Chapter 10
Parasites and Diseases

Jaime Gómez-Gutiérrez and José Raúl Morales-Ávila

Abstract The Antarctic krill *Euphausia superba* is among the most studied species of the Order Euphausiacea in biological and ecological aspects; however, reports of their parasites and diseases are relatively scarce. A worldwide overview of all parasites known for 48 out 86 extant euphausiid species includes 17 distinct types of epibionts, pathogens, parasites, and parasitoids. So far, only seven of them have been reported interacting with *E. superba* [epibionts: exuviotrophic ciliates (Foettingeriidae) and microplanktophagous ciliates (Suctoridae, *Ephelota*), pathogens: chitinoclastic bacteria and fungi; and trophically transmitted endoparasites: Apicomplexans (Gregarinidae, *Cephaloidophora*), nematode infecting krill's eggs (under laboratory conditions), and histophagous parasites: Apostomatida ciliates of the family Pseudocollinidae]. The epibionts have interspecific associations that strongly depend on the krill's moult cycle, discarding them at each moulting event. Their colonization and intensity show a remarkable synchronization with the krill moulting process at individual, school, and population levels. The social and sometimes highly dense swarms and schools of *E. superba*, its keystone trophic function (both as voracious predator and as prey to multiple predators) should make it a critical vector for trophically transmitted parasites in the food web. However, *E. superba* interacts with a relatively low diversity of epibionts, pathogens, and parasites, in comparison with parasite diversity known for relatively well-studied temperate (*Meganyctiphanes norvegica*, *Euphausia pacifica*) and subtropical (*Nyctiphanes simplex*) euphausiid species. The apparently low parasite diversity of *E. superba* is likely associated with its Antarctic zoogeographic pattern; where, parasites have not invaded the Antarctic krill with the same evolutionary success as have occurred with other euphausiid species from tropical, subtropical, temperate, and even Arctic ecosystems.

Keywords Pathogens • Diversity • Prevalence • Intensity • Social behaviour

J. Gómez-Gutiérrez (✉) • J.R. Morales-Ávila
Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, La Paz, Mexico
e-mail: jagomezg@ipn.mx; jrmoralesa@gmail.com

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10.1 Introduction

The Antarctic and non-Antarctic krill were separated approximately 20 Mya (Patarnello et al. 1996) and the Antarctic krill *Euphausia superba* Dana 1850 diverged from *Euphausia crystallorophias* Holt and Tattershall 1906 about 2.7 Mya (D'Amato et al. 2008). The high latitudes inhabited by Antarctic krill species are characterised by extreme changes in seasonal conditions, with very low food availability, long periods of darkness and a massive expansion of sea ice in autumn and winter. Thus, Antarctic krill evolved in a year-round gelid ecosystem with multiple overwintering behavioural and physiological strategies and complex interspecific consumer interactions with planktonic, benthic, and nektonic preys, predators, epibionts, pathogens, and parasites (Seear et al. 2012). These last three groups of organisms, seem to be more diverse in euphausiid from tropical, subtropical, temperate, and Arctic ecosystems than in Antarctic ecosystems; where some of them seem not to have successfully invaded the Antarctic Ocean (Klimpel et al. 2010). Seear et al. (2012) suggested that pathogen and parasites likely are responsive to latitudinal clines in environmental factors such as temperature. For example, at the Antarctic Peninsula, winter temperatures are typically below 0 °C, whereas they largely remained at or above 0 °C year-round at northward latitudes (i.e. South Georgia). It is likely that many disease agents are unable to exist below freezing point, but they may otherwise survive, infect and lead to disease above such temperatures (Seear et al. 2012).

Parasitism appeared early in biological evolution as an extremely common, diverse, and successful consumer interaction (Lafferty 1999; Lafferty and Kuris 2002). It became a relevant connection node for the diversification of complex life cycles of parasites; that sometimes during their ontogeny interacts with multiple host species at distinct trophic levels. *E. superba* is frequently considered a waist-wasp species in the Antarctic Ocean ecosystem (Atkinson et al. 2004). It has been proposed that this species strongly influences energy flow and species assemblages in the Antarctic pelagic realm that are complementary with hydro-climatic feedback interactions. This keystone species represents a colossal available biomass population for epibiontic, ectoparasitic, and endoparasitic organisms.

A healthy krill, with a metabolism in steady-state (in homeostasis), has a transparent body (an adaptation to decrease the risk of visual predators in the water column), red-brown chromatophores, a translucent digestive gland (hepatopancreas), relatively large hepato-somatic index (proportion of the hepatopancreas and the cephalothorax length), fast and synchronized heartbeat, active peristaltic movements of the intestine, energetic and synchronous swimming movements, and regular growth, moulting, and gonad development rate and functions. The pathognomonic (characteristic of specific diseases) in euphausiid is, so far, not well studied worldwide compared with decapods of commercial value. However, among the multiple symptoms of sickness or physiological response to epibionts, pathogens, or parasites in euphausiids include lack of transparency of the body (usually an opaque or pale whitish coloration, which indicates mechanical damage or lack of homeostasis in the individual), black spots on their exoskeleton, opaque colouration, and/or non-functional chromatophores. Additionally, gross signs

include coloured and mostly opaque or/and pulsing movements in the digestive gland, a relative small hepato-somatic index (proportion size of hepatopancreas/cephalothorax length), and a contracted intestine that sometimes lacks peristaltic movements (signs of prolonged fasting). Also, slow or desynchronized heartbeat, sluggish or erratic swimming capabilities (that sometimes can separate them from their conspecifics, lingering behind the krill schools), irregular or slow growth (including shrinking), moulting, and gonad development (including re-absorption or castration), and in case of pathogens and histophagous ciliates (parasitoids), cause death of the krill host. In recent years, ecologists have come to recognize the enormous influence of parasites and disease in regulating animal populations (Gómez-Gutiérrez et al. 2003; Kuris et al. 2008).

The Antarctic krill is a voracious omnivore that requires highly energy intake to fuel continuous swimming in the water column ($\leq$20 cm s^{-1}). Despite this high-energy intake, this species shows relatively slow growth rates (its longevity ranges from 4 to 7 years) that can reach one of the largest body sizes for epipelagic species in the order Euphausiacea (up to 65 mm total length) (Baker et al. 1990). This species forms some of the largest aggregations, swarms, and schools known for any species of the order Euphausiacea, with maximum reported regional biomass of about two million tonnes, distributed over an area of 100–450 km^2 at densities of up to 2000 individuals m^{-3} and annual estimated biomass ranging between 100 and 500 million tonnes (wet mass) (Macaulay et al. 1984; Watkins 2000; Atkinson et al. 2009; Nowacek et al. 2011). Antarctic krill populations represent a colossal amount of biomass that potentially can interact with epibionts, pathogens, and parasites. Hamner (1984) observed natural synchronized moulting in *E. superba* schools and also a predator-induced pattern of moulting that he called "decoy moulting". These synchronized krill moulting events must have a direct effect on survival, feeding, and infection strategies of epibionts, chitinoclastic bacteria, and gregarines (Apicomplexa), which their life cycles are strongly coupled with krill's moult cycles.

Two landmark monographs summarized most of the published information about parasites of euphausiids before the 1980s decade (Mauchline and Fisher 1969; Mauchline 1980). Then, it was apparently unknown the presence of epibiont, pathogens, and parasites of *E. superba*. There have been almost 35 years without any updated monograph to show what is currently known about interspecific associations of krill with other species, except predator-prey interactions (Mauchline and Fisher 1969; Mauchline 1980, see Chap. 9, Trathan and Hill 2016). Although an extensive review of parasites of marine zooplankton mentioned several euphausiid parasites (Théodoridès 1989), this review did not explicitly mention *E. superba* interaction with epibionts, pathogens, or parasites. We performed a meta-analysis review of reports of epibionts and parasitic organism of crustaceans of the order Euphausiacea published between 1885 and 2013 (120 publications including about 360 records including personal observations in *E. superba* reared in the Australian Antarctic Division, Tasmania Australia krill laboratory, Aug 2009–Jul, 2010). This worldwide review of literature provides us a relatively broad perspective about the diversity, prevalence patterns, intensity, parasite-host size ratio, availability of microhabitats for parasites in euphausiids, and the association of parasitism with the host reproductive strategies to better

understand emerging patterns of parasite–host co-evolution. Currently, there are 17 different known types of epibionts, pathogens, parasites, and parasitoids infecting krill (107 known taxa reported in 48 of the 86 extant species of the order Euphausiacea) (Fig. 10.1a). The definitions of trophic strategies used in the present review were defined and explained in detail in Lafferty and Kuris (2002). They report eleven trophic strategy categories based in four dichotomies: (1) number of victims that an individual attacks throughout the life-history stage (to distinguish predators vs. parasites), (2) whether a successful attack eliminates the fitness of the host (to define castrators and parasitoids), (3) if the host must die to further parasite development (to define parasitoids), and (4) presence or absence of density-dependent pathology (macroparasites vs microparasites). Combining these four dichotomies defines seven types of parasitism (typical parasite, pathogen, trophically transmitted typical parasite, trophically transmitted pathogen, parasitic castrator, trophically transmitted parasitic castrator, and parasitoid), three forms of predation (micropredator, social predator, and solitary predators) and, when one considers obligate and facultative combinations of these forms, four types of predators (Lafferty and Kuris 2002). Several of these types of interspecific interactions have been observed in *E. superba* (Table 10.1). All euphausiid's epibionts and parasites have different life strategies, ranging from epibionts (epizootic diatoms, suctorida, and exuviotrophic ciliates, and chitinoclastic bacteria), and ectoparasites (Dajidae isopods), mesoparasites [Ellobiopsidae and Rhizocephalan, this last is a highly uncertain report (Mooney and Shirley 2000)], potential pathogens (bacteria and fungi), hyperparasitic ciliates (*Phtorophyra* sp.), trophically transmitted endoparasites (Apicomplexa, Cestoda, Trematoda, Nematoda, and Acanthocephala), and parasitoids (dinoflagellates, and histophagous Apostomatida *Pseudocollinia* ciliates). With the broad-scale perspective in this chapter, we compared the diversity, prevalence, and intensity of the parasites that are associated with *Euphausia superba* to conceptualize how much is currently known about those interspecific associations in this pivotal species of the Antarctic Ocean. Although *E. superba* (and other krill species) has been the focus of multiple observational and experimental studies; so far in *E. superba*, only 7 out of 17 previously known types of epibionts, pathogens, parasites, and parasitoids that interact with euphausiids have been documented (Fig. 10.1b). These include: epibionts: (1) exuviotrophic apostome ciliates (unidentified species) of the family Foettingeriidae (Kittel and Rakusa-Suszczewski 1988; Rakusa-Suszczewski and Nemoto 1989; Stankovic and Rakusa-Suszczewski 1996) likely of the genus *Gymnodinoides*, but sometimes incorrectly identified cysts of ciliates (found attached to their appendages) of the genus *Ephelota* spp. (Stankovic et al. 2002), (2) microplanktophagous ciliates of the family Ephelotidae (genus *Ephelota*) (Stawiszyńska-Janas and Kittel 1982; Stankovic et al. 2002; Tarling and Cuzin-Roudy 2008), pathogens: (3) chitinoclastic bacteria of the genus *Psychrobacter* and *Pseudoalteromonas* (Miwa et al. 2008) and (4) fungus *Metschnikowia australis* (Donachie and Zdanowaski 1998); and trophically transmitted endoparasites: (5) Apicomplexa (three species of the genus *Cephaloidophora*, family Gregarinidae) (Avdeev 1985, 1987; Avdeev and Avdeeva 1989; Kawaguchi et al. 1999; Takahashi et al. 2003, 2004, 2008, 2009, 2011),

