)									?	?	?	○
<i>Aiella pagelli</i> (Kroyer, 1863) (as <i>A. macrotrachelus</i> (Brian, 1906) (Lernaeopodidae)												○
<i>Salmincola californiensis</i> (Dana, 1852) (Lernaeopodidae)												○
<i>Peniculus minuticaudae</i> Shilno, 1956 (♀) (Pennellidae)												○
<i>Gonophysema guillemarensis</i> Bresciani and Lützen, 1960 (♀) (incertae sedis)												○
<i>Cucumaricola notabilis</i> Paterson, 1958 (Cucumaricolidae)												○
<i>Neomysidion rahotsu</i> Ohtsuka, Boxshall and Harada, 2005 (Nicothoidea)												○

planktonic
 infective
 parasitic
 semi-parasitic
 abbreviated
 feeding
 ? unknown

Fig. 1. Life cycle of representatives of symbiotic copepods. Note abbreviated naupliar stages. * represents only adults showing different pattern from those of other congeners. Based on: Paterson (1958); Kabata and Cousens (1973); Kawatow et al. (1980); Alston et al. (1996); Kearns (2004); Ohtsuka et al. (2004a, c, 2007, 2009); Boxshall (2005); Itoh and Nishida (2007, 2008); Dojiri et al. (2008); Suarez-Morales (2011); Ismail et al. (2013); Venmathi Maran et al. (2013, 2016); Huys (2014); Otake et al. (2016).

interfacing between hosts and the water column, while adult males are truly planktonic without any interaction with the host (Urawa et al. 1980a, b; Ohtsuka et al. 2004a). In the Caligidae, most species follow the above generalized life cycle, but adults of some species most likely show a dual life mode like some ergasilids (Ho and Lin 2004a; Venmathi Maran and Ohtsuka 2008; Suárez-Morales et al. 2012; Venmathi Maran et al. 2012a, b, 2016). In some species of the mesoparasitic family Pennellidae, pre-mated adult females and adult males are planktonic prior to mating in the water column (Kearns 2004; Ismail et al. 2013). Extremely aberrant life cycle types are found in the protelean life cycle of the Monstrillidae and Thaumatopsyllidae, in which the earliest naupliar stage is infective, and non-feeding adults remain truly planktonic during mating and dispersal (Malaquin 1901; Grygier and Ohtsuka 1995, 2008; Dojiri et al. 2008; Suárez-Morales 2011). The present paper briefly reviews the planktonic phases displayed by different groups of symbiotic copepods, and discusses their evolutionary and adaptive strategies.

Patterns of Planktonic Phases in Life Cycle

In general, symbiotic copepods primitively have six naupliar (NI–NVI) and six copepodid (CI–CVI) stages, the last of which corresponds to the adults, thus showing the maximum number of 12 developmental stages (Raibaut 1996; Boxshall 2005; Huys 2014). A typical example of such a complete life cycle in symbiotic copepods is displayed by the “Saphirella”-like forms (= *Hemicyclops* Boeck, 1873 and related genera) whose six naupliar stages actively feed (Fig. 1). Their first copepodid stage is frequently recorded as being abundant in coastal waters (Itoh and Nishida 1991), thus leading to the erroneous assumption that they are holoplanktonic during the entire life cycle (Gooding 1988; Itoh 2006). Their subsequent five copepodid stages are known to be loosely associated with benthic animals including ghost shrimps and polychaetes (Itoh and Nishida 2007, 2008).

The number of naupliar stages among symbiotic copepods is highly variable (i.e., 0, 1, 2, 3, 4 to 6), depending on the group and feeding types (Fig. 1). The planktotrophic

forms are characterized by the development of basal antennary and mandibular elements (Izawa 1986, 1987; Alston et al. 1996; Dojiri et al. 2008; Itoh and Nishida 2008), but these elements are absent from the lecithotrophic forms (Carton 1968; Kawatow et al. 1980; Urawa et al. 1980a; Izawa 1986, 1987; Grygier and Ohtsuka 1995, 2008; Ohtsuka et al. 2009). Lecithotrophic nauplii are common to most truly parasitic taxa belonging to the orders Cyclopoida (including “Poecilostomatoida”) and Siphonostomatoida (Paterson 1958; Carton 1968; Izawa 1986, 1987; Raibaut 1996; Boxshall 2005; Ivanenko et al. 2007). Nauplii generally play a key role in dispersal, irrespective of their feeding strategy. Some species of the Nicothoidae (Paterson 1958; Boxshall 2005; Ohtsuka et al. 2007; Huys 2014) and Pennellidae (Boxshall 2005; Ismail et al. 2013; Huys 2014) are devoid of naupliar stages, and directly hatch as an infective copepodid. Remarkably, the aberrant families, Monstrillidae and Thaumatopsyllidae have infective nauplii (Fig. 1).

