Chapter 2
Krill-Parasite Interactions

2.1 Krill–Parasite Interaction Is Multispecific and Highly Complex

Expanding on the recent review of the diseases and parasites of *Nyctiphanes simplex* (Gómez-Gutiérrez et al. 2010) and *E. superba* (Gómez-Gutiérrez and Morales-Ávila 2016), we review all the available, worldwide reports of epibionts and parasites of species of the Order Euphausiacea published between 1885 and 2017 (128 publications, including about 248 records). We add our own observations carried out on euphausiids waters off from Oregon (USA), Tasmania (Australia), Concepción (Chile), the Pacific coast of Mexico, the Gulf of California and the Gulf of Mexico. All this information provides us a relatively broad and coherent perspective about the diversity, prevalence patterns, intensity, parasite–host size ratios, and availability of microhabitats for parasites on and inside euphausiid bodies, as well as the association of parasitism with the host reproductive strategies. A good understanding emerges of parasite–host co-evolution (Figs. 2.1a, b and 2.2a, b). Currently, there are 18 different types of epibionts, pathogens, parasites, and parasitoids infecting krill (107 known taxa reported from 49 of the 86 extant species of the Order Euphausiacea) (Fig. 2.1a, b).

Euphausiids and their symbionts have co-evolved to a point at which parasites (1) affect almost all stages of the life cycle of euphausiids (except for the early larvae, nauplius-to-metanauplius stages); (2) increase in diversity, prevalence, and parasitic intensity with euphausiid age, a direct association of known parasitic diversity with krill size (Table 2.1); (3) that epibionts and ectoparasites generally do not affect the fitness of their hosts; but (4) several pathogens, mesoparasites, and endoparasites can decrease the host fitness to zero by castration (i.e., Ellobiopsidae and several helminth worms) or death (parasitoid dinoflagellates and apostome ciliates of the genus *Pseudocollinia*); (5) do not transmit vertically from parent to offspring (no evidence exists that a pathogen or parasite developing in the gonad infects the embryo during the embryonic development process) and all
endoparasites seem to infect euphausiids by trophic transmission; (6) have not co-evolved differently in broadcast-spawning species or those forming an ovigerous sac (Gómez-Gutiérrez et al. 2012, 2010; Gómez-Gutiérrez and Morales-Ávila 2016); (7) species of genera Euphausia, Meganyctiphanes, Nyctiphanes, Thysanoessa, and Nematoscelis possesses the most diverse and better-known parasitic fauna; (8) relatively little known for Nematobrachion, Pseudo euphausia and Stylocheiron; and (9) not symbionts are known at present from species of Bentheuphausia, Tessarabrachion or Thysanopoda (Table 2.1). Currently, there are no records of viral infections in any of the 86 extant species of
the Order Euphausiacea; although it is highly likely that infections exist in nature, because viral infections are widely known in decapods harvested by commercial fisheries and aquaculture farms.

**Fig. 2.2** Worldwide meta-analysis of (a) Means (colour bars and black dots) and range of prevalences (%). (b) Mean parasite/host size ratio (colour bars and black dots) and ranges of parasite/host size ratios for taxonomic groups of epibionts and parasites. *Red circles* indicate small unicellular parasitoids that can convert all host biomass into parasitoid biomass, albeit due their high intensity (>8500 cells) and high reproductive rates. The Rhizocephala mesoparasite is excluded from this figure because the only record includes only one infected specimen (Mooney and Shirley 2000)
Parasitic associations have considerable impacts on the dynamics of euphausiid populations, because they can decrease host school density, fecundity, growth rate, and body size (certainly shrinking and perhaps gigantism), reduce body condition or modify external appearance and behaviour making them more vulnerable to predators. Although parasites obtain energy from virtually every trophic level within a marine food web, they have been traditionally thought to contribute little to biomass and energy flow in marine ecosystems. However, estimates of parasite diversity indicate that among about 1.4 million marine species, about 40% are

Table 2.1 Type of parasites detected in euphausiids per developmental phase with an estimation of stage-dependent parasite intensity reported in literature (ordered from gradient of almost innocuous to causing death of the host)

<table>
<thead>
<tr>
<th>Euphausiid developmental phase</th>
<th>Type of parasites</th>
<th>Eggs</th>
<th>Calyptopis</th>
<th>Furcilia</th>
<th>Juvenil</th>
<th>Adult (male)</th>
<th>Adult (female)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bacillariophyta (epibiont)</td>
<td>×</td>
<td>NS</td>
<td>&lt;2</td>
<td>&lt;50</td>
<td>&lt;1000</td>
<td>&lt;1000</td>
<td></td>
</tr>
<tr>
<td>Ciliophora Suctorida (epibiont)</td>
<td>1</td>
<td>NS</td>
<td>&lt;2</td>
<td>&lt;5</td>
<td>&lt;100</td>
<td>&lt;1000</td>
<td></td>
</tr>
<tr>
<td>Ciliophora (exuviotrophic)</td>
<td>×</td>
<td>×</td>
<td>&lt;5</td>
<td>&lt;15</td>
<td>&lt;300</td>
<td>300</td>
<td></td>
</tr>
<tr>
<td>Ciliophora (hyperparasite)</td>
<td>×</td>
<td>×</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Bacteria (chitinoclastic)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>&lt;300</td>
<td>&lt;300</td>
<td>&lt;300</td>
<td></td>
</tr>
<tr>
<td>Bacteria (in digestive tract)</td>
<td>×</td>
<td>NS</td>
<td>ND</td>
<td>&lt;1 x 10^6</td>
<td>&lt;1 x 10^6</td>
<td>&lt;1 x 10^6</td>
<td></td>
</tr>
<tr>
<td>Fungi</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Apicomplexa (“Sporozoa”)</td>
<td>?</td>
<td>&lt;36</td>
<td>&lt;36</td>
<td>&lt;29</td>
<td>&lt;8000</td>
<td>&lt;8000</td>
<td></td>
</tr>
<tr>
<td>Cirripedia Rhizocephala</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>1*</td>
<td>1*</td>
<td></td>
</tr>
<tr>
<td>Isopoda Dajidae</td>
<td>×</td>
<td>×</td>
<td>1*</td>
<td>1</td>
<td>1 (2)</td>
<td>1 (2)</td>
<td></td>
</tr>
<tr>
<td>Eellobiopsida Thalassomyces</td>
<td>×</td>
<td>×</td>
<td>1*</td>
<td>1</td>
<td>1 (2)</td>
<td>1 (2)</td>
<td></td>
</tr>
<tr>
<td>Cestoda</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Trematoda</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Nematoda</td>
<td>1*</td>
<td>×</td>
<td>1*</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Acanthocephala</td>
<td>×</td>
<td>×</td>
<td>NS</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Dinoflagellata (parasitoids)</td>
<td>1 to 1 x 10^4</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td></td>
</tr>
<tr>
<td>Ciliophora Pseudocollinia</td>
<td>×</td>
<td>×</td>
<td>&lt;1 x 10^3</td>
<td>×</td>
<td>rare</td>
<td>&gt;8500</td>
<td></td>
</tr>
</tbody>
</table>