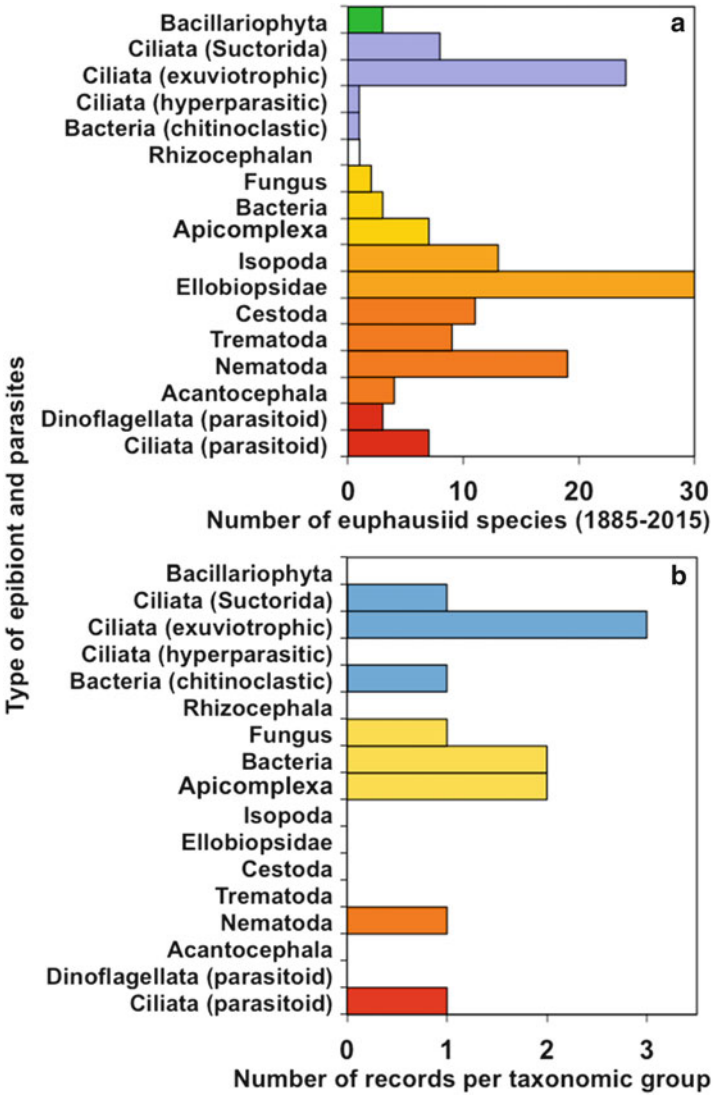

Fig. 10.1 (**a**) Meta-analysis of the 17 types of epibionts (*green* and *blue* bars), pathogens (*light orange bars*), trophically transmitted parasites (*dark orange bars*), and "parasitoids" (*red bars*) that interact with euphausiids (Order Euphausiacea) around the world from a review of 120 published works from 1885 to 2013. (**b**) Types of parasites so far reported for the Antarctic krill *Euphausia superba*

(6) Nematoda (unidentified larvae L1 infecting eggs of *E. superba*) (Robert King and Jaime Gómez-Gutiérrez, pers. observ.), and parasitoids: (7) Apostomatida histophagous ciliates (Stankovic and Rakusa-Suszczewski 1996) probably belonging to the family Pseudocollinidae (Gómez-Gutiérrez et al. 2012; Lynn et al. 2014) (Fig. 10.1b, Table 10.1). Circumstantial evidence suggest potential viral inclusions

Table 10.1 List of epibiont, pathogen, parasite, and parasitoids species assemblage reported interacting with the Antarctic krill *Euphausia superba* in the Antarctic Ocean. Trophic strategies assigned according with criteria of Lafferty and Kuris (2002)

Kuris and Lafferty (2002) classification	Type of parasite	Family	Genus and species	Krill life phase vulnarable	Parasite size range (μm) (μm)	Parasite mean size (mm)	Krill TL length (mm)	Parasite/ host total length ratio	Prevalence		Intensity	Region of study	References
									Range (%)	Mean (%)			
Epibiont (planktophagous)	Ciliata	Suctoridae	*Ephelotas* spp.	Juvenil and adult	40–420	0.157	65.0	0.002				Southern Ocean, Admiralty Bay	Stawiszyńska-Janas and Kittel (1982)
Epibiont (planktophagous)	Ciliata	Suctoridae	*Ephelotas* spp. (three forms-sizes)	Juvenil and adult	100, 200–250, 450–500	0.250	58.0	0.0043	35–72	55	<95	Southern Ocean, south of Australia	Rakusa-Suszczewski and Nemoto (1989)
Epibiont (exuviotrophic)	Ciliata	Suctoridae	*Ephelotas* spp.	Juvenil and adult			65.0				42	Southern Ocean 63.38 S, 127.10 E	Stankovic and Rakusa-Suszczewski (1996)
Epibiont (planktophagous)	Ciliata	Suctoridae	*Ephelotas* spp.	Juvenil and adult	40–420	0.157	65.0	0.002	<1 %	0.0005	20,000	Southern Ocean, Elephant Island, the South Orkneys, King George Island and Bransfield Strait	Stankovic et al. (2002)
Epibiont (planktophagous)	Ciliata	Suctoridae	*Ephelotas* spp.	Juvenil and adult	40–420	0.157	58.0	0.003	0–35 %	0.35	281	Southern Ocean, South Georgia 54.5S, 37W	Tarling and Cuzin-Roudy (2008)
Epibiont (exuviotrophic)	Ciliata	Foettingeriidae	Unknown spp. (three forms)	Juvenil and adult	27, 38, 46	0.038	54.0	0.0007		84		King George Island, Elephant Island and in the Bransfield Strait	Kittel and Rakusa-Suszczewski (1988)
Epibiont (exuviotrophic)	Ciliata	Foettingeriidae	Unknown spp. (three forms)	Juvenil and adult	35–45, 75–87, 30–37	0.044	55.0	0.0008	100	100	382, 902, 8	Almiratly Bay (an annual cycle) and Wedell Sea	Rakusa-Suszczewski and Filcek (1988)

Epibiont (exuviotrophic)	Ciliata	Foettingeriidae	Unknown spp. (three forms)	Juvenil and adult	35–87	0.061	58.0	0.0011	100	100	<1000	Southern Ocean, south of Australia	Rakusa-Suszczewski and Nemoto (1989)
Epibiont (exuviotrophic)	Ciliata	Foettingeriidae	Unknown spp.	Juvenil and adult			65.0	0.0000	84–100 %	90	450	Southern Ocean, 63.38 S, 127.10 E	Stankovic and Rakusa-Suszczewski (1996)
Epibiont (exuviotrophic)	Ciliata	Foettingeriidae	Unknown spp., erroneously identified as *Ephelota*	Juvenil and adult	70	0.007	65.0	0.0001	0–80 %	0.8	20,000	Elephant Island	Stankovic et al. (2002)
Oportunistic pathogen	Bacteria	g-proteobacteria	*Psychrobacter*	Juvenil and adult	1–2		65 0		2–42 %	0.0350		Southern Ocean, South Georgia	Miwa et al. (2008)
Oportunistic pathogen	Bacteria	g-proteobacteria	*Pseudoalteromonas*	Juvenil and adult	1–2		65.0		2–42 %		0.0350	Southern Ocean, South Georgia	Miwa et al. (2008)
Opportunistic parasite	Fungus	Yeast	*Metschnikowia australis*	Juvenil and adult	45	0.005	65.0	0.0001				Southern Ocean, King George Island	Donachie and Zdanowaski (1998)
Trophically trasmitted parasite	Apicomplexa	Gregarinidae	*Cephaloidophora pacifica*	Juvenil and adult	140–155	0.016	65.0	0.0002	76.4	0.7640	1848	East Pacific and Indian Sector of the Southern Ocean	Avdeev (1985)
Trophically trasmitted parasite	Apicomplexa	Gregarinidae	*Cephaloidophora indica*	Juvenil and adult	102–238	0.024	65.0	0.0004	44.5	0.4450	229	East Pacific and Indian Sector of the Southern Ocean	Avdeev (1985)
Trophically trasmitted parasite	Apicomplexa	Gregarinidae	*Cephaloidophora pacifica*	Juvenil and adult	18–76	0.008	65.0	0.0001	90–100	0.9640		Antarctic Peninsula, Near Syowa station, Pacific and Indian sector the Southern Ocean	Takahashi et al. (2004, 2008)
Trophically trasmitted parasite	Apicomplexa	Gregarinidae	*Cephaloidophora pacifica*	Juvenil and adult	18–76	0.008	65.0	0.0001			195	Southern Ocean, South Georgia	Takahashi et al. (2003, 2008)

(continued)

Table 10.1 (continued)

Kuris and Lafferty (2002) classification	Type of parasite	Family	Genus and species	Krill life phase vulnarable	Parasite size range (μm) (μm)	Parasite mean size (mm)	Krill TL length (mm)	Parasite/ host total length ratio	Prevalence		Intensity	Region of study	References
									Range (%)	Mean (%)			
Trophically trasmitted parasite	Apicomplexa	Gregarinidae	*Cephaloidophora pacifica*	Calyptopis to adult	50	0.005	13.0	0.0004	14–79.6	0.4	256	Indian sector of the Southern Ocean	Takahashi et al. (2011)
Unknown	Nematoda	Unknown	Unknown spp.	Eggs								Laboratory Australian Antarctic Division (AAD)	King and Gómez-Gutiérrez (pers observ)
Trophically transmitted castrator	Helminth	Unknown	Unknown spp.	Juvenil and adult	200–1000	0.100	65.0	0.0015	6 %	0.06	50	Southern Ocean, South Georgia	Miwa et al. (2008)
Parasitoid	Cilia	Pseudocollinidae	Unknown spp.	Adults	80–333	0.18	65	0.0028				Southern Ocean, 63.38 S, 127.10 E	Stankovic and Rakusa-Suszczewski (1996)

present within R-cells of the hepatopancreas in <1 % of sampled *E. superba* (Bateman, Hicks, Tarling, Soeffker and Stentiford, WG-EMM-2015/23). However, further studies must confirm such histological observations. However, it is difficult to visualize whether historical research efforts to study epibionts and parasites of *E. superba* (circa 1982 to present) are a precise representation of the apparently low diversity of epibiont and parasitic interactions with this species or whether parasitological studies of *E. superba* are in their infancy. In either case, considerable parasitological research effort remains to be carried out in the Antarctic Ocean in the future to discover the ecological function and consequences of epibiont and parasitic interactions.

Infectious agents—bacteria, fungi, or parasites cause most diseases described in the present chapter. Conditions due to non-infectious causes like cancer (although some cancer can be viral induced), diseases related to prolonged fasting, high levels of persistent organic pollutants (POP), heavy metals, or other toxic substances are not covered in this chapter (Yamamoto et al. 1987; Corsolini et al. 2002; Nash et al. 2008; Poulsen et al. 2012). Aside from the eco-physiological studies of Poulsen et al. (2012) the negative health effects of toxic substances have not been specifically tested and their health consequences are poorly understood. Sub-lethal narcosis (immobility) was observed in non-feeding larval stages of *E. superba* from p,p′-dichlorodiphenyl dichloroethylene (p,p′-DDE) body residues of 0.2 mmol/kg p.w. (Poulsen et al. 2012).

Overall, little is known about euphausiid immune response (i.e. melanization, enhancement of encapsulation, hemocytes, opsonin formation, antibacterial or antifungal activity, production of free radicals, and oxidative stress responses among others), behaviour, influence of epibionts and parasites in the metabolic and reproduction rates, resulting in a poor and fragmented understanding about the effect of epibionts, pathogens, parasites, and parasitoids on euphausiids and presumably zooplankton and nekton krill's predators. However, recently were published two pioneer studies about *E. superba*'s immune system (Seear et al. 2012; Zhao et al. 2013). Seear et al. (2012), using gene expression techniques [cDNA microarrays and quantitative (qPCR)], reported the first *E. superba* study of immune gene expression in any euphausiid species worldwide. *E. superba* showed two major immune gene types: (1) Cathepsins (C and K) localized in the lysosomes and endosomes that degrade intracellular or endocytosed proteins and (2) C-type lectins that contribute to innate immune responses in invertebrates, including prophenoloxidase activation, enhancement of encapsulation, nodule formation of hemocytes, opsonin formation, antibacterial activity, antifungal activity, and injury healing. Seear et al. (2012) mentioned that haemocyanin may also be an additional contributor to the krill immune system given that, in addition to being an oxygen carrier, it is known to have antiviral, antibacterial, and antifungal properties. However, this research did not experimentally challenge krill with any parasite or pathogen (krill was not infected), but detected the expression of genes associated with previously known immune function in shrimps infected with bacteria or virus. Zhao

et al. (2013) obtained and purified a preliminary antimicrobial polypeptide (CMCC-1) from *E. superba*. This polypeptide showed cell cytoplasmic membrane destruction and inhibited cell division at the logarithmic phase against the pathogenic bacteria *Staphylococucs aureus*. Despite these research efforts, still being a poorly and fragmented perspective about the effect of parasites upon *E. superba* at the individual, aggregation, population, and species levels. In this chapter, we summarize the parasitological knowledge about the interaction of *E. superba* with each taxonomic group: epibionts, pathogens, parasites, and parasitoids.