Copepodids of symbiotic copepods are usually feeding-stages, whose food items depend on a variety of hosts (Fig. 1). The permanent association with a host commences at the first, second or sixth (adult) copepodid stage (Boxshall 2005). In Caligidae and most other symbiotic families, the first copepodid is the infective stage. In the Ergasilidae, the first to fifth copepodid stages, adult males and pre-mated adult females are semi-planktonic, while postmated adult females infect fish hosts (Urawa et al. 1980b; Kearn 2004). The feeding habits of these semi-planktonic stages remain largely unknown. Kearn (2004) hypothesized that ergasilid copepodid stages and unmated adults feed on planktonic organisms. On the other hand, considering that the mouthparts of free-swimming copepodids resemble those of parasitic adult females, it may be inferred that they are able to feed on tissues and blood of any kind of fish host. This is indirectly supported by Alston et al. (1996), who obtained all copepodid stages of *Ergasilus briani* Markevich, 1933 in an experimental tank using the tench *Tinca tinca* (Linnaeus, 1758).

In some fish-parasitic families such as the Caligidae and Ergasilidae, adult females of some species are also free-swimming, and exhibit a dual mode of life involving switching between the host and the water column (Ho and Lin 2004a; Ohtsuka et al. 2004a, c; Venmathi Maran and Ohtsuka 2008; Venmathi Maran et al. 2012a, b, 2016; Suarez-Morales et al. 2012).

Some species of Pennellidae and Caligidae require both an intermediate and a definitive host (Bush et al. 2001; Kearn 2004; Hayward et al. 2011; Ismail et al. 2013; Huys 2014; Venmathi Maran et al. 2016). In these cases, adults are temporarily planktonic, actively searching for a new host.

Bizarre Life Cycle

In the Monstrillidae and Thaumatopsyllidae, the first nauplius is the infective stage, the subsequent stage(s) are endoparasitic, and adults are truly planktonic and non-feeding, lacking mouthparts (Suárez-Morales and Tovar 2004; Huys 2014; Suárez-Morales et al. 2014). The life cycles of these families have to a great extent been elucidated by Malaquin (1901), Caullery and Mesnil (1914), and more recently by Suárez-Morales and Tovar (2004), Dojiri et al. (2008), and Suárez-Morales et al. (2014). Differences between these two groups are found in the number of naupliar and copepodid stages in their life cycle. In the Monstrillidae, the life cycle consists of only one planktonic, infective lecithotrophic naupliar stage, at least 3 endoparasitic copepodid stages, and non-feeding planktonic adults (Fig. 1) (Malaquin 1901; Grygier and Ohtsuka 1995, 2008; Suárez-Morales 2011; Suárez-Morales et al. 2014). Huys (2014) regarded the early endoparasitic stages as naupliar

stages. From Malaquin's (1901) illustrations of the endoparasitic stages, two forms can be differentiated: sack-like bodies without and with paired absorptive processes. These may correspond to naupliar and copepodid stages, respectively. According to Malaquin's (1901) detailed observations, the naupliar body has vitelline tissues during these first endoparasitic stages and the feeding tubes are clearly underdeveloped and probably not functional. Therefore, it is likely that they do not feed on the host fluids until the individuals molt into successive copepodid stages in which the absorptive processes are fully developed. In contrast, thaumatopsyllids have one planktonic/infective and one or more endoparasitic naupliar stages, plus five or six non-feeding planktonic copepodid stages including adults (Fig. 1) (Suárez-Morales and Tovar 2004; Dojiri et al. 2008; Hendler and Dojiri 2009).

In these two groups, the presence of non-feeding planktonic adults implies very limited dispersal abilities. Development in free-living copepods generally takes 2-4 weeks from nauplii to copepodids, and 1-2 months or longer for adults (Hendler and Dojiri 2009). This duration is clearly abbreviated in the non-feeding adult stage, and more significantly affected in monstrillids than in thaumatopsyllids, because the former has a single planktonic instar (the adult) while the latter has 6 (copepodids I-V and adult). Furthermore, monstrillid adults can be locally abundant in the water column, particularly during nighttime or at dusk (Sale et al. 1976, 1978; Suárez-Morales 2001; Grygier and Ohtsuka 2008), thus suggesting an effective synchronized mating strategy to compensate for their short longevity. In contrast, the planktonic phase of the thaumatopsyllid *Caribeopsyllus amphiodiae* Ho, Dojiri, Hendler and Deets, 2003 seems to be ca. 3 days during the development from first to sixth copepodids, with adults surviving 3–27 days in culture (Hendler and Dojiri 2009).