ND = parasite studied, but no available quantitative intensity data. NS = No studied, but probable interaction. The number between parentheses shows unusual intensity reports. * = rare observations, possibly accidental interactions, × = unlikely interaction. No record exists of symbionts for nauplius, pseudometanauplius, and metanauplius development stages.

Parasitic associations have considerable impacts on the dynamics of euphausiid populations, because they can decrease host school density, fecundity, growth rate, and body size (certainly shrinking and perhaps gigantism), reduce body condition or modify external appearance and behaviour making them more vulnerable to predators. Although parasites obtain energy from virtually every trophic level within a marine food web, they have been traditionally thought to contribute little to biomass and energy flow in marine ecosystems. However, estimates of parasite diversity indicate that among about 1.4 million marine species, about 40% are
parasites; food-web studies estimate that about 75% of the links in food webs involve a parasite (Dobson et al. 2008; Kuris et al. 2008; Poulin 2007, 2014). In coastal estuaries, parasite biomass may exceed the biomass of several top predators, such as birds (Kuris et al. 2008), suggesting that the ecological role of parasites in the carbon flux in marine ecosystems is substantial, though largely unknown and frequently overlooked. Most studies of parasites of euphausiids estimate prevalences, but not the abundances of the parasites or their hosts; those are pre-requisites to estimate the biomass of parasites in the pelagic ecosystem (Morales-Avéila et al. 2015; Morales-Avéila 2016). The parasite–host volume or biomass ratios seem to be better indicators of infection levels, although they are relatively more complicated to estimate than classical indices, such as intensity (number of parasites per hosts) or prevalence (proportion of infested/infected hosts in the population). Such ratios could allow assessment of the energetic and fitness costs for the host (Wedekind et al. 2000; Poulin 2007, 2014). Biomass production within organisms is not limited to the organism itself: parasites can “steal” a portion of the metabolic products that would otherwise be allocated to host growth or other functions, and use it for the production of parasite biomass (Poulin 2007).

Estimation of parasitic biodiversity in euphausiids is a complex task because taxonomic description of parasitic species is limited and our ignorance is geographically biased (we know disproportionately much less about parasites in the tropics than in higher latitudes). There are numerous cryptic species with relatively few genetic studies to distinguish them; current named names are probably invalid taxa, and synonymous with species described earlier, among others causes. The parasites that interact with 34 euphausiid species have not been studied so far (including Bentheuphausia, Tessarabrachion, and Thysanopoda species). This is most likely because there are only a few trained taxonomists in this specialty, especially in the tropics, where most euphausiid biodiversity resides (Brinton 1962; Brinton et al. 2000; Poulin and Morand 2000; Dobson et al. 2008; Poulin 2014). Parasites of most of the tropical and subtropical euphausiid species have not been extensively studied compared with those of North Atlantic, Mediterranean Sea and Northwest Pacific species, for which most studies of parasites have been carried out. A particular exception is the subtropical species Nyctiphanes simplex of northwestern Mexico that has been studied for many types of parasites (Gómez-Gutiérrez et al. 2010, 2012, 2015a, b; Lynn et al. 2014; Morales-Avéila et al. 2015). Studies of euphausiid parasites in the Indian Ocean are virtually non-existent (Sebastian 1970). According to Dobson et al. (2008) and Poulin (2014), there is no credible way to estimate how many viruses, bacteria, fungi and protozoa exist. The biological diversity of the first three of those taxonomic groups is virtually unstudied in euphausiids, and new protozoan species are still being discovered (Gómez-Gutiérrez et al. 2006, 2012; Lynn et al. 2014). Thus, any attempt at estimating total parasite biodiversity is possibly flawed by insufficient current knowledge (Poulin 2014).

Exuviotrophic ciliates with typically high prevalence (>70%) and intensities (>900 per krill host) within euphausiid populations seem to have no negative impact at the individual level, but perhaps they influence the amount of carbon flux via exuviae drifting into deeper waters. In contrast, apicomplexan gregarines may drive significant negative effects in health of euphausiids (Lear 1963; Lindley
1978; Landers et al. 2006; Avdeev 1985, 1987; Avdeev and Vagin 1987; Takahashi et al. 2003, 2004, 2008). All of the known histophagous parasitoids of euphausiids are unicellular. Blastodiniales (Family Chytridiiniaceae) and Syndiniales dinoflagellates (Gómez-Gutiérrez et al. 2009) and *Pseudocollinia* spp. parasitoid ciliates (Gómez-Gutiérrez et al. 2003, 2004, 2006, 2010, 2012, 2015a, b; Lynn et al. 2014) can efficiently transform the entire individual euphausiid biomass into protist biomass in <3 days (Fig. 2.2b), sometimes causing epizootic events and annihilating large parts of a swarm. Macroparasites of euphausiids, like helminths, usually have low prevalences (<1%), likely with negligible impacts on population levels (Smith 1983a, b; Hurst 1984a, b; Gregori et al. 2012, 2013, 2015b), but they convert a large amount of the substance of the host to parasite body biomass, sometimes causing decrease of fecundity, castration of the host or lowering its growth (Shields and Gómez-Gutiérrez 1996; Morales-Avila et al. 2015).