10.2 Black Spot Pathogenic Chitinoclastic Bacteria

Lear (1963) was likely the first to mention the occurrence and significance of chitinoclastic bacteria in pelagic waters and zooplankton. Currently is unclear the diversity, density, and relative abundance of bacteria in euphausiid digestive tract and what proportion they have gut-symbiotic or gut-parasitic interactions. Bacteria inhabiting the euphausiid digestive system (stomach, intestine, and digestive gland) are several orders of magnitude more concentrated ($1.6–5.7 \times 10^6$ bacteria mg^{-1}) than in sea water (Rakusa-Suszczewski and Zdanowski 1989). It is unlikely that such high densities are explained by feeding filtering because bacteria are small (<1 μm), suggesting that bacteria reside and multiply in their stomachs (Fevolden and Eidsa 1981; Donachie 1995; Donachie et al. 1995; Donachie and Zdanowski 1998; Denner et al. 2001) (Table 10.2). Bacterial communities collected from the digestive tract of euphausiids (*E. superba*, *E. crystallorophias*, *Thysanoessa macrura* G. O. Sars, 1883) have been studied to understand the role of bacteria in krill spoilage (Kelly et al. 1978) and the digestive function of bacteria and krill health (Donachie and Zdanowski 1998). These studies used culture-dependent techniques, likely resulting in a considerable underestimation of bacterial diversity because only a relatively small fraction of these bacteria can be successfully cultivated from gastrointestinal tracts of invertebrates and vertebrates (10–50 %) (Zoetendal et al. 2004). Overall, Arctic and Antarctic euphausiid species have less diverse bacterial biota than subtropical species (Aguilar-Méndez et al. 2008). The dominant cultured bacteria in *E. superba* are γ-proteobacteria (*Pseudomonas* is ubiquitous in the stomachs of polar krill and *Moraxella*), followed by lower densities of Firmicutes, Actinobacteria, Flavobacteria, and β-proteobacteria (Table 10.2). Stomach bacteria in *E. superba* participate in host digestive processes by producing enzymes and dietary co-factors contributing to proteolytic, lipolytic, and chinitolytic enzyme pools (Rakusa-Suszczewski and Filcek 1988; Dabrowski et al. 1983; Rakusa-Suszczewski and Zdanowski 1989; Donachie et al. 1995; Cieśliński et al. 2005, 2007). It is evident that most bacteria in stomachs of euphausiids participate in digestive processes of the host. Miwa

et al. (2008) reported that bacteria may cause potential pathogenic effect when opportunistically increase their numbers when interact with infection inflicted by other krill parasites (Fig. 10.2a, b). Bacteria also have been observed associated with histophagous ciliate infections of northeast Pacific region krill species that, in extreme high intensities, may lead to bacteraemia events (Gómez-Gutiérrez et al. 2012, 2015; Lynn et al. 2014) (Table 10.2). Miwa et al. (2008) is the only published report that specifically proposes that pathogenic bacteria infect *E. superba* (unknown for all other euphausiid species) from South Georgia region causing black spots in different parts of the cephalothorax and trunk (Fig. 10.2a). Their histological observations revealed that the black spots were melanised nodules composed of hemocytes surrounding either bacteria or

Table 10.2 Chronological list of bacterial densities and strain richness associated with Antarctic krill (*Euphausia superba*, *Euphausia crystallorophias*, and *Thysanoessa macrura*)

Euphausiid species	Microbiota	Bacterial densities	References
E. superba	Coryniform like, *Pseudomonas*, *Moraxella* like, *Alcaligenes*, *Acinetobacter*, *Flavobacterium*, *Micrococcus*, *Vibrio*, *Bacillus*	0.875 CFU mg^{-1}	Kelly et al. (1978)
E. superba	*Moraxella* like, *Pseudomonas*, *Alteromonas*	1×10^3 CFU mg^{-1}	Fevolden and Eidsa (1981)
E. crystallorophias	*Moraxella* like, *Alcaligenes*, *Flavobacterium*, Vibrionaceae, *Planococcus*, *Brochothrix thermosphacta Alteromonas*, *Pseudomonas*	0.56 CFU mg^{-1}	Fevolden and Eidsa (1981)
E. superba	*Corynebacterium*, *Micrococcus*, *Pseudomonas*, *Alcaligenes*, *Moraxella*, *Bacillus*, *Flavobacterium*, *Arthrobacter*	3.59×10^6 CFU mL^{-1}	Turkiewicz et al. (1982)
E. superba	*Clostridium bifermentans*, *C. sporogenes*, *C. subterminale*, *Clostridium*	Not estimated	Dabrowski et al. (1983)
E. superba	Cocci	5.7×10^8 cells mg^{-1}	Rakusa-Suszczewski and Zdanowski (1989)
E. superba	*Clostridium bifermentans*, *C. sporogenes*, *C. subterminale*, *Clostridium*	Not estimated	Dabrowski et al. (1983)
E. superba	*Flavobacterium*, *Flavobacterium breve*, *Pseudomonas vesicularis*, *Weeksella virosa*, *Moraxella*, *Pasteurella*, *Aeromonas*, *Vibrio*	1.09×10^5 CFU mg^{-1}, 3.28×10^6 mg^{-1} AODC	Donachie (1995), Donachie et al. (1995)
T, macrura	*Pseudomonas*	3.23×10^3 CFU mg^{-1}, 2.22×10^5 AODC mg^{-1}	Donachie (1995), Donachie et al. (1995)

(continued)

Table 10.2 (continued)

Euphausiid species	Microbiota	Bacterial densities	References
E. superba	Gram negative cocci, Gram negative bacilli	1.09×10^5 CFU mg^{-1}, 3.28×10^6 mg^{-1} AODC	Donachie and Zdanowsky (1998)
E. superba	*Psychrobacter proteolyticus*	Not estimated	Denner et al. (2001)
T. macrura	*Pseudoalteromonas*	Not estimated	Cieśliński et al. (2005)
E. superba	*Pseudoalteromonas*	Not estimated	Cieśliński et al. (2007)
E. superba	*Pseudoalteromonas*, *Psychrobacter*	Not estimated	Miwa et al. (2008)
E. superba	*Non-identified*, SEM Fig. 10.2	Not estimated	Gómez-Gutiérrez unpubl. data

All bacteria were isolated from the digestive tract of krill, except bacteria isolated from black spot melanomas located at the surface of the Antarctic krill exoskeleton. *Pseudoalteromonas*, *Psychrobacter*, *Staphylococcus*, and *Vibrio* are potentially opportunistic pathogenic bacteria (Miwa et al. 2008). Chitinoclastic bacteria may also be opportunistic pathogens (Review information modified from Aguilar-Méndez et al. (2008))

amorphous material (Fig. 10.2b). In 2007, 42 % of the krill had melanised nodules, but prevalences usually range from 2 to 5 %. Most of the nodules had an opening on the body surface of krill (Miwa et al. 2008). Three bacterial strains were isolated from these black spots and classified as *Psychrobacter* or *Pseudoalteromonas*, based on sequences of 16S rRNA gene analysis (Table 10.2).

We have observed chitinoclastic bacterial infection that cause considerable injury, that eventually resulted in death, from live *E. superba* specimens transported from the Antarctic Sea to the Australian Antarctic Division krill laboratory (AAD) located at Kingston, Tasmania, Australia (Robert King and Jaime Gómez-Gutiérrez, pers. observ.) (Fig. 10.2c). Scanning Electron Microscope (SEM) images of *E. superba* black spots and areas with visible black injuries (in cephalothorax, appendages, trunk, and telson) were rapidly colonized by opportunistic rod-shaped bacterial colonies (Fig. 10.2d–f). Specimens developed black spots in the overwhelming high-density tanks where krill are regularly transported in the R/V Aurora Australis. In this case, although bacteremia can eventually cause the death of krill, bacteria cannot be considered, in the strict sense, a parasitoid because bacteria do not require the death of the host to complete their life cycle and they have a density-dependent virulence in the host (Lafferty and Kuris 2002).

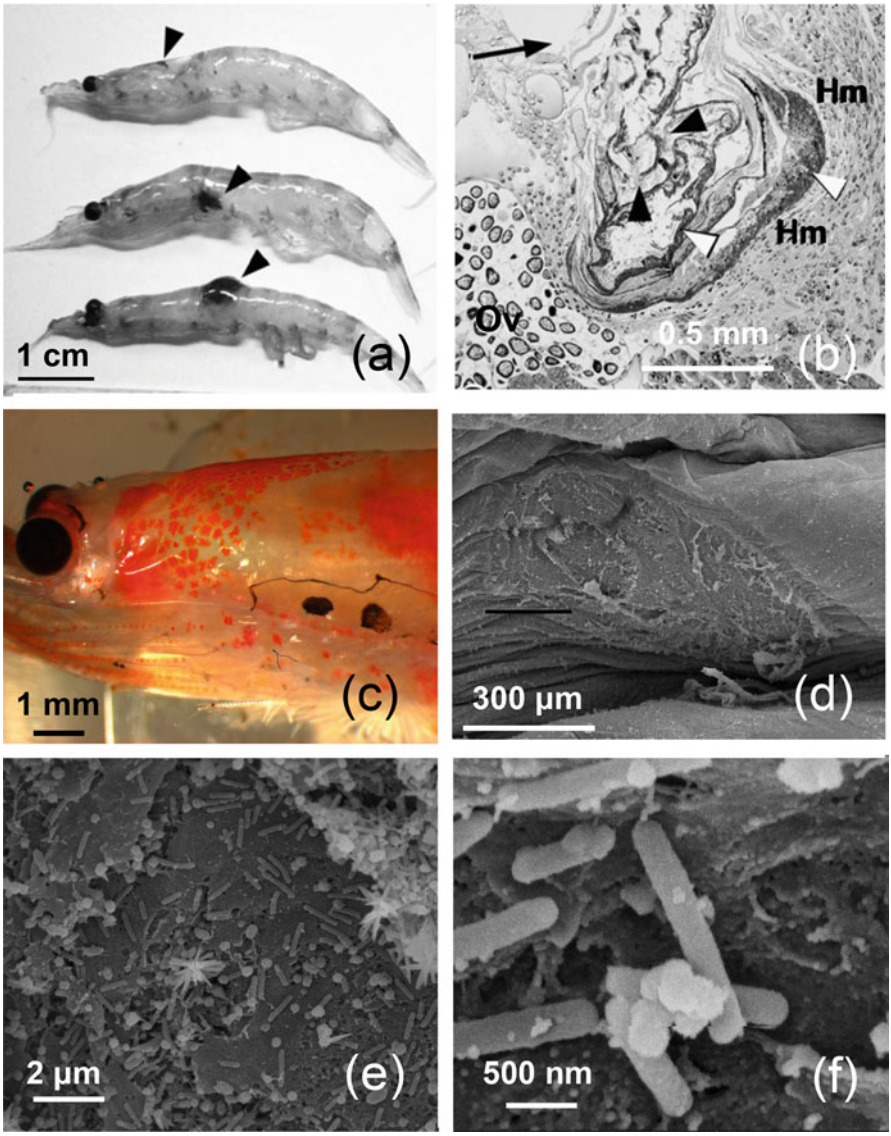

Fig. 10.2 (**a**) Antarctic krill *Euphausia superba* bearing black spots (*arrowheads*). The numbers on the scale are in cm, (**b**) A transverse section of dorsal part of the cephalothorax of a krill with a typical melanised nodule. Bacterial mass (*black arrowheads*) is encapsulated by melanin layers (*white arrowheads*), which is further surrounded by hemocytes (Hm). The *arrow* indicates the opening of the lesion to outside of the body. *Hp* hepatopancreas, *Ov* ovary. HE stain (**a**, **b** reprinted from Miwa, S., Kamaishi, T., Matzuyama, T., Hayashi, T. and Naganobu, M. Histopathology of Antarctic krill, *Euphausia superba*, bearing black spots. Journal of Invertebrate Pathology 98, 280–286, Copyright (2008), with permission from Elsevier). **c** *Black* spot caused by chitinoclasitic bacteria affecting *E. superba* maintained under laboratory conditions in the Australian Antarctic Division, Tasmania, Australia. Scanning electron microscope micrographs show (**c**) zoom of the wound and (**d**–**f**) high population density of rod-shaped chitinoclastic bacteria (**c** Photos and **d**–**f** SEM images taken by JG-G)

10.3 Endoparasitic Apicomplexa (Family Gregarinidae)

Apicomplexan gut-living gregarines, commonly but incorrectly known as sporozoans, infect the digestive tract of annelids and several crustacean taxa (Cirripedia, Amphipoda, Mysidacea, Decapoda, and Euphausiacea) (Dobson 2002; Takahashi et al. 2008). All species are parasites of animals. The apicomplexa infect the stomach, intestine, and midgut gland (hepatopancreas) of euphausiids. Currently, it is known that 7 out the 62 named species of the genus *Cephaloidophora* (Family Cephaloidophoridae), one species of the genus *Lateroprotomeritus*, and several reports of undescribed gregarines are trophically transmitted apicomplexa gregarines of euphausiids from the Mediterranean Sea, Barents Sea, and the Antarctic Ocean (Théodoridès and Desportes 1975; Avdeev 1985; Avdeev and Avdeeva 1989; Théodoridès 1989; Timofeev 2001). So far, gregarines have been reported in only seven euphausiid species (*E. superba*, *M. norvegica*, *Nematoscelis megalops*, *N. atlantica*, *Thysanoessa macrura*, *T. raschii*, and *Stylocheiron abbreviatum*) (Table 10.3). Although most apicomplexan species have monoxenous life cycles involving a single invertebrate host, gregarines are endoparasites relatively difficult to detect (particularly in preserved specimens) due their small cell size (71–144 μm average total length) and the location inside the intestine or the hepatopancreas. Apicomplexan gregarines have a trophic transmission strategy (orofaecal route) and they sometimes attain high prevalences (up to 90 %) in the krill species so far studied. Therefore, it is likely to find new euphausiid hosts with gregarine infections and perhaps new species of gregarines identified with molecular methods.