Abbreviated Development

Reduction in the number of developmental stages, in particular naupliar instars, is common in symbiotic copepods in contrast to free-living taxa which typically display the ancestral complement of stages (i.e., six nauplii, six copepodids) (Raibaut 1996; Kearn 2004; Boxshall 2005; Huys 2014). The number and duration of these developmental stages appear to have been evolutionarily determined by feeding, predator-avoidance and reproductive strategies of symbiotic copepods, the life modes of host organisms, and other biological/environmental factors (see Hendler and Dojiri 2009). An extreme abbreviated case is found in the nicothoid *Neomysidion rahotsu* Ohtsuka, Boxshall and Harada, 2005 infecting mysids, in which only two stages are known: one copepodid stage for dispersal and infection, and the reproductive adult (Ohtsuka et al. 2005, 2007). The absence of entire naupliar stages seems to be related to the swarming behavior of the host mysid *Siriella okadai* Ii, 1964, occurring in surface waters at night (Ohtsuka et al. 2007), thus suggesting high local host availability for the infective stage during that time. The abbreviation of the copepodid stages is presumably due to the small size of the host organism. In fish-parasitic copepods, the full number of copepodid stages is common. Similarly, the ascidian endoparasite *Gonophysema gullmarensis* Bresciani and Lützen, 1960 shows highly abbreviated developmental stages, with one lecithophic nauplius, one copepodid, an onychopodid (a reduced preadult larva), and adults (Bresciani and Lützen 1961).

Planktonic Adults of Caligidae and Ergasilidae

The elucidation of the caligid life cycle has been hampered by defining the correct number of developmental stages (Ho and Lin 2004a), but this dispute was settled recently

(Ohtsuka et al. 2009; Hamre et al. 2013; Venmathi Maran et al. 2013). The caligid development includes two naupliar, one copepodid (Fig. 2A–C), four chalimus stages, and the adult in the genus *Caligus* Müller, 1785 (Fig. 1), and two naupliar, one copepodid, two chalimi, two preadult stages, and the adult in *Lepeophtheirus* von Nordmann, 1832.

The occurrence of adults of the Caligidae in plankton samples has previously been attributed to their accidental detachment from the host fish (Ho and Lin 2004b; Venmathi Maran and Ohtsuka 2008; Venmathi Maran et al. 2016). Although some species like *Caligus undulatus* Shen and Li, 1959 frequently occur in the plankton, their hosts remain unknown (Venmathi Maran et al. 2016). Their ovigerous adult females were also found from plankton, but carried relatively fewer eggs per egg-string in comparison with congeners known from fish hosts (Venmathi Maran and Ohtsuka 2008; Ohtsuka et al. 2009). In *C. undulatus*, the number of eggs per string is at most 4, but in other congeners obtained from fish hosts off Japan and Taiwan, the number reaches up to 253 (Ohtsuka et al. 2009), thus implying that planktonic adults have limited access to food, possibly only during temporary contact/infection on fish. This behavior may be considered as an anti-predation strategy to avoid being consumed by cleaners, although it renders the parasites more vulnerable to predation by planktivorous fish (Venmathi Maran and Ohtsuka 2008; Venmathi Maran et al. 2016).

In three species of *Caligus*, host switching from wild intermediate fish to farmed definitive fish has been reported in Norway (Heuch et al. 2007), Australia (Hayward et al. 2008, 2009, 2011), and Japan (present study). In Norway, wild lumpfish *Cyclopterus lumpus* Linnaeus, 1758 seems to serve as an infection reservoir for *Caligus elongatus* von Nordmann, 1832 before it eventually infects farmed Atlantic salmon *Salmo salar* Linnaeus, 1758 (Heuch et al. 2007). In Australia, only adults of *Caligus chistos* Lin and Ho, 2003 parasitize farmed southern bluefin tuna *Thunnus maccoyii* (Castelnau, 1872), and cause eye damage eventually leading to blindness (Hayward et al. 2008, 2009). Hayward et al. (2011) discovered that Degen's leatherjacket *Thamnaconus degeni* (Regan, 1903) residing outside the tuna cages serves as the wild intermediate host for chalimi development. In Japan, a similar phenomenon occurs in *Caligus sclerotinosus* Roubal, Armitage and Rohde, 1983 (Fig. 2D), a species that might have been introduced from Australia to Japan (Ho et al. 2004). It has spread among farms of red seabream *Pagrus major* (Temminck and Schlegel, 1843) in western Japan (Ho et al. 2004; Ohtsuka et al. 2010) and Korea (Venmathi Maran et al. 2012c). We document herein the prevalence and intensity of *C. sclerotinosus* on farmed *P. major* in Uwajima, Shikoku, Japan, from May 2006 to October 2007 (Fig. 3). In total, we examined 205 individuals of *P. major* and recovered 2,052 individuals of *C. sclerotinosus* from the hosts (mean standard length: 27.3 to 294.5 mm) (Fig. 3A). Among the caligids examined, only 3 chalimi (0.2%) were found on one occasion (December 2006) during the entire investigation period, and the remaining samples consisted primarily of adults (97.2%) and several unidentified, damaged individuals (2.6%) (Fig. 3B). Prevalence was constantly high, except for August 2006 (0%), reaching 100% in July 2006 and from December 2006 to October 2007, with mean intensity ranging between 1.4 (October 2006) and 26.3 (June 2007) (Fig. 3A). The intermediate host of *C. sclerotinosus* is still unknown. In these two cases, actively swimming adults searching for definitive hosts are regarded as a re-infective stage (Heuch et al. 2007). It is unknown whether such host switching is restricted to fish farms or not.