Ecologists and evolutionary biologists are well aware of the relevance of predation, and they do consider the roles of parasites in the control of population structure. Most parasites, at some point in their lineage, evolved from predatory organisms (Lafferty and Kuris 2002). Thus, parasites are the most ubiquitous and diverse trophic form transferring carbon throughout food webs; that is deduced from the fact that each species has a diverse community of parasites. Thus, parasites outnumber the species obtaining their energy by other trophic strategies, such as chemiotrophy, autotrophy, coprophagy, herbivory, omnivory and carnivory.

Euphausiids are associated with at least 18 general types of symbionts: 5 ectoparasites, 2 mesoparasites and 11 categories of endoparasites in 55 genera (38 of them identified to species level and more than 110 records without species names). The report of a Rhizocephalan parasitizing *Thysanoessa inermis* (Mooney and Shirley 2000) is unique and is considered, so far, to be a case of accidental parasitism (Table 2.1, Fig. 2.1a). Parasites are better studied from the furcilia to adult phases, with only four types of parasites known to attack eggs (suctorian ciliates, parasitoid dinoflagellates (Blastodinian and syndinian-like dinoflagellate) and nematodes) (Gómez-Gutiérrez et al. 2009; Gómez-Gutiérrez and Morales-Avila 2016). One type of parasite (a “sporozoan”) has been reported from the calyptopis larval stage of *Meganyctiphanes norvegica* (Macdonald 1927), and an apicomplexan gregarine infects calyptopis and furcilia larvae of the *Euphausia superba* (Takahashi et al. 2011) (Table 2.1). It is likely that larvae (calyptopis and furcilia) are not frequently affected by parasites, because they are constrained by the small available the surface, volume and biomass for parasite infection and proliferation. However, studies to detect parasites in earlier euphausiid life stages and careful observations of those life stages must be extended in the future (Table 2.1). For example, we have observed gregarine infections in calyptopis and furcilia life stages of *Nyctiphanes simplex* and *Nematoscelis difficilis* from the Gulf of California (Gómez-Gutiérrez, personal observation). However, prevalence and intensities of most parasites consistently increase with increasing host biomass and age (Gómez-Gutiérrez et al. 2006, 2010, 2012; Lynn et al. 2014) (Table 2.1). Except for *Pseudocollinia* ciliates, which almost exclusively infect adult females, parasites of euphausiids generally do not have significant sex bias with respect to their hosts.
Among the euphausiid species that have been studied, a diverse parasitic assemblage has been noted, varying interspecifically (i.e. with the host species) as functions of body size, swarming behaviour, vertical distribution and zoogeography. For example, the neritic subtropical euphausiid *Nyctiphanes simplex* has at least 12 distinct types of ectoparasites and endoparasites, affecting up to 14% of the population (Gómez-Gutiérrez et al. 2010). Parasites not included in that count are recently discovered *Pseudocollinia* ciliates (Gómez-Gutiérrez et al. 2012), trematodes (Morales-Ávila et al. 2015) and apicomplexans in furcilia, juvenile and adults of *N. simplex*. Others yet to be reported occur in *Nematoscelis difficilis* (Gómez-Gutiérrez unpublished data). Thus, parasite assemblages seem to have significant impacts on population levels, but are strongly dependent on euphausiid abundance, population dynamics, three-dimensional distributions and social behaviour. If high host diversity in the tropics leads to lower densities of each euphausiid host, and oligotrophic conditions lead to smaller host sizes (less biomass for parasites per individual host), then some host-specific parasites might be unable to maintain viable populations in the tropics, reducing parasitic diversity and prevalence. However, that prediction could be wrong if parasites in tropical ecosystems are also smaller than those in higher latitudes. The largest euphausiid species, *E. superba* in the Southern Ocean, actually seems to have low diversity of symbiotic organisms and apparently lacks interactions with macroparasites (Gómez-Gutiérrez and Morales-Ávila 2016) and relative small krill subtropical species, *Nyctiphanes simplex*, seem to have diverse parasitic species assemblages (Gómez-Gutiérrez et al. 2010).