Avdeev (1985) discovered and described the first two species of apicomplexa gregarine parasites, *Cephaloidophora pacifica* (Fig. 10.3a–c) and *Cephaloidophora indica* (Fig. 10.3d–f), infecting digestive tract of the Antarctic krill *E. superba*, being more prevalent the species *C. pacifica* (75 % of 1848 specimens examined) than *C. indica* (44.5 % of 229 specimens examined) (Table 10.3). Avdeev and Avdeeva (1989) later described two additional species, *Cephaloidophora thysanoessae* infecting *Thysanoessa macrura*, and *Cephaloidophora antarctica* infecting *E. superba*. Following the apicomplexa description by Levine (1988), it appears that the ciliates found reproducing in the gut of *E. superba* (Kawaguchi and Toda 1997) were actually gregarine parasites. Although, they have been studied mostly from adult euphausiid specimens, there are records that Apicomplexa (Eugregarinida) also infect *E. superba* calyptopis and furcilia larval phases (Takahashi et al. 2011). Currently, *C. pacifica* (host *E. superba*) is the best-studied gregarine species infecting euphausiids worldwide, partially because its high prevalence, broad circumpolar distribution, and a significant research effort carried out first by Russian (Avdeev 1985, 1987; Avdeev and Vagin 1987; Avdeev and Avdeeva 1989), followed by Japanese scientists (Takahashi et al. 2003, 2004, 2008, 2009, 2011), and more recently by British scientists (Bateman et al. 2015).

Avdeev (1987) first described the development of gregarines of *E. superba* and Takahashi et al. (2009) conceptualized the known life cycle of gregarines (Order

Table 10.3 Apicomplexa gregarines of the genera *Cephaloidophora* and *Lateroprotomeritus* (the last one of unclear taxonomic affiliation) reported infecting several Antarctic krill *Euphausia superba* and *Thysanoessa macrura*

Gregarine species	Krill host	Size (μm)	Average prevalence (%)	Location (likely distribution range)	Source
C. pacifica	*E. superba*	140–155	76.4 (1848)	East Pacific and Indian Ocean sector of Southern Ocean	Avdeev (1985)
C. indica	*E. superba*	102–238	44.5 (229)	East Pacific and Indian Ocean Sector of Southern Ocean	Avdeev (1985)
C. pacifica	*E. superba*	100	100 (1165)	Kosmonavtov Sea	Avdeev (1987)
C. pacifica	*E. superba*				Avdeev and Vagin (1987)
C. pacifica	*E superba*	No data	No data	Circumpolar	Spiridonov (1996)
C. indica	*E superba*	No data	No data	Antarctic Indian region	Spiridonov (1996)
C. pacifica	*E. superba*	18–76	96.4	Antarctic Peninsula, near Syowa Station, Pacific and Indian sector of the Southern Ocean	Takahashi et al. (2004, 2008)
C. pacifica	*E. superba*	18–76	(195)	South Georgia Region	Takahashi et al. (2003, 2009)
C. pacifica	*E. superba*	40–50	69.7 % (256)	Antarctic Indian region	Takahashi et al. (2011)
C. thysanoessae	*T. macrura*	130–217	29.0 (17)	East Pacific and Indian Sector of the Southern Ocean	Avdeev and Avdeeva (1989)
C. antarctica	*T. macrura*	47–142	2	East Pacific and Indian Ocean Sector of the Southern Ocean	Avdeev and Avdeeva (1989)

The number in parenthesis is the number of krill specimens examined during each study. *Cephaloidophora pacifica* is a species currently considered Antarctic circumpolar

Eugregarinida) (Fig. 10.4). Gregarines typically have high prevalences in the *E. superba* population (up to 87 %). The gregarine parasites have six life stages (Avdeev 1987). Four endoparasitic stages occur inside the digestive tract in krill (sporozoite, cephalin, gamont, and syzygy) and two presumably outside the krill hosts (gametocyst and oocyst), which probably infect an intermediate planktonic host (likely a copepod) (Fig. 10.4). After the gregarine enter the host's intestine, sporozoites excyst from the oocyst and attach to the epithelium (cephalin stage). Cephalins have bodies divided into anterior epimerite, protomerite, and posterior deutomerite and are commonly located in the hind-gut epithelium of their host and liberated into the intestinal lumen. The early developmental stages take place mostly intra-cellularly. The gamont stage, which follows, is mostly found in the

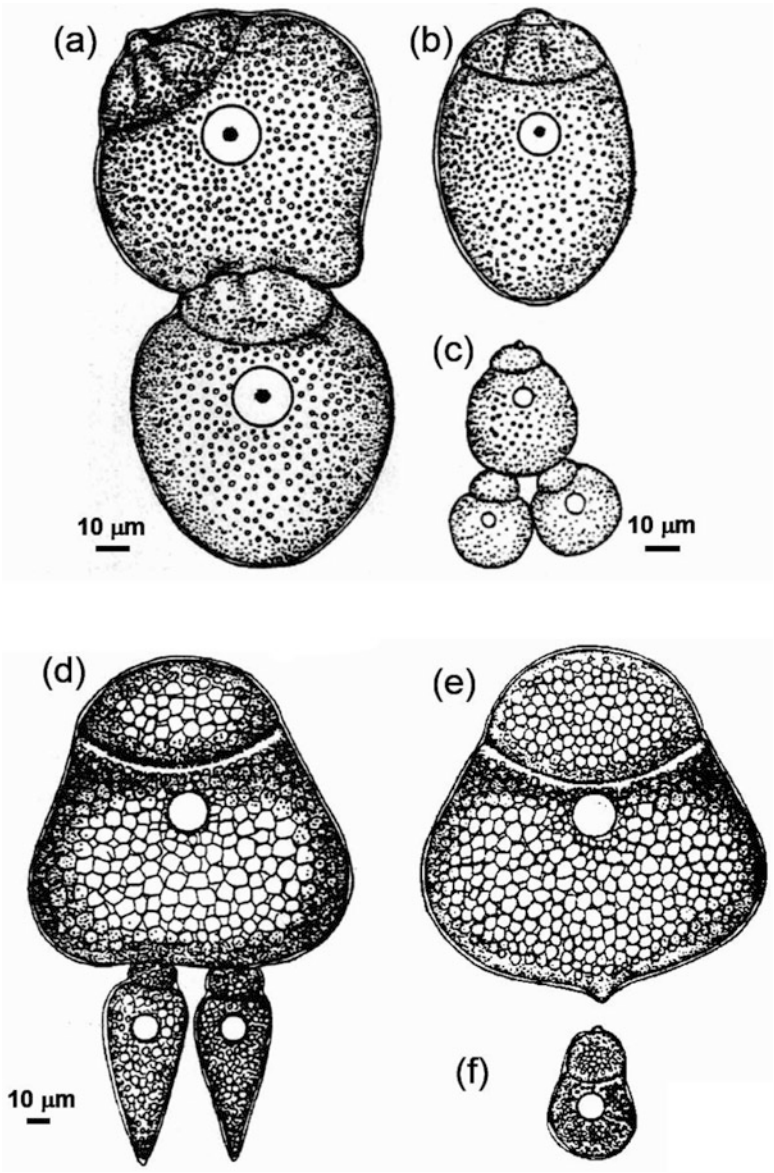

Fig. 10.3 Apicomplexa Gregarinidae that infect *Euphausia superba*. *Cephaloidophora pacifica* (**a**) mature syzygy, (**b**) mature gamont, and (**c**) immature syzygy. *Cephaloidophora indica* (**d**) mature gamont, (**e**) mature syzygy, and (**f**) immature syzygy (Figures are reproduced with permission from Parasitology, Avdeev 1985)

intestinal lumen, as well as the diverticulum of the mid-gut gland. After maturation, they associate head to tail (syzygy) to produce a reproductive gametocyst that will be shed in the host's faeces. Within a few days, mature gametocysts release infective oocysts into the environment to continue the cycle (Fig. 10.4) (Takahashi

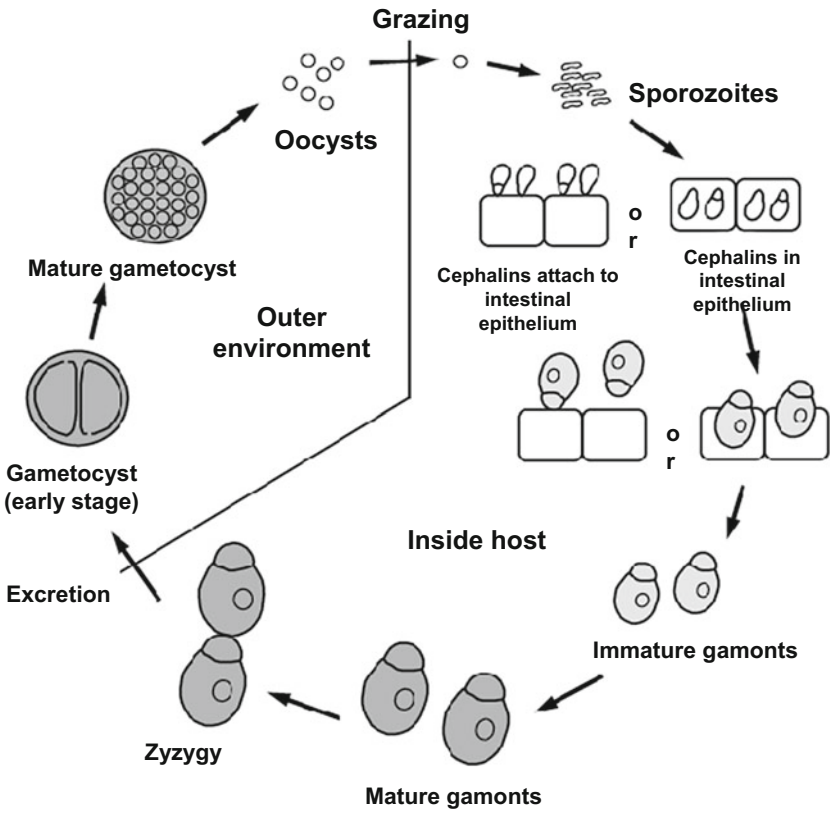

Fig. 10.4 Known general life cycle of gregarines (Order Eugregarinida) (Diagram reproduced from Takahashi et al. (2009) originally published in Polar Biology with kind permission from Springer Science and Business Media)

et al. 2009). The high infection and sometimes high intensity of this parasite prompted Avdeev (1987) to suggest that it must have a pathological effect. Kawaguchi et al. (1999) and Takahashi et al. (2009, 2011) using scanning and transmission electron microscopy concluded that gamonts in the diverticulum appear to damage microvilli, which uptake digested nutrients and secrete various enzymes, and destroy hepatic cells in the mid-gut gland having a significant impact on the nutritional state of the Antarctic krill host. The strategy of gregarines parasitizing the hind-gut epithelium during the cephalin stage may be a positive compromise, not causing a fatal impact on the host, while securing a suitable habitat (Takahashi et al. 2009). *E. superba* frequently attain relatively high gregarine infection rates that may exit in faeces. Because *E. superba* spends most of its life in the epipelagic strata (200 m depth) and produces rapidly sinking faecal pellets, apicomplexans may also sink with faeces, but this process has never been explicitly investigated.