In the Ergasilidae, some species show a dual mode of life similar to that found in some Caligidae. Generally, copepodid stages I–V of representatives of *Ergasilus* von Nordmann, 1832 and related genera occur in the plankton, while the adult males die after mating

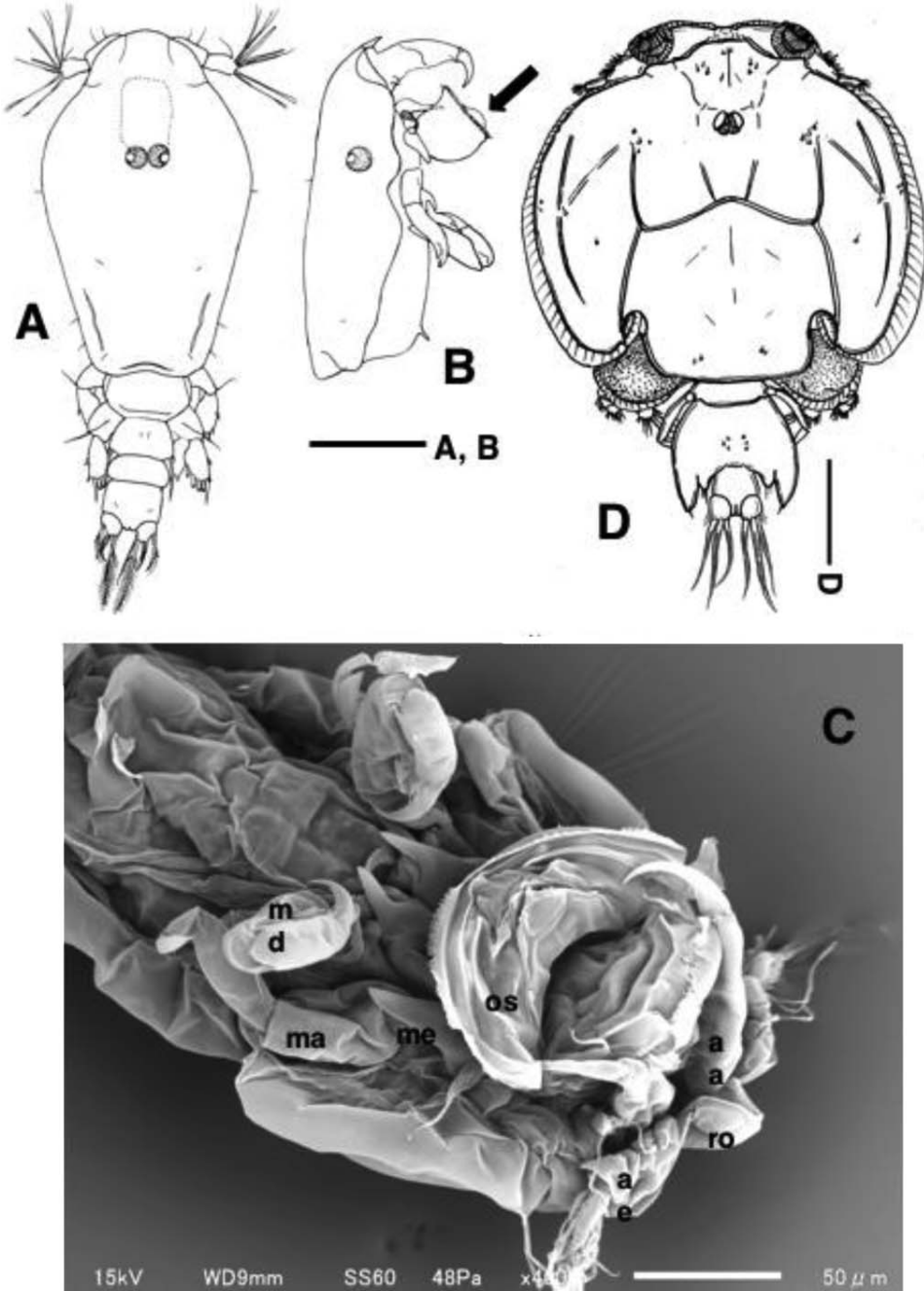


Fig. 2. *Caligus sclerotinosus* Roubal, Armitage and Rohde, 1983. (A) Copepodid I, dorsal view; (B) Cephalothorax of copepodid I, lateral view, with large oral cone indicated by arrow; (C) SEM micrograph of ventral view of cephalothorax of copepodid I. ae: antennule; aa: antenna; ma: maxilla; md: maxilliped; me: maxillule; os: oral sucker; ro: rostrum; (D) Adult male, dorsal view. Scale bars = 0.2 mm (A, B); 0.05 mm (C); 0.5 mm (D).