Kamiya et al. (2014) suggest three universal predictors of parasite diversity across animal host species: body size, host geographical range dimensions and host population density; and they demonstrated that latitude is not a consistent predictor of parasite species richness. Two other well established laws in parasite ecology are that (1) within a parasite population, parasites are aggregated among host individuals and (2) the prevalence of infection within a locality is generally positively correlated with the mean number of parasites per host (intensity), when comparing different parasite species (Moran and Guégan 2000; Poulin 2007). Based on “island biogeography theory,” and assuming similar parasite transmission rates for relatively benign parasites, it would be expected that longer-lived or larger individual (or both) euphausiid hosts would offer more potential sites for parasites than shorter-lived and small euphausiid hosts (Kuris et al. 1980) (Table 2.1). This is a key inference, because it predicts that eggs and larvae (with development times from a few days to a week and with small individual biomass) are less likely to be attacked by parasites, and by a smaller number of parasitic types, than juveniles and adults. If this is true, small euphausiid species, such as *Stylocheiron microphthalmalma* and *S. suhmi* (<7 mm and likely longevity <1 year) should have relatively less diverse parasitic fauna that larger species, such as *E. superba* (length 65 mm, longevity of several years) or *Thysanopoda* spp. (lengths up to 150 mm) (interspecific vulnerability). Thus, biovolume must be a paramount feature regulating successful invasion of new euphausiid hosts (Poulin 2007). For example, Lindley (1978) did an interspecific comparison of the infestation by apostome ciliates of euphausiid species of different sizes, arguing that large species, such as
*Meganyctiphanes norvegica* had higher prevalences (16.1%) than smaller species, such as *Thysanoessa longicaudata* (3.4%). *Nyctiphanes couchi*, which is only slightly larger than *T. longicaudata*, also has relatively higher prevalences (12.9%). So far, this trend of larger and more abundant euphausiids having more diverse parasitic assemblages (Gómez-Gutiérrez et al. 2010) seems to hold, but given the large intraspecific variability this trend may be of minor significance (Morales-Ávila 2016). However, unlike actual islands, host species are not devoid of parasites when newly diverged from parent species, rather they can inherit parasites from them, mostly independently of their body size, population density or other characteristics (Poulin 2007). For example, D’Amato et al. (2008) postulated that *Nyctiphanes simplex*, currently distributed to the south in the California Current System, Gulf of California and northern part of the Humboldt Current, is the ancestral species of the neritic genus *Nyctiphanes*. Thus, *N. simplex* split by dispersal into new species in the following chronological order: *N. australis* (Australia), *N. capensis* (Benguela Current) and *N. couchi* (North Sea and Mediterranean Sea). In theory, coevolutionary processes would occur among each *Nyctiphanes*–parasite species assemblage predicting that greater similarities in parasitic fauna should be expected in proportion to the distances among their biogeographical distribution ranges (Poulin 2007). However, testing that prediction awaits future parasite-host metapopulation studies. Their allopatric phylogenetic origins may explain why helminths of *N. simplex* are mostly cestodes (98%) in the Pacific (Gómez-Gutiérrez et al. 2010; Morales-Ávila 2016; Morales-Ávila et al. 2015), while *N. couchi* is predominantly infected with acanthocephalans in the Atlantic (Gregori et al. 2012, 2013) and why is likely that parasitoid *Pseudocollinia* ciliates may have broader distributions that those currently reported, so far, from the North-eastern Pacific (Lynn et al. 2014).

So far, infections in nauplii and metanauplii have never been observed, likely because of their small body size (small biomass) and short development times, from hours to a few days (Ambriz-Arreola et al. 2015). Interestingly, the Antarctic krill *E. superba*, with 65 mm total length, has a comparatively less diverse symbiotic biota than many smaller species, such as the subtropical *Nyctiphanes simplex*, with 19 mm total length (Gómez-Gutiérrez et al. 2010; Gómez-Gutiérrez and Morales-Ávila 2016), suggesting latitudinal changes in parasite species assemblages.

Eggs of broadcast-spawning euphausiids can be infected with four types of parasites: (1) epibiont suctorian ciliates (Ephelotidae), (2) mesoparasitic Blastodinian dinoflagellates of the genus *Chytriodinium*, (3) an undescribed endoparasitoid, a syndinian-like dinoflagellate (Dogiel 1906; Cachon and Cachon 1968, 1987; Gómez-Gutiérrez et al. 2009) and (4) nematode larvae (Gómez-Gutiérrez and Morales-Ávila 2016). More diversely affected, adults of euphausiid species are parasitized with all the types of parasites currently known, except endoparasitic dinoflagellates (Shimazu 2006; Gómez-Gutiérrez et al. 2010; Gregori et al. 2015a, b). Several studies have shown positive correlations between host size and intensity of infection, regardless of the host’s sex for exuviotrophic apostome and suctorian ciliates (Lindley 1978; Tarling and Cuzin-Roudy 2008; Sheridan et al. 2000), eugragarine apicomplexans (Takahashi et al. 2003, 2008) and *Pseudocollinia* spp. ciliates (Gómez-Gutiérrez et al. 2006, 2012, 2015a; Lynn et al. 2014). This more
extended range of infections may be because larger and older euphausiids that have higher feeding rates, provide more energy (biomass) for the parasites and have longer intermoult periods facilitating higher intensity of several ecto- and endoparasites (Fig. 2.2b). Certainly parasite evolution has been controlled in part by the size and age of the host, habitat complexity, feeding habits, social behaviour (numbers, density, and dynamics of the swarms and schools), biogeography and distance from potential sources of infection (a function of host population density), as has been observed in other crustaceans (Kuris 1974; Kuris et al. 1980). Parasites having the highest estimated prevalences are similar in some ways, because (1) they are quite easy to observe (like Ellobiopsidae or suctorian ciliates), (2) they cause negligible damage to the host (exuviotrophic ciliates) or (3) they have efficient transmission among hosts (Fig. 2.2a). The coevolution of parasites and their hosts must be associated with the proportional sizes of parasite and host, and with how much energy parasites can obtain from the hosts. The largest parasite-to-host size proportion is for helminths some of which, like the Anisakidae (nematodes), can be slightly longer than the host when extended after dissection (Hurst 1984a, b; Gómez-Gutiérrez et al. 2010; Gregori et al. 2015b). Other parasites, such as the histophagous dinoflagellates and ciliates have small cell sizes in comparison with the krill host. When Pseudocollinia ciliates produce transmission cells inside the host, they virtually transform all the host’s biomass into parasite biomass, which makes them lethal (Fig. 2.2b). Except for the histophagous microparasites, macroparasites overall have a small range of size and produce relatively moderate negative effects on the hosts due their relatively low prevalences. Mesoparasites (Ellobiopsidae and Rhizocephalan) may cause castration because they obtain a substantial amount of energy from the host, and they may even feminize their crustacean hosts (Rhizocephalan feminization of males is known in decapods) (Mathieson et al. 1998). Trematoda, Cestoda, Acanthocephalan and Nematoda typically have large parasite-to–euphausiid host proportions. However, they do not necessarily always castrate the host (Fig. 2.2b). For instance, cestodes and acanthocephalans have been reported to infect ovigerous females of N. simplex (Morales-Avila et al. 2015; Morales-Avila 2016). There are no reports of trematodes or nematodes infecting ovigerous females. The supply of energy and nutrients should ultimately determine how much biomass could be sustained; for parasites, therefore, host metabolic rate should be a key determinant of total biomass (Poulin 2007).