Krill moult every 3–90 days depending on the temperature of their environment (Kawaguchi et al. 2006; Tarling et al. 2006). Their moults include parts of their

stomachs and hind-guts, which are covered with cuticle (Ikeda et al. 1984). These biological characteristics of krill do not facilitate the reproductive process of gregarine parasites. If the gametocysts are ejected within the faecal pellets, they may rapidly sink out of the normal vertical range of krill. The sinking velocity of Antarctic krill faecal pellets is estimated to be from 50 to 800 m day^{-1} (Cadee et al. 1992). This process decreases the chance of re-infection with gametocysts in the hosts, and does not support the high prevalences (100 %) sometimes observed in krill. However, Takahashi et al. (2003) observed a possible strategy for avoiding the discharge induced by moulting. The highly motile gamont stage may move to a safety zone where no shedding occurs. Non-motile syzygy and/or gametocysts in early stages of their reproductive development may be discharged during the host's moulting and excretion activities. A possible explanation for this high prevalence rate is the social behaviour of *E. superba* swarms or schools (Hamner 1984; Hamner et al. 1983, 1989), which would increase the chance of krill eating their faecal pellets (coprophagy) and moults before they sink.

Several studies show that *C. pacifica* infects the digestive tract of *E. superba* with average intensities from 87 to 493 cells $krill^{-1}$ (maximum intensity = 8505 cells $krill^{-1}$) from different locations (Takahashi et al. 2003, 2004, 2008, 2009). Although *C. pacifica* occurs in most *E. superba* populations, its pathologic effect varies greatly. It has been described as low-intensity infection (probably with negligible or minor negative effects) to high intensities in the hepatopancreas in some individuals. In the digestive gland, gamonts reproduce destroying the hepatopancreas tissue that clot the diverticula and loses tissue compactness. With cumulative clots, the hepatopancreas changes its normal coloration (green-yellow to yellow-brown) and becomes dark and opaque (Avdeev and Vagin 1987; Takahashi et al. 2009). These gregarines have a close interspecific association with *E. superba* in all dissected specimens (n = 93) and widely distributed in the Southern Ocean albeit highly aggregated, which is typical of parasites living in marine hosts (Takahashi et al. 2003, 2004, 2008, 2009, 2011).

Unlike other *E. superba*'s parasites that, so far, little is known about their biogeographic distribution, gregarine distribution has been studied in large part of the *E. superba* distribution range in the Antarctic Ocean. Avdeev (1985) described *C. pacifica* that parasitizes *E. superba* throughout most of its range, except the eastern Indian sector where *C. indica* infects *E. superba*. Further studies speculated how these two gregarine species diverged from *E. superba* populations with a biogeographic and paleoceanographic perspective (Dolzhenkov et al. 1987; Spiridonov 1996). However, the biological tag role of the gregarines is still highly controversial and requires future genetic studies. Takahashi et al. (2008) demonstrated that the circumpolar Antarctic distribution of *C. pacifica* infecting *E. superba*, shows little evidence of a supposed geographic and even taxonomic separation between *C. pacifica* and *C. indica*. The current perspective is that *C. pacifica* is present in virtually all of the *E. superba* range, indicating a stable seasonal and parasite-host interaction. Although intensity varies greatly, this is usually >70 % of the infected population (Takahashi et al. 2008, 2009, 2011). Its role on the health of *E. superba* deserves more detailed investigation. On-going

systematic histological work carried out by Bateman, Hicks, Tarling, Soeffker and Stentiford (WG-EMM-2015/23, CCAMLR 2015) considered the prevalence of pathogens and diseases in krill collected across the Scotia Sea during the austral summer (Mar–Apr, 2009). Compared to other marine crustaceans, the krill were relatively disease free, with the main parasite being *Cephaloidophora pacifica*.

10.4 Yeasts

Turkiewicz et al. (1982) isolated white budding yeasts from *E. superba*'s alimentary canal. Later, nine psychrophilic yeast strains were isolated from the stomach of *E. superba*, two of them identified as *Leucosporidium antarcticum* and *Metschnikowia bicuspidata australis* (Donachie and Zdanowski 1998). *Leucosporidium antarcticum* is endemic in the Antarctic Sea but not *Metschnikowia*, which has a broader biogeographic distribution range. The yeast *Metschnikowia kamienski* infests the copepod *Eurytemora velox* (Fize et al. 1970). However, the functional biological association between yeast and krill is still unexplored and certainly poorly understood (Donachie and Zdanowski 1998). Based on the free-living habitat of these psychrophilic yeasts and very low abundance (<1 % of the cultured counts), such yeast infections might be opportunistic, presumably with considerably low prevalence rates, although with so far unknown effect on *E. superba* populations. The diversity, pathology, epizootiology, and ecological function of fungi of any euphausiid species in the world are virtually unknown and deserve future research.

10.5 Ciliata

Members of the Class Phyllopharyngea and Oligohymenophorea have evolved in association with Crustacea (Bradbury 1994). The Subclass Suctorida epibionts of euphausiids are ciliates with tentacles that feed on planktonic organisms and reproduce by multiple budding (Stankovic et al. 2002; Tarling and Cuzin-Roudy 2008). The Subclass Apostomatia ciliates that infest (carried out by ectoparasites) or infect (carried out by endoparasites) euphausiids have life cycles that involve at least four distinct, specific feeding strategies, typically reproducing by palintomy or fission: (1) exuviotrophic ciliates (epibionts) that feed exuviotrophically from moult exudates (probably originated as scavengers of the exoskeleton; although the scavenger-feeding mode is now extremely rare), (2) planktotrophic suctorians, (3) histophagous endoparasitic ciliates (parasitoids), and (4) hyperparasitic ciliates (Capriulo and Small 1986; Bradbury 1994; Stankovic and Rakusa-Suszczewski 1996; Landers et al. 2006; Gómez-Gutiérrez et al. 2003, 2006, 2012, 2015; Lynn et al. 2014). The ciliates interacting with *E. superba* are: (1) epizoic sessile predatory suctorian ciliates of the family Ephelotidae that likely cause

hydrodynamic drag on krill swimming and may make the host more vulnerable to visual predators (Nicol 1984; Stankovic and Rakusa-Suszczewski 1996; Stankovic et al. 2002; Tarling and Cuzin-Roudy 2008), (2) exuviotrophic ciliates of the family Foettingeriidae that also cause hydrodynamic drag of the swimming host (Lindley 1978; Kittel and Rakusa-Suszczewski 1988; Rakusa-Suszczewski and Nemoto 1989; Stankovic and Rakusa-Suszczewski 1996; Stankovic et al. 2002; Landers et al. 2006, 2007), and (3) histophagous Apostomatida ciliates (Family Pseudocollinidae) that invariably kill the adult hosts being considered as a parasitoid (Capriulo and Small 1986; Capriulo et al. 1991; Stankovic and Rakusa-Suszczewski 1996; Gómez-Gutiérrez et al. 2003, 2006, 2012; Lynn et al. 2014). The last type was originally reported in *E. superba* as unidentified endoparasitic ciliates that "may have a negative (lethal) consequence for the host" (Stankovic and Rakusa-Suszczewski 1996). Because photographs of ciliates from Stankovic and Rakusa-Suszczewski (1996) resemble in size (40 μm) and morphology to the only endoparasitic ciliates known that infect krill (histophagous parasitoid ciliates of the genus *Pseudocollinia*) (Gómez-Gutiérrez et al. 2006, 2012; Lynn et al. 2014) we interpret those ciliates inside *E. superba* must be also histophagous ciliates of the family Pseudocollinidae because their endoparasitic microhabitat (photographed inside the *E. superba* legs). Transmission pathways and identification of these organisms in krill should be further investigated (Gómez-Gutiérrez et al. 2015), particularly since planktonic protozoans are a significant part of the diet of *E. superba* (Schmidt et al. 2006).

10.5.1 Epibiotic Suctorian Ciliates (Subclass Suctorida, Order Exogenida, Family Ephelotidae)

Stawiszyńska-Janas and Kittel (1982) probably provided the first confirmed report of trophic sessile stage suctorian epibionts attached on *E. superba* and *E. crystallorophias* exoskeleton. More detail was provided in further publications (Rakusa-Suszczewski and Filcek 1988; Rakusa-Suszczewski and Nemoto 1989; Stankovic and Rakusa-Suszczewski 1996; Stankovic et al. 2002; Tarling and Cuzin-Roudy 2008).

Ephelotidae epibiont prevalence depends on krill social behaviour and density of the swarms and schools, intermoult period, and size of the host. Several authors suggest that larger, older krill are more likely to be infested than smaller and younger krill (Rakusa-Suszczewski and Filcek 1988; Rakusa-Suszczewski and Nemoto 1989; Stankovic et al. 2002). This hypothesis was explicitly tested and confirmed by Tarling and Cuzin-Roudy (2008), who observed higher prevalences in older krill (Fig. 10.5). Nicol (1984) specifically proposed that, since euphausiids from surface swarms were mature individuals mostly, the high prevalences are the result of senility or delayed ecdysis in reproductive animals. Tarling and Cuzin-Roudy (2008) confirmed that Ephelotidae prevalences were positively correlated

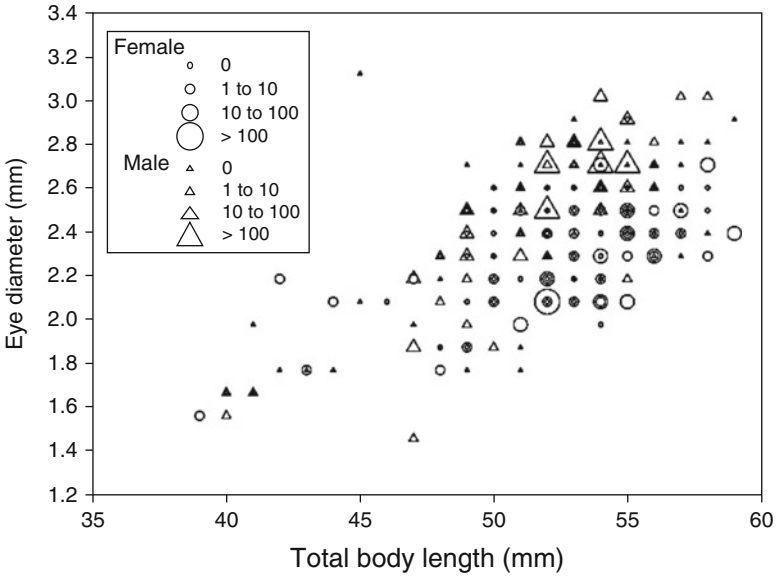

Fig. 10.5 The relationship between body length, eye diameter, and level of suctorian infection in male and female adult krill. Note that symbols are superimposed on each other where body length and eye diameter coincide (Diagram reproduced from Tarling and Cuzin-Roudy (2008) originally published in Polar Biology with kind permission from Springer Science and Business Media)

with eye diameter and the pre-moult stage in *E. superba*. Krill specimens in pre-moult stage were infested as high as 66 % compared to 0 % prevalence in those krill in post-moult stage (Fig. 10.5).

Suctorian ciliates found on juvenile and adult *E. superba* have been invariably identified as *Ephelota* spp. because taxonomy of the genus *Ephelota* has not been firmly established (Nicol 1984; Stankovic et al. 2002; Tarling and Cuzin-Roudy 2008). Rakusa-Suszczewski and Nemoto (1989) proposed that at least three distinct *Ephelota* undescribed species infected *E. superba*, apparently separated per size and type of cyst attachment (body width: small 100 μm, medium 150–175 μm, and large 450–500 μm). Most recently, Stankovic et al. (2002), using small subunit rDNA (SS rDNA), suggested that feeding and budding stage adult suctorians were all members of the same, yet-to-be-named, *Ephelota* species that infected *E. superba* collected from the King George Island region. Further genetic analyses of *COI* from a more extensive range of regions could test whether the *Ephelota* infesting euphausiids is a cosmopolitan species or a multi-species assemblage with distinct biogeographic patterns. Stankovic et al. (2002) also suggested that Antarctic and non-Antarctic ciliate species of *Ephelota* diverged much earlier than Antarctic and non-Antarctic euphausiid species, perhaps implying *Ephelota* species are generalist rather than specialized epibionts of euphausiids.