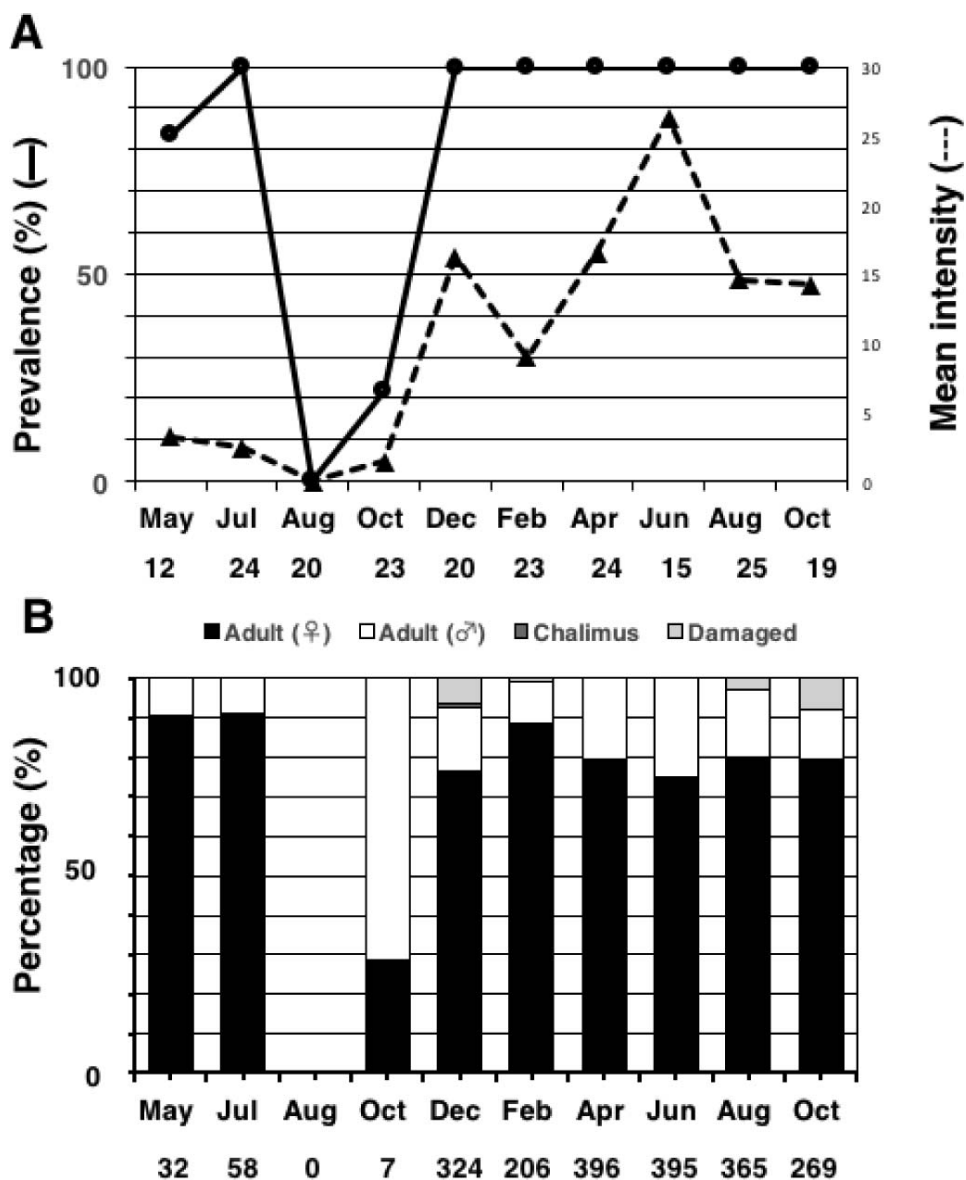


Fig. 3. Prevalence and mean intensity (A) and stage composition (B) of *Caligus sclerotinosus* Roubal, Armitage and Rohde, 1983 infecting farmed *Pagrus major* (Temminck and Schlegel, 1843) in Uwajima City, Japan, from May 2006 to October 2007. Numbers below months indicate total number of hosts collected and total number of parasites examined, respectively.

in the water column, and mated adult females become parasitic (Urawa et al. 1980a; Alston et al. 1996; Kearns 2004). However, the occurrence of ovigerous adult females of some ergasilids has been reported in plankton communities (Ohtsuka et al. 2004a, c). They have a relatively slender cephalothorax, not expanded like *Ergasilus lobus* Lin and Ho, 1998 [see Fig. 2A in Lin and Ho (1998)], and carry relatively fewer eggs in each sac com-

pared to other congeners permanently attached to host (Ohtsuka et al. 2004a), indirectly suggesting that these show a dual mode of life like that observed in *Caligus undulatus*. In Japanese waters, the enigmatic genus *Limnoncaea* Kokubo, 1914 was originally described from plankton samples (Kokubo 1914) and was later found to encompass species of two ergasilid genera, *Ergasilus* and *Thersitina* Norman, 1905, rendering it a junior subjective synonym of *Ergasilus* (Ohtsuka et al. 2004a, b, c).