2.2 Social Behaviour, Parasite Life Cycles, and Infection Mechanisms

Social behaviour is fun and adaptive, but also is dangerous.

J. Gómez-Gutiérrez 2009

The most characteristic feature of euphausiids is aggregation behaviour. Euphausiids vary in social behaviour from species whose individuals are solitary swimmers to those with social interactions resulting in formation of swarms or schools, as
particularly observed in the Antarctic krill, *Euphausia superba*, individuals of which swim in the same direction (“polarized”) (Hamner et al. 1983, 1989; Ritz 1994, 2000; Hamner and Hamner 2000; Ritz et al. 2011; Tarling and Fielding 2016). Goodall-Copestake et al. (2010) investigated the genetic variation among *E. superba* sampled from different swarms in the Scotia Sea, reporting no significant swarm-related genetic structuring. However, their large amount of sequence data confirmed high genetic diversity within swarms. The implication is that swarms do not constitute discrete genetic units and that there is mixing among swarms on both small and large scales. Thus, epibionts and parasites interact with individuals within swarms that have high genetic diversity. Kawaguchi et al. (2010) further proposed the hypothesis that krill must disperse from swarms at regular intervals in order to flush out waste products, parasites and pathogens and replenish oxygen concentrations. Krill social behaviour is closely associated with multiple, significant ecological and physiological processes, including conservation of energy, reproduction, food search, predator avoidance, parasitic interactions, moult-cycle timing and others. There is an ontogeny of krill social behaviour (Ritz 1994, 2000; Tarling and Fielding 2016). Small, faster growing krill tend to form larger and more tightly packed swarms, and their internal state (maturity, body condition) appears to have a greater influence on swarm structure than does the local external environment (Tarling et al. 2009; Spiridonov and Casanova 2010; Décima et al. 2010; Kawaguchi et al. 2010).

Euphausiid species that form dense schools/aggregations interact with more diverse parasitic assemblages than more dispersed species, because parasite transmission is facilitated by close host social interactions and host abundance (Gómez-Gutiérrez et al. 2010) (Fig. 2.3). Crustaceans form distinct social groups, and close association with conspecifics has been postulated to deliver both costs and benefits to individuals of gregarious species. Ritz (1994) explicitly defined such terms to avoid ambiguity: aggregations (groups of conspecific individuals without any connotation of mutual attraction), swarms (discrete social groups with members evenly spaced but not coordinated), schools (discrete social groups with members evenly spaced and usually facing the same direction), and shoals (groups within which are distinct subgroups of swarms and/or schools). Social behaviour provides protection from predation, ensures repeated mating, high genetic variability within the population and close interaction among krill individuals, but it may also increase krill feeding competence that influence the infection rates of trophically transmitted parasites and infestation of ectoparasites. A meta-analysis of species diversity and prevalences of parasites of *E. superba*, *N. simplex* that form large schools and/or swarms, *Nematoscelis difficilis* that forms aggregations and *Stylocheiron affine* that likely lives in dispersed, low density populations, indicates that aggregative behaviour facilitates evolution and transmission of parasites among individuals shaping distinct infracommunities. Décima et al. (2010) demonstrates that seven of the eight euphausiid species numerically dominant in the California Current have a size-dependent patchiness, with stronger patchiness in the smallest size classes, followed during growth by an abrupt decrease in patchiness, and then an increase again at the largest sizes. That is true for euphausiid species
with both sac-spawning and broadcast-spawning strategies, reflecting the needs to
mate, to interact in the search of food and to avoid predators (Fig. 2.3). Tarling et al.
(2009) proposed that, at the mesoscale level, the structure of swarms switches from
predominantly large and tightly packed to smaller and more diffuse as krill grow
and mature. It is clear that changes in patchiness occur during ontogenetic devel-
opment for species in the California Current; this must be tested in other euphausiid
species around the world. There is observational evidence that the aggregative
behaviour of *Euphausia superba* may start as early as the furcilia IV (Hamner
et al. 1989). Interestingly, parasitoid ciliates like dinoflagellates (Gómez-Gutiérrez

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**Fig. 2.3** Patchiness index ($I_{mod}$) as a function of euphausiid length (mean ± 95\% C.I. *Black arrows* indicate euphausiid length at onset of sexual maturity. Body size dependence of euphausiid spatial patchiness (Reprinted from Décima et al. (2010) with permission from Limnology and Oceanography)
et al. 2009) or Pseudocollinia ciliates species (Capriulo and Small 1986; Gómez-Gutiérrez et al. 2010, 2012) have been consistently detected only in eggs and the larger individuals in the population. This suggests that strong gregarious behaviour facilitates parasitism within the krill population relative to that in species with lower densities and longer nearest-neighbour distances.

Several pioneering studies mention the role of social behaviour in the parasitic infections of euphausiids (Hamner 1984; Nicol 1984; Gómez-Gutiérrez et al. 2010), and this interaction was reviewed by Gómez-Gutiérrez and Morales-Ávila (2016). According to Kuris et al. (1980, page 571) “from a parasite’s point of view, individual host organisms are unequivocal islands. Infection is equivalent to immigration of the parasite population. Extinction represents the loss of a parasite population either through natural death of the parasites with short life spans, competition from other parasite populations, or host defensive responses”. Thus, euphausiids may be regarded as islands for parasites at several levels of organization: (1) individuals, (2) aggregations, swarms, or schools (sensu Ritz 1994, 2000; Ritz et al. 2011), (3) populations, (4) species and (5) perhaps species assemblages with similar biogeographic affinities. Poulin (2007) proposes that parasite communities are organized in a hierarchical manner, with infracommunities consisting of all parasites of all species found together in one individual host and component communities representing the sum of all infracommunities (all parasites of all species found within a host population). Euphausiids have an interspecific, and size-dependent intraspecific variability of social behaviour (patchiness), likely being more aggregated in the egg, early larval and adult phases than in the late larval, juvenile and young adult phases (Décima et al. 2010).