The epizootiology of suctorian ciliates indicates that they are not frequently detected, but when present, large numbers of krill seem to be infested (Tarling and

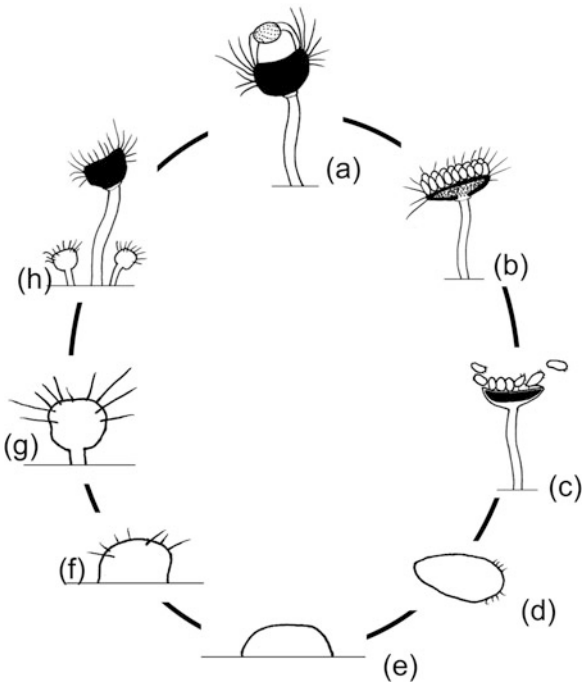

Fig. 10.6 Known general life cycle of suctorian ciliates (Family Suctoridae) in euphausiids. (**a**) Adult (tentacles are used to capture prey and to suck nutrients out of them), (**b**, **c**) adult at budding reproductive stage, (**d**) young swarmer cell with two rings of cilia, (**e**) sessile cell, (**f**) sessile cell developing tentacles, (**g**) young cell with non-contractile stalk, and (**h**) young and adult cells are frequently observed in the same host (*Euphausia pacifica* and *Nematoscelis difficilis*) because life cycle is shorter than the intermoult period (Gómez-Gutiérrez, pers. observ)

Cuzin-Roudy 2008). Intensity varies, with an average of 11 individuals of *Ephelota* spp. per krill, with the suctorian adult phase having a stalk and tentacles (Rakusa-Suszczewski and Nemoto 1989; Stankovic and Rakusa-Suszczewski 1996; Stankovic et al. 2002). Stankovic et al. (2002) interpreted that massive numbers of cysts attached on krill's appendages (ranging from 120 to 900 phoront cysts per host) were also suctorian ciliates. We currently interpret, as earlier studies like Rakusa-Suszczewski and Nemoto (1989), that those ciliate cysts are actually apostome exuviotrophic ciliates (Class Oligohymenophorea, Subclass Apostomatia) that are highly prevalent in krill (Lindley 1978; Landers et al. 2006, 2007), rather than suctorian ciliates (Class Phyllopharingea, Subclass Suctorida) that infest with significantly fewer intensities. The suctorians feed by trapping prey with prehensile and pipe-like suctorial tentacles. The reproductive phase produce budding cells. During the budding process, the tentacles disappear, and a crown of buds emerges in the anterior area of the cell; these swim (transmission stage) and later adhere to the crustacean cuticle, such as *E. superba*. The adhering cell develops protruding tentacles and a short stalk that eventually develop into a solid cylindrical structure. Suctorida ciliates feed and reproduce by budding continuously in the same host resulting in suctorians individuls of different sizes in the same krill host. This overlapping cohort occurs because suctorians complete their life cycle in only few hours (Fig. 10.6). Our direct observations under shipboard laboratory conditions of cyst ciliates swimming inside the *Euphausia pacifica* moult (Oregon coast) show that they are exuviotrophic feeders (growing

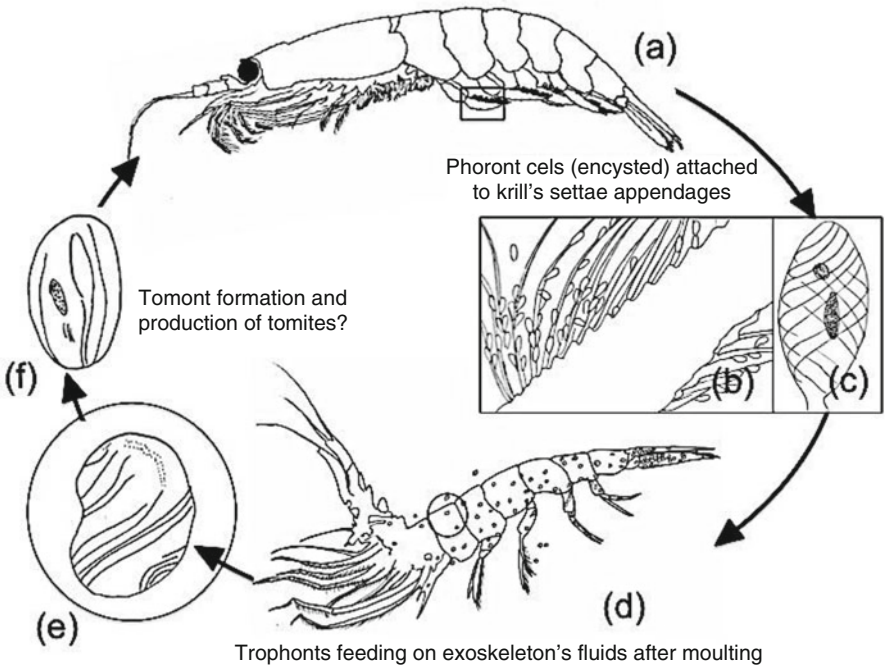

Fig. 10.7 Known general life cycle of apostome exuviotrophic ciliates (Family Foettingeriidae) in *Euphausia superba*. (**a**) *E. superba* infested with phoront cysts of the Apostome ciliates, (**b**) zoom of the krill appendages showing how ciliate cysts attach to setae and (**c**) cyst showing ciliate row pattern (Draw based from photographs of Stankovic et al. 2002), (**d**) trophont cells feeding on exoskeleton's fluids after the krill moulted, (**e**) detail of trophont cell, and (**f**) so far little studied tomont (reproductive) and tomite (transmission) stage inferred from Landers et al. (2006)

and changing coloration as they ingest more moult's fluid) and reproduce by cell division (Landers et al. 2006). Thus, our perception is that ciliate cysts attached to krill's appendages do not feed neither reproduce like suctorian ciliates attached on the cephalothorax and abdomen of *E. superba*.

10.5.2 Epibiotic Exuviotropic Ciliates (Subclass Apostomatia, Order Apostomatida, Family Foettingeriidae)

The Foettingeriidae exuviotrophic ciliates (encysted phoront stage) infest appendages of the euphausiids (thoracic limbs and pleopods, on setae, and between setae) of juveniles and adults of both sexes with intensities up to 900 phoront cysts per

host (Lindley 1978; Stankovic and Rakusa-Suszczewski 1996) (Fig. 10.7a–c). When the krill moults, the ciliates excyst into a feeding stage (trophont) that feeds on the fluids of the exuvia (Fig. 10.7d–e), transforming into a reproductive tomont stage that divides by fission to produce multiple tomites (the transmission stage) before infecting another crustacean host as a phoront (Fig. 10.7f). These exuviotrophic ciliates seem to complete their life cycle exclusively infesting krill (Landers et al. 2006, Fig. 10.7a–f). Their prevalence is usually closely related with the proportion of individuals in the population in the intermoult and premoult stages. Postmoult krill do not bear phoronts attached to their swimming appendages (Tarling and Cuzin-Roudy 2008).

Protistan epibionts were first noted as phoronts (resting cysts) on nine krill species in the North Atlantic with prevalences ranging from 3 to 16 % (Lindley 1978). Similarly, at least three different forms of unidentified encysted phoront cysts were later discovered on *E. superba* in the Antarctic Ocean (Kittel and Rakusa-Suszczewski 1988; Rakusa-Suszczewski and Filcek 1988; Rakusa-Suszczewski and Nemoto 1989; Stankovic and Rakusa-Suszczewski 1996; Stankovic et al. 2002). All these epibiont phoront ciliates were not assigned to any genus or species because their life cycle was then unknown due to the virtually exclusive examination of preserved samples. However, Rakusa-Suszczewski and Filcek (1988) suggested their "form 1" was similar to *Spirophrya* ciliates observed from various crustaceans. *Gymnodinioides pacifica* Landers et al. 2006 was the first exuviotrophic ciliate properly named that infest the thoracic and abdominal appendages of six krill species in the Oregon coast, USA (Landers et al. 2006, 2007). Under laboratory conditions, they observed how these phoronts have an exuviotrophic ectocommensal life cycle strategy (Landers et al. 2006). Lindley (1978) identified as Apostomatida ciliates the cysts attached to swimming appendages of several euphausiid species that inhabit in the North Atlantic and Banas (1981), Kittel and Rakusa-Suszczewski (1988), Rakusa-Suszczewski and Filcek (1988) also reported similar taxonomic assignation to cysts attached on *Euphausia superba* from the Antarctic Sea. However, Stankovic et al. (2002), based on SS rDNA evidence, assigned such phoront stages to Suctoridae (*Ephelota* spp.) (see their Figs. 6a–d, 7, and 8), concluding that all cysts that infest *E. superba* belong to one so far non-described species of *Ephelota* and suggested that Lindley's (1978) interpretation of exuviotrophic ciliates was incorrect. The Stankovic et al. (2002) interpretation is not correct, based on evidence obtained from ciliates from *E. superba* and other krill species in the world: (1) A search of GenBank (Jan, 2014) of the 18S rDNA sequences (with a current considerably greater amount of information than was available in 2002) shows that *Ephelota* species (Phyllopharingea, Suctoria, Exogenida, Ephelotidae) are closely related to Suctorida species of the Order Endogenidae (Acinetidae), while the genus *Gymnodinoides* cysts from euphausiid appendages (Oligohymenophorea, Apostomatida; Foettingeriidae) are actually closely associated with histophagous species of the genus *Pseudocollinia* (Olygomenophorea, Apostomatida, Pseudocolliniidae family). The family Ephelotidae and Foettingeriidae actually belong to distinct classes and therefore is unlikely they

are the same species, as suggested by Stankovic et al. (2002). Stankovic et al. (2002) possibly analysed a conservative part of the 18S rDNA; more precise species identification can be done using cytochrome oxidase (*COI*) mitochondrial gene (Hebert et al. 2003); (2) Direct observations of live ciliates show distinct feeding strategies: the resting cysts (tomite stage attached to the krill's appendages) excyst and transform into the feeding stage (trophont) that feeds osmotrophycally from the fluids of the moult (exuviotrophic strategy); the suctorian ciliates (Ephelothidae) have a raptorial feeding strategy, using their prehensile tentacles. This means that Foettingeriidae actually obtain energy from the krill's moult fluids, while the Ephelotidae species use krill exclusively as a substrate (basibiont) without obtaining energy from krill; (3) Reproduction of both types of ciliates are distinct. The Foettingeriidae tomont cells reproduce using typical ciliate cell division, while the Ephelothidae reproduce using multiple budding from a crown (relatively unusual in ciliates); (4) Both ciliates that infect *E. superba* (in similar life phases) show distinct morphologic features: (a) In Stankovich et al. (2002) their Fig. 7 shows a phoront cell with nine kineties (typical of apostome Foettingeriidae phoronts cells) (compare with our Fig. 10.7c) rather than 12–18 rows (typical of suctorian phoront cells); (b) The swarmer stage (tomite transmission stage) of suctorian cells have their ciliates restricted to rings around the anterior end and not spiraled around the cell, like Foettingeriidae ciliates, and (c) Stankovich et al. (2002) mention the encysted ciliates have a "stalk of the cyst" (see their Fig. 8, showing a TEM image), which is in fact a typical Foettingeriidae apostome peduncle attachment secreted by the cell during the encysting process that it is distinct from the *Ephelota* stalk that develops as a solid cylindrical structure; and (5) Suctorian cells attached to euphausiids show considerably smaller intensities per host and prevalence in the population than Foettingeriidae ciliates attached to the euphausiid appendages (Tarling and Cuzin-Roudy 2008; Gómez-Gutiérrez pers. observ.). In short, there are several lines of evidences that ciliates of the genus *Ephelota* and *Gymnodinoides* that infest euphausiids are different species from a distinct classess, having distinct consumer, reproductive, and life cycles strategies (Landers et al. 2006, 2007; Fernandez-Leborans 2013). Further *COI* gene analyses could provide the required precision to distinguish species and solve the taxonomic discrepancies about the identification of ciliates in *E. superba* and other krill species worldwide.