Symbiotic Copepods on Plankters

Many copepods are symbiotically associated with phyto- or zooplanktonic organisms, and may complete their entire life cycle in planktonic communities. Associations between host plankters and symbiotic copepods are summarized in Table 1. Copepod symbioses in plankton communities are rare in comparison with those in benthic communities, partly because of the relatively lower diversity, shorter longevity, and smaller size (except for jellyfish and colonial forms like salps) of potential planktonic hosts (cf. Karplus 2014). Surprisingly, no record of the occurrence of symbiotic copepods has been reported from copepods and euphausiids in contrast to mysids (e.g., Mauchline 1998; Boxshall and Halsey 2004; Gómez-Gutiérrez et al. 2010). Two types of copepod symbionts on plankters can be recognized: (1) both naupliar and copepodid stages associated with the host (i.e., Miraciinae); (2) only copepodid stages, including adults, symbiotic on plankters (all other known cases). Although nauplii and copepodids of Miraciinae were thought to feed on *Trichodesmium* (Cyanobacteria) (Tokioka and Bieri 1966; Huys and Böttger-Schnack 1994; O'Neil and Roman 1994), gut content and stable isotope analyses (Eberl et al. 2007) have recently suggested that these copepods utilize the filamentous cyanobacteria as a habitat rather than a food source. All naupliar stages of a miraciinid *Macrosetella gracilis* (Dana, 1847) seem to be unable to swim (see Tokioka and Bieri 1966). Harpacticoids such as *Parathalestris cronii* (Krøyer, 1842) associated with floating macroalgae (Ingólfsson and Ólafsson 1997; Huys 2016) may also belong to the first type.

The complete life cycle of the truly parasitic species *Cardiodectes bellottii* (Richiardi, 1882) (as *C. medusaeus* (Wilson, 1908)) (Pennellidae) was described by Ho (1966) and Perkins (1983). The copepodid of *C. medusaeus* infects planktonic gastropod molluscs (i.e., Cavoliniidae and Janthinidae) as intermediate hosts, and then metamorphoses into the first chalimus stage (Ho 1966; Perkins 1983). After three molts of the chalimi on the hosts, adult females and males mate in the water, and then actively seek the definitive myctophid fish host. In this species, the planktonic phase comprises the copepodid and pre-copulatory adults. This species appears to lack a naupliar stage.

The life cycle of two nicothoids, *Hansenulus* Heron and Damkaer, 1986 and *Neomysidion* Ohtsuka, Boxshall and Harada, 2005, were unraveled by Heron and Damkaer (1986) and Ohtsuka et al. (2007), respectively. The planktonic/infective copepodid attaches to the mysid body surface, and finally lodges itself within the host marsupium involving either no or a few molts. Other genera and species of nicothoids were described from mysids by Hansen (1897).

Copepodids and adults of some species of the Macrochironidae are associated with medusae (Ohtsuka et al. 2015). However, the occurrence of host medusae in the plankton is seasonally limited for several months (Ohtsuka et al. 2012). In addition, free-swimming adults of some macrochironids have been described from the Indo-West Pacific (Wilson 1950; Browne and Kingsford 2005; Mulyadi 2005; Ohtsuka et al. 2012) and it is likely that during the absence of their main hosts, these copepods are able to utilize other host

Table 1. Copepods associated with planktonic organisms.