Theoretical frameworks indicate that although spatial distribution is influenced by behaviour of individuals and by variability of the flow resulting in variable survival of the krill individuals, behavioural mechanisms can only account for the formation of relatively small aggregations, of a few meters at most (Verdy 2008; Verdy and Flierl 2008). This theoretical prediction is challenged by observations of large concentrations of krill sometimes named “super-swarms” (Watkins and Murray 1998; Gómez-Gutiérrez et al. 2010; Nowacek et al. 2011). Turbulent environments are favourable to the evolution of social behaviour because interactions between social groups, perhaps involving variability of the flow at different scales, might provide an additional mechanism to the formation of large swarms and schools (Verdy and Flierl 2008). That might increase the probability of parasite transmission among host individuals from different swarms. It is clear that social behaviour varies interspecifically and intraspecifically, from cases with individuals as solitary swimmers to social interactions forming aggregations, initially accumulated by water circulation and fronts. These processes are likely more important for calyptopis and furcilia. Swarms and schools involve more nektonic behaviour, gathering groups of juveniles or adults, typically of similar sizes. Those with formally defined schools swim in a coordinate direction, as do Antarctic krill E. superba (Hamner 1984; Ritz 1994; Ritz et al. 2011; Brierley and Watkins 2000; Nowacek et al. 2011). The subtropical Nyctiphanes simplex has quite diverse
and dynamic social behaviours, forming aggregations as early as calyptopis I (Gómez-Gutiérrez, personal observation). It typically forms daytime surface aggregations of larvae and adults (Gendron 1992) and temporary epibenthic aggregations during their daily vertical migrations when constrained by relatively shallow water (Robinson and Gómez-Gutiérrez 1998; Gómez-Gutiérrez and Robinson 2006). It can occur in dense shoals, sometimes monospecific, about 70 m thick, as tracked with echo sounders (Gómez-Gutiérrez et al. 2010). This highly diverse social behaviour co-evolves with both predator and symbiont life cycle strategies. Hamner (1984) specifically discussed parasite transmission within swarms, and among swarms and schools. He noted that krill infected with a then unknown parasite (whitish appearance) seemed to be positioned at the back part of the schools likely debilitated and with slower swimming capabilities.

Near-surface swarming behaviour of krill with observed densities ranging from 100 to $1.8 \times 10^6$ ind. m$^{-3}$ (in the larval calyptopis stage) may decrease the nearest neighbour distances and facilitate parasite infection (Hamner 1984; Nicol 1984; O’Brien 1988; Gendron 1992; Siegel 2005). Trophically transmitted parasites should successfully infect euphausiids if their preys are in the path of a social aggregation. Kaartvedt et al. (2005) showed that saithe, *Pollachius virens* a piscivorous fish, patrol swarms of *Meganyctiphanes norvegica*, apparently preying on planktophagous predators attracted to the krill, rather than on the krill itself. Massive *M. norvegica* aggregations (volumes estimated at 380,000 m$^3$ with densities of 200 ind. m$^{-3}$) attract predatory fish, which potentially become the next in a sequence of hosts. In this case, Kaartvedt et al. (2005) mention that blue whiting, *Micromesistius poutassou*, are the most likely deep-living predators of krill and prey for saithe. Thus, the social behaviour of krill likely has a direct effect on the efficiency of parasite transmission from krill to predators. For krill, patrols of piscivores may add to the generally accepted anti-predator benefit of their swarming behaviour, but at the cost of enhanced transmission of parasites from krill to krill (for parasites that spend most of their life cycle parasitizing krill, for example ellopbiopsiids, suctorian ciliates, or *Pseudocollinia* ciliates). The fact that krill swarms influence the small-scale distributions of large piscivores emphasizes the key role of krill in oceanic ecosystems. Parasites must adapt to these tangled trophic pathways and ontogenetic social behaviours.

Daytime surface swarms of several euphausiid species may promote higher prevalences of epibionts, ectoparasites, mesoparasites and endoparasites. For example, surface swarms of *Meganyctiphanes norvegica* had higher prevalence of epibiont suctorians (8–82%) than krill specimens collected at greater depths offshore (2%) in Bay Fundy, Canada (Nicol 1984). Surface swarms of *Nyctiphanes australis* usually had *Thalassomyces fagei* mesoparasitic infections at prevalences of 2–6%; but paradoxically, in this particularly case higher prevalence (14–63%) it was observed in euphausiids not forming swarms 2 days after a mass-stranding event (O’Brien 1988). That suggests that infected animals may separate from the other individuals forming a social aggregation. It is clear that krill behaviour aggregation is not the only factor increasing chances of parasite infections. Other factors like parasite life cycle, parasite active search of the host, morphological and
physiological adaptations to infect and overcome host immune system also influence the parasite success to transmit and develop throughout their life cycles.

It is expected that euphausiid species with distinct social behaviours interact with distinct parasites and likely with distinct prevalence rates. Gómez-Gutiérrez et al. (2010) and Morales-Avila et al. (2015) demonstrated that Nycitiphanes simplex, which forms dense swarms and attains high population densities and wide distribution off northwestern Mexico, has a more diverse parasite assemblage (5 ectoparasites and 6 endoparasites) than Nematoscelis difficilis Hansen, 1911, which is considerably less abundant and does not form dense swarms (four ectoparasites and one endoparasite). Komaki (1970) found trematodes (in metacercaria stage) and Thalassomyces only in the most abundant euphausiid (Euphausia similis) in Suruga Bay, Japan, but in none of the 11 other species less abundant regionally. All this suggests that several parasites have come to require host species with high abundance and compact swarming/schooling behaviour to complete their life cycles during the long-term evolutionary process of co-adaptation.