10.5.3 Endoparasitic Histophagous Ciliates (Parasitoids)

Stankovic and Rakusa-Suszczewski (1996) is the only report of an unidentified endoparasitic histophagous ciliate infection of *E. superba* [mentioned as "intramuscular *Apostoma* trophonts"] (see their Figs. 10.1, 10.2, 10.3, and 10.4)

observed from preserved krill specimens. Although this study was reported after the first publication of endoparasitic ciliates infecting *Thysanoessa inermis* in the Bering Sea (Capriulo and Small 1986; Capriulo et al. 1991), Stankovic and Rakusa-Suszczewski (1996) did not associate them with ciliates of the then known endoparasitic *Collinia beringensis*. Currently it is known that all endoparasitic ciliates that infect krill are obligate histophagous ciliates of the genus *Pseudocollinia*, family Pseudocollinidae (Gómez-Gutiérrez et al. 2003, 2006, 2012; Lynn et al. 2014) observed in at least seven of the most abundant krill species from the northeast Pacific (Bering Sea to Gulf of California) and northwest Atlantic Ocean (Kulka and Corey 1984; Lynn et al. 2014). If future morphological and molecular evidence show that endoparasitic ciliates that infect *E. superba* reported by Stankovic and Rakusa-Suszczewski (1996) actually belong to the genus *Pseudocollinia*, this would be the first published record of histophagous apostome ciliates in the southern hemisphere. They interpreted these endoparasitic ciliates as associated with the phoront cysts (Foettingeriidae) that adhere to the appendages setae and reporting a potential link in a life cycle. However, it is well established that they are actually distinct ciliate species with distinct life cycles, morphology, and feeding strategies (although phylogenetically closely related) (Landers et al. 2006, 2007; Lynn et al. 2014). However, Stankovic and Rakusa-Suszczewski (1996) correctly interpreted that those endoparasitic ciliates "may have a negative (lethal) consequence for the host", being so far the only known parasitoid reported infecting *E. superba*. We use the term "parasitoid" with caution, because, although dinoflagellates and histophagous ciliates infecting krill match with the typical characteristic of the parasitoid definition (i.e. which must kill its host to continue their life cycle), the fact that they occur with remarkable high intensity per krill-host, is quite anomalous when compared with for the typical terrestrial parasitoid definition (Gómez-Gutiérrez et al. 2015).

10.6 Trophically Transmitted Helminths (Nematoda)

Helminths (Trematoda, Cestoda, Acanthocephala and Nematoda) include generalist trophic transmitted endoparasites that infect plankton and nekton in different life phases. In the Australian Antarctic Division krill state-of-art laboratory located at Kingston, Tasmania (Australia), we observed small, unidentified nematodes (<400 μm length) inside just-hatched eggs (with intensity of one or rarely two nematodes) of *E. superba* reared under laboratory conditions (Robert King and Jaime Gómez-Gutiérrez pers. observ., Fig. 10.8a,b). As far as we know, this is the first record of a nematode infecting eggs of any krill species worldwide and, the only report of occurrence of any helminth parasitizing *E. superba*. Although there

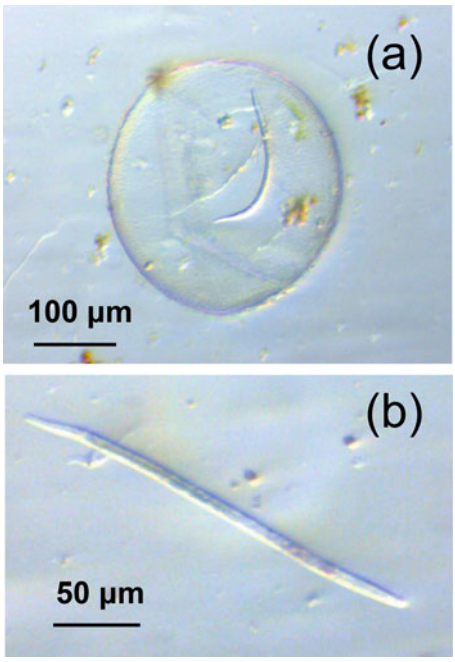

Fig. 10.8 Parasitic nematode found in eggs of *Euphausia superba* reared under laboratory conditions. (**a**) Unidentified larvae of nematode occurring inside just-hatched eggs. (**b**) Nematode (<400 µm length) freed from *E. superba* egg (Robert King and Gómez-Gutiérrez, pers. observ. at Australian Antarctic Division, Kingston, Tasmania, Australia)

are numerous records of helminth infections in Antarctic fish, seabirds, and marine mammals, so far, despite considerably research effort to find such helminthic infections, there are no published records of helminth infecting *E. superba* in the field (Kagei 1969, 1974, 1979; Kagei et al. 1978). Earlier studies reported that the Antarctic krill *E. superba* is free of *Anisakis* spp. infection [34,879 specimens analysed (Kagei 1974; Kagei et al. 1978) and 91,771 specimens analysed (Kagei 1979)]. The same was proposed for Antarctic marine mammals (Kagei and Kureha 1970). However, this perspective is changing because recent research efforts show life cycle biology, specificity, and geographical distribution of Tramatoda, Cestoda, Acanthocephala and Nematoda of Antarctic fishes (Rocka 2006). *Anisakis simplex* and *Anisakis pegreffii* infect migratory myctophids (*Gymnoscopelus nicholsi* and *Electrona carlsbergi*, intermediate hosts that feed on Antarctic krill), and other krill's predators like minke whales (definitive host), and elephant seal *Mirounga leonine* (accidental host) in the Antarctic (Klimpel et al. 2010). So far, the main invertebrate host vectors of such nematode infections are unknown. The endemic myctophid *Electrona antarctica* did not have nematode infections. The occurrence in migrating myctophids coupled with rare findings from other teleosts and regular introduction events through migrating whales lead them to conclude that *A. simplex* and *A. pegreffii* were introduced from northern latitudes outside the Antarctic. Seal worms of *Contracaecum* and *Pseudoerranova* genera clearly dominate the

Antarctic anisakid nematode fauna infecting fish, seals, and cetaceans, but so far, evidence suggest those nematodes species do not infect *E. superba* (Kagei 1974, 1979; Kagei et al. 1978). The icefish *Chaenocephalus aceratus* (especially specimens >30 cm total length) are heavily infected with the nematode *Contracaecum* spp., but no nematodes are found in fish <22 cm in males or females. Larvae of nematodes are often long living, resulting in an accumulation in the fish and a positive correlation between length and age and infection intensity (infection rates increases rapidly for *C. aceratus* >22 cm and attains a mean level >90 %). The reason for infection with nematodes can be deduced from the food items of the Channichthyidae. *Ch. aceratus* feeds on fish, krill, mysids, amphipods, and tunicates and *Champsocephalus gunnari* feeds mainly on krill (Permitin and Traverdiyeva 1972). Krill, however, is not a intermediate host for nematodes in the Southern Ocean (Kagei 1974, 1979; Kagei et al. 1978), so it is not surprising that *Ch. gunnari* is free of nematodes as well as the krill-eating small *Chionodraco* sp. and juveniles (<22 cm) of *Ch. aceratus*. As they grow larger (>22 cm), the latter two Channichthyidae change their main diet to potential intermediate hosts of nematodes; and the *Contracaecum* sp. infection prevalences increase (Siegel 1980a, b). Thus, observational evidence, so far available, indicates that *E. superba* really seems to be "clean" of helminths as concluded Siegel (1980a, b). Evidently, scientists must focus on investigating helminthic infections in the Antarctic ecosystems because they have been detected in several krill predators that migrate seasonally to this gelid ocean during the high-production austral spring and summer (Klimpel et al. 2010).

10.7 The Role of Swarming Behaviour in the Transmission of Parasites and Pathogens

Kuris et al. (1980) proposed based on biogeography island theory "individual host organisms are unequivocal islands where infection is equivalent to immigration of the parasite population and extinction represent the loss of a parasite population either from natural death of the parasites with short life spans, competition from other parasite populations, and/or host defensive responses". Thus, *E. superba* may be regarded as islands for parasites at several levels of organization: (1) individuals, (2) aggregations, swarms, or schools, and/or (3) populations. The euphausiids have an interspecific, and likely size-dependant intraspecific variability of social behaviour (patchiness) (Décima et al. 2010). It ranges from species where individuals are solitary swimmers to social interactions that result in the formation of aggregations, swarms, or even schools at different spatial and time scales (Hamner 1984; Ritz 1994; Ritz et al. 2011; Watkins 2000; Nowacek et al. 2011). Krill social behaviour is closely associated with multiple, significant ecological and physiological processes like reproduction, food searches, predator avoidance strategies, moulting,

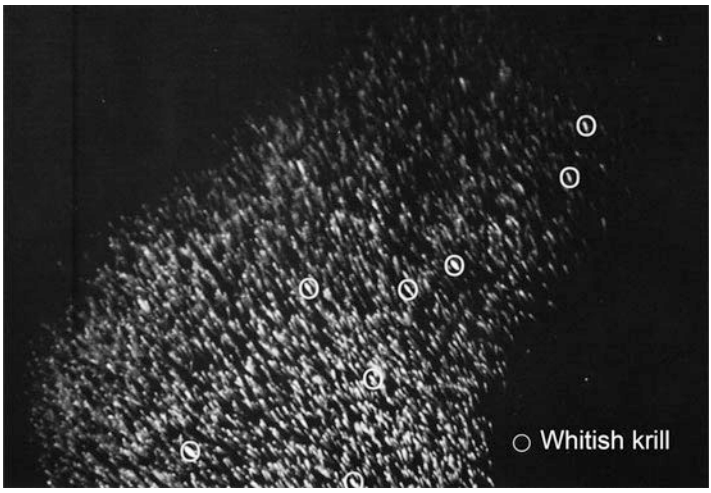

Fig. 10.9 School of *Euphausia superba* in Croker Passage off Antarctic Peninsula. Swimming direction in photo is obliquely downward from *left* to *right*. No individuals occur outside the school. Within the school, krill are closely packed at extremely high density. Unhealthy, whitish animals (*circles*) are easily distinguished (Photo reproduced with permission Koninklijke Brill NV (1984) from Hamner W. M., Aspects of schooling of *Euphausia superba*, Journal of Crustacean Biology)

and parasitic transmission, among others. Hamner (1984) specifically discussed the possible parasite transmission within swarms and among swarms and schools of *E. superba*. Euphausiids species that form dense schools/aggregations seem to interact with a more diverse parasitic assemblage than those that form low-density aggregations because parasite transmission is facilitated by social interaction (Gómez-Gutiérrez et al. 2010). Krill surface swarming behaviour with densities ranging between 100 individuals m^{-3} to 1.5×10^6 individuals m^{-3} may decrease the nearest neighbour distance that facilitates parasite transmission (Fig. 10.9) (Hamner 1984; Hamner et al. 1983; Nicol 1984). This suggests that several parasites require host species with dense and high abundance and compact swarming/schooling behaviour to complete their life cycles during the long-term evolutionary process of speciation. Aggregating behaviour of *E. superba* can develop in early larval stages, as young as furcilia IV (Hamner et al. 1989), possibly enhancing parasitic transmission after the ontogenetic formation of social aggregations and swarms. Hamner (1984) observed that *E. superba* swarms sometimes have opaque ("whitish") individuals (presumably necrotic) positioned behind the schools that are unable to swim as fast as healthy individuals and indicating that schooling may have zoonotic disadvantages (Fig. 10.9). The causes of opaque appearance in *E. superba* are still unknown. It is well known that apostome histophagous ciliates change the colour of the krill host (Gómez-Gutiérrez et al. 2006, 2012), but in *E. superba* it is unknown because histophagous

endoparasitic ciliates were observed only in frozen kill specimens (Stankovic and Rakusa-Suszczewski 1996).

Based on the biogeography island theory (Kuris et al. 1980) and assuming similar parasite transmission rates of relatively less virulent parasites, it would be expected that long-lived euphausiid hosts with larger individual biomass would offer longer and more potential sites (or microhabitats) for parasites than short-lived with small individual biomass euphausiid hosts. This is a paramount inference because it would predict that eggs and larvae (with development times within days-week and small individual biomass) are comparatively less likely to be parasitized (or smaller number of parasitic types), than juveniles and adults (intraspecific ontogenetic vulnerability). Additionally, smaller euphausiid species like *Stylocheiron microphthalma* Hansen, 1910 or *Stylocheiron suhmi* G. O. Sars, 1883 (<7 mm and longevity likely <1 year) should have relatively less diverse parasitic fauna than larger species, such as *E. superba* (6.5 cm, longevity of 5–7 years) or *Thysanopoda* species (<15 cm) (interspecific vulnerability). However, an overview of all epibionts and parasites known for 48 of 86 current extant euphausiid species include at least 17 distinct types (epibionts, parasites, pathogens, and parasitoids) (Gómez-Gutiérrez et al. 2010). Only seven of them have been reported in *E. superba* [epibionts: exuviotrophic ciliates (family Foettingeriidae) and microplanktophagous ciliates (family Suctoridae genus *Ephelota*), pathogens: chitinoclastic bacteria and fungus; and trophically transmitted endoparasites: Apicomplexa (family Gregarinidae genus *Cephaloidophora*), Nematoda, and endoparasitic histophagous ciliates (family Apostomatidae)]. The massive and dense aggregations, swarms, and schools of *E. superba*, their keystone function as voracious predators (phytoplankton, benthic microalgae, marine snow, and mesozooplankton), and prey for multiple predator species (macrozooplankton, fish, squids, sea birds, and marine mammal) should make it a critical vector for trophically transmitted parasites in the Antarctic food web. However, comparing parasite diversity of *E. superba* with those for other well studied krill species of the world (*Meganyctiphanes norvegica*, *Euphausia pacifica*, and *Nyctiphanes simplex*), *E. superba* apparently interacts with a relatively low diversity of parasitic taxa (Fig. 10.10). However, future studies must confirm this ontogenetic and interspecific parasite diversity pattern because, so far, relatively few scientists have been studied parasites of krill worldwide. *Euphausia superba*'s diversity, prevalence, and intensity of parasites is less than expected from the theory of island biogeography predicted from the relatively large body size and the colossal *E. superba* population biomass, but consistent with the hypothesis that low temperatures prevailing in the Antarctic Sea are not favourable for parasites and pathogens (Seear et al. 2012). Multiple parasitic taxa diversity with wide global zoogeographic patterns could overlap with *E. superba* range in the circumpolar Antarctic Ocean. Current knowledge indicates that multiple parasites apparently have not invaded the Antarctic ecosystem with the same evolutionary success (Klimpel et al. 2010) as has occurred with euphausiid species in tropical, subtropical, temperate, and even Arctic ecosystems.