Taxon	Host	Reference
Harpacticoida		
<i>Microsetella</i> Brady and Robertson, 1873	appendicularians (including discarded houses), chaetognaths	Ohtsuka and Kubo (1991); Ohtsuka et al. (1993); Steinberg et al. (1994); Huys (2016)
Miracinae Dana, 1846 (<i>Disticolus</i> Huys and Böttger-Schnack, 1994, <i>Macrosetella</i> Scott, 1909, <i>Miracia</i> Dana, 1846, <i>Oculosetella</i> Dahl, 1895)	<i>Trichodesmium</i> Ehrenberg ex Gomont, 1892	Tokitoka and Bieri (1966); Huys and Böttger-Schnack (1994); O'Neil and Roman (1994); Eberl et al. (2007); Huys (2016)
<i>Nitokra medusaea</i> Humes, 1953	<i>Aurelia</i> sp. floating macroalgae	Humes (1953) Huys (2016)
<i>Parathalestris cronii</i> (Krøyer, 1842)		
Siphonostomatoida		
<i>Cardiodectes bellottii</i> (Richiardi, 1882) (as <i>C. medusaeus</i> (Wilson, 1908) or <i>C. sp.</i>)	gastropods (as intermediate hosts)	Ho (1966); Perkins (1983)
<i>Hyalopontius</i> Sars, 1909	unknown	Boxshall and Halsey (2004)
Nicothoidae Dana, 1852 (<i>Aspidocia</i> Giard and Bonnier, 1889, <i>Hansenulus</i> Heron and Damkaer, 1986, <i>Mysidion</i> Hansen, 1897, <i>Neomysidion</i> Ohtsuka, Boxshall and Harada, 2005)	mysids	Hansen (1897); Bowman and Kornicker (1967); Heron and Damkaer (1986); Ohtsuka et al. (2005, 2007)
<i>Pontoecetella</i> Giesbrecht, 1895	unknown	Boxshall and Halsey (2004)
<i>Ratania</i> Giesbrecht, 1893	unknown	Boxshall and Halsey (2004)
Cyclopoidea (formerly Poecilostomatoida)		
Macrochironidae Humes and Boxshall, 1996 (<i>Macrochiron</i> Barady, 1872, <i>Paramacrochiron</i> Sewell, 1949, <i>Pseudomacrochiron</i> Reddiah, 1969)	scyphomedusae, cubomedusae	Reddiah (1968, 1969); Humes (1970); Boxshall and Halsey (2004); Browne and Kingsford (2005); Ohtsuka et al. (2012, 2015)
Oncaeidae Giesbrecht, 1893 (<i>Oncaea</i> Philippi, 1843, <i>Triconia</i> Böttger-Schnack, 1999)	appendicularians (including discarded houses)	Allredge (1972); Ohtsuka and Kubo (1991); Ohtsuka et al. (1993, 1996); Steinberg et al. (1994)
<i>Pseudolubbockia dilatata</i> Sars, 1909	<i>Aegina citrea</i> Eschscholtz, 1829	Gasca et al. (2007)
<i>Sapphirina</i> Thompson, 1829	thaliaceans	Heron (1973); Takahashi et al. (2013, 2015)

medusae and/or other planktonic organisms or even shift from a planktonic to a benthic mode of life, using benthic polyphagous (Ohtsuka et al. 2012).

Copepodid stages and adults of the shallow- and deep-water species of the Oncaeidae (e.g., *Oncaea* Philippi, 1843 and *Triconia* Böttger-Schnack, 1999) are associated with appendicularian houses, in particular discarded ones, on which phyto- and zooplankters still remain and are consumed by the copepods (Alldredge 1972; Ohtsuka and Kubo 1991; Ohtsuka et al. 1993, 1996; Steinberg et al. 1994). The naupliar stages of *Oncaea media* Giesbrecht, 1891 and *Monothula subtilis* (Giesbrecht, 1893) (as *Oncaea subtilis* Giesbrecht, 1893) were described by Malt (1982) based on specimens successfully reared in the laboratory using cultured phytoplankton. The ectinosomatid harpacticoid *Microsetella* Brady and Robson, 1873 and some scolecitrichid genera of calanoid copepods are also associated with occupied, and in particular discarded, appendicularian houses (Ohtsuka and Kubo 1991; Ohtsuka et al. 1993; Steinberg et al. 1994). *Microsetella* is known as a parasite of chaetognaths (Huys 2016).

Copepodids and adults of *Sapphirina* Thompson, 1829 were found to be associated with thaliaceans (Heron 1973; Takahashi et al. 2013, 2015). Copepodids and adult females of *Sapphirina nigromaculata* Claus, 1863 were frequently attached to the chains of nurse and zoid stages of doliolids in the Kuroshio Extension (Takahashi et al. 2013). For *Sapphirina iris* Dana, 1849 there is evidence that the copepod can penetrate the salp body and remain lodged in the host while feeding on it (Gasca et al. 2015). According to Takahashi et al. (2013), the ingestion rate of *S. nigromaculata* on live doliolids corresponded to 29–37% of the copepod body carbon ($5.1\text{--}6.4\ \mu\text{g C ind}^{-1}\text{d}^{-1}$), and the potential population ingestion rate of three dominant sapphirinids linearly increased with the size of the doliolid populations. Doliolids and salps attacked by sapphirinids were sometimes seriously damaged leading to death (Heron 1973; Takahashi et al. 2013), thus suggesting that this interaction can be regarded as predation or parasitoidism rather than commensalism or parasitism (Gasca et al. 2015).

The deep-sea cyclopoid *Pseudolubbockia dilatata* Sars, 1909 was recorded to be associated with the hydromedusa *Aegina citrea* Eschscholtz, 1829 off California using a ROV (Gasca et al. 2007). The presence of early copepodid stages and mated pairs of *P. dilatata* on the host suggests that they utilize it for refuge and mating, although the feeding habits of the symbiont were not determined (Gasca et al. 2007). Potential hosts of the few known holoplanktonic siphonostomatoid families (i.e., Megapontiidae, Pontoeciellidae, Rataniidae) are still unknown, although this order is generally regarded as symbiotic (Boxshall and Halsey 2004).