Descriptions of the species characteristics, life cycles and transmission mechanisms of most euphausiid parasites are badly fragmented and infrequently reported; many are undescribed species. For example, it is unknown whether the ellobiopsid Thalassomyces fagei, one of the most widespread euphausiid parasites, detected in at least 32 euphausiid species (Fig. 2.1b), is a cosmopolitan species or a species complex with weak phenotypic differentiation. Molecular studies likely will clarify whether these and similarly problematic organisms are indeed single species. Genetic information from T. fagei is currently available from only one specimen collected off California (Silberman et al. 2004). Thus, future studies should compare genetic information from specimens from multiple regions around the world to answer the biogeographic and taxonomic questions about this enigmatic mesoparasite.

All parasites feed on the biomass produced by some kind of living organism, and their interspecific host-parasite associations have been classified into three categories: paratenic (transport) host, intermediate host, and final host (Ohtsuka et al. 2000). Those can be applied to euphausiid parasites, but before we can synthesize the knowledge of euphausiid parasites, several additional concepts must be defined: pathogen (any disease-producing agent), parasite (an organism that lives on or in an organism of another species from the body of which it obtains nutriment or protection), castrator (parasite that decrease and inhibit reproduction of the host), parasitoid (parasite that must kill the host to complete it life cycle), micropredator (organism that does not kill the prey but consume biomass from several preys throughout their life cycle) and predator (organism that kill and consume several preys throughout their life cycle) (Lafferty and Kuris 2002). In nature, there exists a broad continuum in trophic strategies that challenge assumptions about where one type of inter-specific association ends and another begins in parasite — host interactions (with overlap of distinct criteria) (Parmentier and Michel 2013). Many bacteria and gregarines located in the euphausiid digestive tract are not necessarily either pathogens or parasites (Kawaguchi and Toda 1997; Águilar-Méndez 2008; Takahashi et al. 2008, 2009; Gómez-Gutiérrez et al. 2015a). We review the biology
and epizootiology of the currently known parasites that infest and infect euphausiids by taxonomic category, using ecological terms defined by Margolis et al. (1982). Lafferty and Kuris (2002) used four life-history dichotomies to distinguish between: (1) Pathogens and parasites are distinguished by the intensity-dependent pathology (defining intensity as number of pathogens or parasites per hosts), pathogens are intensity independent and typical parasites are intensity dependent; (2) predators and parasites by the number of victims that an individual attacks in its life-history, usually one or a few (for those with intermediate hosts) for parasites and significantly more for predators; (3) parasites and parasitoids in that a parasitoid infection must kill the host, while a parasite maintains both itself and the host alive: (4) Castrators and parasitoids because parasitoids must kill the host to complete their life cycles, while castrators keep their host alive and benefit from inhibiting reproduction. Castrators disrupt gonad development and gamete production, in some cases stopping their hormonal regulation, diverting the host’s substance to parasite metabolism. These four life-trait dichotomies distinguish seven types of parasitism and three types of predation interactions (micropredators, social and solitary predators) (Lafferty and Kuris 2002). The seven types of parasitic strategies are: (1) typical parasite, (2) pathogen (host fitness >0, no death of host), (3) parasitic castrator (fitness =0, no death of host), (4) trophically transmitted typical parasite, (5) trophically transmitted pathogen (fitness >0, death of host is certain), (6) trophically transmitted parasitic castrator and (7) parasitoids (fitness =0, death of host is certain).

Perhaps the most obscure part of euphausiid parasitology is the understanding of the infection mechanisms, because (1) complete life cycles of most parasites are unknown, (2) parasites mostly have low prevalences, (3) it is difficult to simulate natural conditions in the laboratory for parasites to complete their life cycles, (4) several parasites require multiple intermediate or final hosts to complete their sequence of metamorphoses, (5) infection is typically a fast, opportunistic process mediated by social behaviours of the host or pheromonal attraction of the parasite to the host and taxonomy in numerous types of parasites of euphausiids still unsatisfactorily established. Therefore, it is quite difficult to observe a host in the moment when it is being infected with any type of parasite. Infection mechanisms usually are assumed based on sparse observational information, rather than fully tested under experimental conditions (Gómez-Gutiérrez et al. 2006, 2015a).

The most obvious mechanism of infection for endoparasites is the trophic pathway (Oshima et al. 1968; Shimazu and Amano 2001), but the pathogenicity and the means for invading other parts of the host body are difficult to test. Shimazu and Amano (2001) experimentally attempted to infest E. pacifica with the L_3 larvae of Anisakis simplex, but though they observed L_3 larvae in the digestive tracts of the euphausiids, those were defecated without creating an infection of the hemocoel, where usually have been observed the helminth parasites (Gómez-Gutiérrez et al. 2010; Gregori et al. 2012, 2013). Gómez-Gutiérrez et al. (2006) carried out several shipboard experiments attempting to infect E. pacifica and T. spinifera with histophagous, parasitoid Pseudocollinia ciliates without success at producing symptoms of infection (although euphausiids always died in infection treatments, but not in controls where potential hosts were healthy euphausiids, decapods or
mysids). Gómez-Gutiérrez et al. (2015a) indirectly tested the trophic mechanism by comparing the bacterial species assemblage from stomachs of non-infected euphausiids to those in the hemocoel of *Pseudocollinia*-infected euphausiids, observing similarities and temporal changes in the assemblages as the infection progressed.

Epizootic events require a mechanism that enables infection of a large number of euphausiids in a swarm or more dispersed population. Cannibalism could be an infection vector, because krill frequently do eat each other; however, it is unlikely to be the driving force of epizootic events in nature, because weaker and dead individuals are left behind a moving krill swarm or school. Field-collected *E. superba* watched in large tanks showed schooling behaviour and frequently showed cannibalism (Price et al. 1988; Nishino and Kawamura 1994; Gómez-Gutiérrez, personal observation); in nature since any given adult would not likely encounter its own offspring, individual fitness might be increased by cannibalistic feeding; but parasitism might be a potential risk for individuals feeding by cannibalism. In the laboratory only single individuals eat dead or moribund animals, and they did not fight each other to get at carcasses (Gómez-Gutiérrez, personal observation). In epizootic events, like the *Pseudocollinia* ciliate infections in Astoria Canyon (Gómez-Gutiérrez et al. 2003), opportunistic cannibals could potentially become infected if the carcass still contained endoparasitoid ciliates. For now transfer of *Pseudocollinia brintoni* by a trophic pathway seems to be the most parsimonious explanation evidenced by molecular similarities among operational taxonomic units of bacteria in the stomachs of healthy specimens to bacteria from hosts of the ciliates (Gómez-Gutiérrez et al. 2012, 2015a). Overall, trophic pathways are likely for many euphausiids parasites (and parasitoids), but transfer mechanism are difficult to establish and prove.

### 2.3 Biodiversity and Size Proportion Between Euphausiid and Parasites

Overall, host body size has a relatively strong effect on the number of parasite taxa a host harbours, regardless of the site of infection and transmission method (Poulin 2007; Kamiya et al. 2014). The theoretical basis of host size as predictor of parasite diversity originates from parallels with island biogeography theory and species-area relationships. Thus larger bodied hosts provide greater space and other resources to parasites and may represent a less ephemeral habitat than small-bodied hosts (Kamiya et al. 2014). However, individual euphausiids typically have low parasite species richness (1–3 symbiont species) with low intensities for macroparasites (i.e. ellobiopsidae, helminth, isopod Dajidae) and high intensities for microparasites (i.e. Apicomplexans, dinoflagellates, parasitoid ciliates). Overall, relative size (mass) of enemy:victim of pathogens-hosts ranges between $10^8$ and $10^4$, typical parasites and micropredators between $10^9$ and $10^2$ and parasitoid and castrators have the largest relative size of enemy:victim ratio $10^5$ to $1:1$ (Lafferty and Kuris 2002). Predators:victim size ranges from predators of the same
body size 1:1 and considerably larger than their prey’s 10^8:1 (Lafferty and Kuris 2002). As far as we known, predators are always slightly larger than their krill prey, but parasitoids are considerably smaller than their krill hosts (Gómez-Gutiérrez et al. 2012, 2015a; Lynn et al. 2014). The epibionts and parasites that are currently known to interact with euphausiids are shown in Figs. 2.1a, b and 2.2a, b, listed in Table 2.1. The degree of damage to the host ranges from that by virtually innocuous epibionts (diatoms, suctorians and apostome phoront ciliates), through commensal or parasitic bacteria and apicomplexans (gregarines) living in the feeding tract or hepatopancreas of the euphausiids, to castrators (Dajidae isopods, Ellobiopsidae, helminth worms) and parasitoids (dinoflagellates and Pseudocollinia ciliates) that affect, in different degrees, the fitness of the host (behaviour, swimming, feeding, growth, reproduction, and survival) (Fig. 2.1a, b).

The parasitoids that infect euphausiids are unicellular protists (quite small parasite–to-host body size ratio), but the infections reach very high intensity (>8500 cells) (Gómez-Gutiérrez et al. 2015a). They actually can convert all euphausiid biomass into parasite biomass except the moult that account about 5% of biomass of the body dry wight (Gómez-Gutiérrez et al. 2003, 2006, 2012, 2015a, b). Several parasites (e.g., helminths) are transmitted trophically when a predatory host feeds on an infected euphausiid intermediate host. Although those parasites do not directly kill their intermediate euphausiid hosts, they require the host’s death (predation) to continue and complete their life cycles (Lafferty and Kuris 2002). Parasites compromise the viability and health of their intermediate euphausiid host to improve transmission to higher trophic levels by impairing swimming capabilities to make them more vulnerable to predation, or they change the coloration of the host. Terrestrial parasitoids (mostly insects) infect hosts with relatively short life spans, weighing only a few grams and with a parasitoid-to-host size ratio between 1:100 and 1:1; which constrains the infection to relatively few parasitoids per host (a small infrapopulation) (Lafferty and Kuris 2002). Euphausioid parasitoids (dinoflagellates and ciliates) are considerably smaller (ratios of 0.018:1), can have larger infrapopulation size, and infect and usually consume the host faster (histophagous ciliates in <3 days) than terrestrial parasitoids (Gómez-Gutiérrez et al. 2003, 2006, 2010, 2012, 2015a). Thus, parasitoids of marine plankton do not fit the traditional concept for insect parasitoids that undergo their larval development within the egg, larva, pupa or adult of the host species (other insects or even small mammals), killing and consuming only one individual host in its life cycle. Rather, a very large number of parasitoids may kill a single krill egg (Gómez-Gutiérrez et al. 2009) or a krill adult (Gómez-Gutiérrez 2004; Gómez-Gutiérrez et al. 2003, 2006, 2012; Lynn et al. 2014). Despite this distinction, population densities of many insect species are regulated by parasitoids, which may be true for krill populations, but so far inadequately studied (Gómez-Gutiérrez et al. 2003).

2.3 Biodiversity and Size Proportion Between Euphausiid and Parasites
rather than more three-dimensional measures or even better estimation of biomass that should be more informative. The supply of energy and nutrients should untimely determine how much parasite biomass could be sustained; this is a key determinant of total biomass of parasite relative to biomass of the host (Poulin 2007; Kamiya et al. 2014).

References


Dogiel V (1906) Beiträge zur Kenntnis der Peridineen. Mittheilungen aus der Zoologischen Station zu Neapel 18(1):1–45 [in German]


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