Interactions between Different Phases and Other Organisms

In addition to the morphological and behavioral differences between the planktonic and symbiotic phases of symbiotic copepods, it is worthwhile to note that some physiological and microbiological phenomena are also involved in the phase change.

Adults and probably chalimi of *Caligus fugu* (Yamaguti, 1936) infecting the toxic tetraodontid puffer are tolerant to its tetrodotoxin (TTX), and are able to accumulate it in their bodies, except for the ovaries and eggs (Ikeda et al. 2006). TTX-free eggs evidently produce TTX-free nauplii, suggesting that TTX accumulation in the adult body is by way of feeding on the toxic host tissues and blood. In the same species, different developmental stages exhibit different physiological reactions to TTX under a certain genetic mechanism, especially that concerning blocking of sodium channels (Chen and Chung 2014).

TTX-producing bacteria were found on the body of *C. fugu* (Venmathi Maran et al. 2007), but their actual interaction is still unknown.

Caligids have been regarded as pests in fish farms in many geographic regions (Ho and Lin 2004a; Johnson et al. 2004; Shinn et al. 2015). Economic losses caused by these pathogenic copepods on farmed Atlantic salmon *Salmo salar* Linnaeus, 1758 are estimated at US\$480 million annually (Shinn et al. 2015). Usually, these copepods feed on the host skin, tissues and blood, causing physical damage and inflammation and finally leading to death (Nylund et al. 1993; Dojiri and Ho 2013). Secondary microbial infections occur via open wounds, thus enhancing the economic losses (Nylund et al. 1993; Dojiri and Ho 2013). Nylund et al. (1993) showed that infectious salmon anaemia (ISA) caused by *Aeromonas salmonicida* (Lehmann and Neumann, 1896) was horizontally transferred by *Lepeophtheirus salmonis* (Krøyer, 1837). Madinabeitia et al. (2009) also found the presence of the pathogenic bacterium *Lactococcus garvieae* (Collins, Farrow, Phillips and Kandler, 1984) on *Caligus longipedis* Bassett-Smith, 1898 infecting the striped jack *Pseudocaranx dentex* (Bloch and Schneider, 1801) suffering from lactococcosis in Japan. This study showed that the adults of *C. longipedis* carrying *L. garvieae* could be potential agents for the transmission of the bacteria between host fish. Therefore, the adults of some species of caligids may act as vectors of diseases among cultured fish. However, the microhabitats of these bacteria on and in the bodies of caligids remain unknown (Nylund et al. 1993). Pathogens likely spread by way of host switching of caligids, ergasilids, and other good swimmers carrying them.

Evolutionary and Adaptive Strategies of the Planktonic Phase in Symbiotic Copepods

Symbiotic copepods generally have one or more planktonic phases. However, the number and duration of developmental stages and feeding type of the planktonic phase vary between taxonomic groups (Fig. 1). Heterochrony is greatly important to determine developmental timing of reproductive and somatic gene expressions (Gould 1977), and has been considered an important mechanism in the evolution of the Copepoda (Huys and Boxshall 1991). Progenesis is conspicuous in some symbiotic copepods such as *Neomysidion* and the Thaumatopsyllidae.

What sort of evolutionary factors drive such different modes of life of symbiotic copepods? Hendler and Dojiri (2009) discussed the evolution of the bizarre thaumatopsyllids, and regarded predator avoidance as the most important factor. The endoparasitic metanauplii of *Caribeopsyllus amphiodiae* grow in the stomach of its ophiuroid host for 5 months contrasting with a very short duration of its planktonic phases. The microhabitat provides the metanauplii with refuge and sufficient food, while free-living nauplii are generally exposed to high mortality caused by predation (Hendler and Dojiri 2009).

The availability of hosts for symbiotic copepods may also be essential to determine the number and duration of the planktonic phase. In some cases, the aggregated distribution of host animals enhances infection efficiency of some ectoparasites due to their horizontal transfer (Brown and Brown 1986). Therefore, swarming hosts may represent a factor that accelerates the abbreviation of lecithotrophic naupliar stages for dispersal.

On the other hand, phylogenetic constraints are also remarkable in the evolution of symbiotic copepods. In the Caligidae, the number of developmental stages is so far known for 18 species, infecting a variety of coastal and oceanic fish, and has proven to be remarkably constant (8 stages in total in both *Caligus* and *Lepeophtheirus*) (Ohtsuka et al. 2009;

Madinabeitia and Nagasawa 2011; Hamre et al. 2013; Venmathi Maran et al. 2013; Huys 2014). The encounter and accessibility of ecologically diversified hosts for highly host-specific caligids seems to be greatly variable, but the number of developmental stages in the family appears nevertheless to be phylogenetically conservative. Some adaptive strategies may compensate for the conservative phylogenetic constraints. It may be possible that reproductive strategies of the symbionts are synchronized with the hosts' aggregating behavior, such as breeding and swarming. Such synchronization would enhance the infection efficiency and the life cycle flexibility, as caligids do in fish farms switching from single to multiple hosts.

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