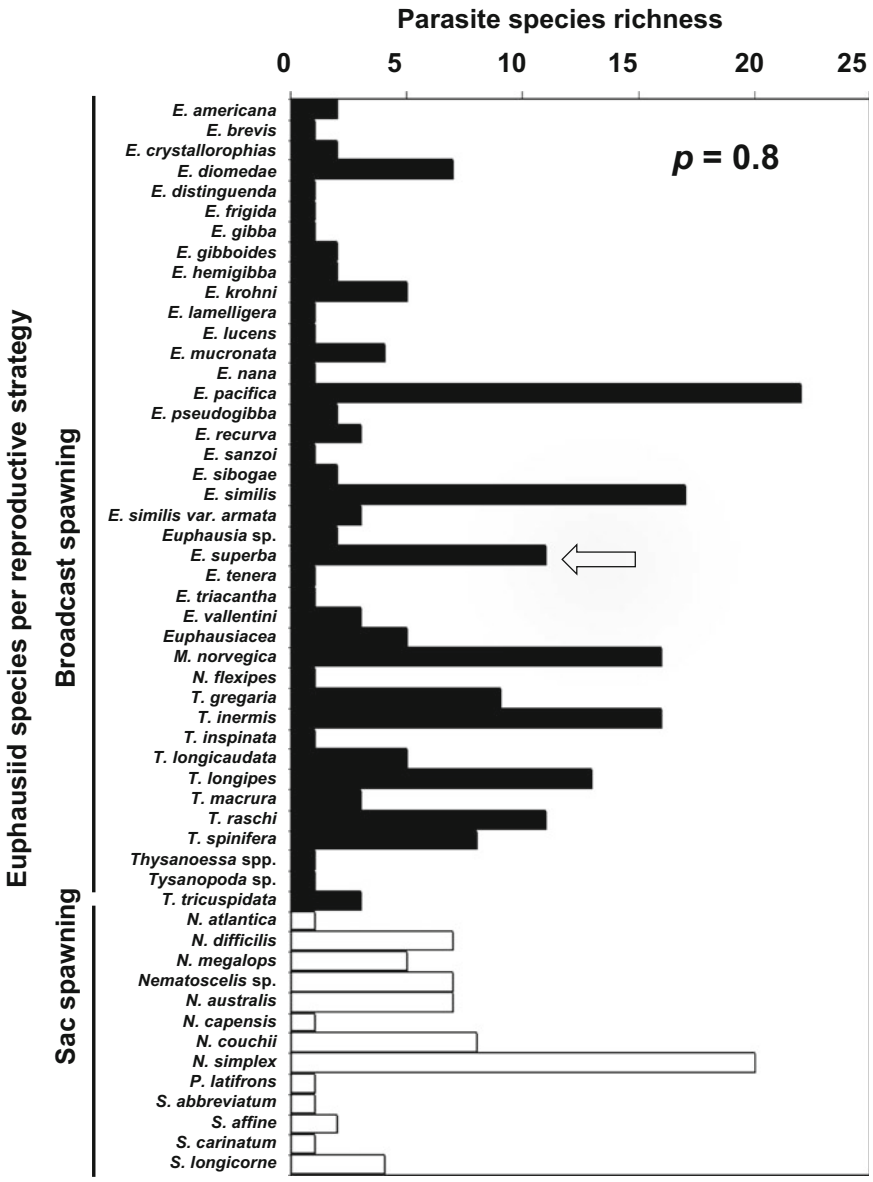

Fig. 10.10 Meta-analysis of epibiont, mesoparasite, parasite, and parasitoid species richness known for each of the 48 out of 86 current extant euphausiid species around the world, comparing krill species of relatively better known symbiotic relationship with the Antarctic krill *Euphausia superba*, comparing species with distinct reproductive strategies (broadcast versus sac-spawning species), from 1885 to 2013 (120 publications) plus personal observations (Gómez-Gutiérrez)

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References

Aguilar-Méndez MJ, López-Cortés A, Gómez-Gutiérrez J (2008) Bacterial diversity associated with parasitoidism of the ciliate *Collinia* spp. in euphausiids from the Gulf of California. Paper presented at the 12th International Society on Microbial Ecology (ISME). Microbial diversity: sustaining the blue planet, Cairns, Australia, August 17–22, 2008

Atkinson A, Siegel V, Pakhomov E et al. (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432(7013):100–103

Atkinson A, Siegel V, Pakhomov EA et al (2009) A re-appraisal of the total biomass and annual production of Antarctic krill. Deep-Sea Res I 56:727–740

Avdeev VV (1985) New species of gregarines of genus *Cephaloidophora* parasites of *Euphausia superba*. Parasitology 1:1–6

Avdeev VV (1987) Certain specific characteristics of the development of gregarine *Cephaloidophora*, a parasite of *Euphausia superba*. Parasitology 21(4):580–582

Avdeev VV, Avdeeva NV (1989) On gregarine fauna from planktonic crustaceans from Antarctica. In: Lebedev BI (ed) Parasites of animals and plants: collected papers. Far East Division of Russian Acad. Sci, Vladivostok, pp 40–44

Avdeev VV, Vagin AV (1987) Pathogenic effect of gregarine *Cephaloidophora pacifica* Avdeev on the organism *Euphausia superba* Dana. Parasitology 21(6):741–743

Banas PT (1981) Apostomatous ciliate association with the antarctic krill, *Euphausia superba* (Master's thesis, Texas A and M University)

Bateman K, Hicks R, Tarling G et al (2015) Chiller killers – first steps towards identifying krill pathogens. Paper presented at the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), Working Group on Ecosystem Monitoring and Management (WG-EMM-2015/23). Warsaw, Poland, 6–17 July 2015

Bradbury PC (1994) Parasitic protozoa of molluscs and crustacea. In: Kreier JP (ed) Parasitic protozoa, vol 8, 2nd edn. Academic, San Diego, pp 139–263

Cadee GC, Gonzalez H, Schnack-Schiel SB (1992) Krill diet affects fecal string setting. Polar Biol 12:75–80

Capriulo GM, Small EB (1986) Discovery of an apostome ciliate (*Collinia beringensis* n. sp.) endoparasitic in the Bering Sea euphausiid *Thysanoessa inermis*. Dis Aquat Organ 1:141–146

Capriulo GM, Pedone MJ, Small EB (1991) High apostome ciliate endoparasite infection rates found in the Bering Sea euphausiid *Thysanoessa inermis*. Mar Ecol Prog Ser 72:203–204

Cieśliński H, Kur J, Bialkowska A et al (2005) Cloning, expression, and purification of a recombinant cold-adapted beta-galactosidase from Antarctic bacterium *Pseudoalteromonas* sp. 22b. Protein Expr Purif 39:27–34

Cieśliński H, Bialkowska A, Dlugolecka A et al (2007) A cold-adapted esterase from psychrotrophic *Pseudoalteromas* sp. strain 643A. Arch Microbiol 188:27–36

Corsolini S, Romeo T, Ademollo N et al (2002) POPs in key species of marine Antarctic ecosystem. Microchem J 73(1):187–193

D'Amato ME, Harkins GW, de Oliveira T et al (2008) Molecular dating and biogeography of the neritic krill *Nyctiphanes*. Mar Biol 155:243–247

Dabrowski J, Mierzejewski J, Skoczek A (1983) Isolation of mesophilic anaerobes from Antarctic krill (*Euphausia superba*). Acta Microbiol Pol 32:95–98

de C Baker A, Boden BP, Brinton E (1990) A practical guide to the euphausiids of the world. Natural History Museum Publication, London

Décima M, Ohman MD, Robertis AD (2010) Body size dependence of euphausiid spatial patchiness. Limnol Oceanogr 55(2):777–788

Denner EB, Mark B, Busse HJ et al (2001) *Psychrobacter proteolyticus* sp. nov., a psychrotrophic, halotolerant bacterium isolated from the Antarctic krill *Euphausia superba* Dana, excreting a cold-adapted metalloprotease. Syst Appl Microbiol 24:44–53

Dobson EE (2002) Phylum Apicomplexa Levine, 1970: order Eugregarinorida Léger, 1900. In: Lee JJ, Leedale G, Patterson D, Bradbury PC (eds) Illustrated guide to the Protozoa, 2nd edn. Society of Protozoologists, Lawrence, pp 205–288

Dolzhenkov VN, Avdeev VV, Tirnonin VP (1987) To the problem of the population structure of the Antarctic krill *Euphausia superba* Dana. In: Makarov RR (ed) Biological-oceanographical investigations of the Pacific sector of Antarctic. VNIRO Publishers, Moscow, pp 176–186 (in Russian)

Donachie SP (1995) Ecophysiological description of marine bacteria from Admiralty Bay (Antarctica), and the digestive tracts of selected euphausiidae. In: Rakusa-Suszczewski S, Donachie SP (eds) Microbiology of Antarctic marine environments and krill intestine, its decomposition and digestive enzymes. Department of Antarctic Biology, Polish Academy of Sciences, Warsaw, pp 101–196

Donachie SP, Zdanowski MK (1998) Potential digestive function of bacteria in krill *Euphausia superba* stomach. Aquat Microb Ecol 14:129–136

Donachie SP, Saborowski R, Gerrit P et al (1995) Bacterial digestive enzyme activity in the stomach and hepatopancreas of *Meganyctiphanes norvegica* (M. Sars, 1857). J Exp Mar Biol Ecol 188:151–165

Fernandez-Leborans G (2013) Epibionts on the krill (*Euphausia pacifica*) from the E coast of Japan. Acta Zool (Stockholm) 94:167–176

Fevolden SE, Eidsa G (1981) Bacteriological characteristics of Antarctic krill (Crustacea; Euphausiacea). Sarsia 66:77–82

Fize A, Manier JF, Maurand J (1970) Sur un cas d'infestation du copepoda *Eurytemora velox* (Lillj) par une levure du genre *Metschnikowia kamienslu*. Ann Parasitol Hum Comp 45:357–363

Gómez-Gutiérrez J, Peterson WT, Robertis AD et al (2003) Mass mortality of krill caused by parasitoid ciliates. Science 301:339

Gómez-Gutiérrez J, Peterson WT, Morado FJ (2006) Discovery of a ciliate parasitoid of euphausiids off Oregon, USA. *Collinia oregonensis* n. sp. (*Apostomatida*: *Colliniidae*). Dis Aquat Organ 71:33–49

Gómez-Gutiérrez J, Robinson CJ, Kawaguchi S et al (2010) Parasite diversity of *Nyctiphanes simplex* and *Nematoscelis difficilis* along the Northwestern coast of Mexico. Dis Aquat Organ 88:249–266

Gómez-Gutiérrez J, Strüder-Kypke M, Lynn D et al (2012) *Pseudocollinia brintoni* gen. nov. sp. nov. (Apostomatida: Colliniidae) a parasitoid ciliate infecting the euphausiid *Nyctiphanes simplex*. Dis Aquat Organ 99:57–78

Gómez-Gutiérrez J, López-Cortez, A, Aguilar-Méndez MJ et al (2015) Histophagous ciliate *Pseudocollinia brintoni* and bacterial assemblage interaction with krill *Nyctiphanes simplex*: I. Transmission process. Dis Aquat Organ. 116:213–226. doi:10.3354/dao02922

Hamner WM (1984) Aspects of schooling of *Euphausia. superba*. J Crust Biol 4:67–74

Hamner WM, Hamner PP, Stran SW et al (1983) Behavior of Antarctic krill, *Euphausia superba*: chemoreception, feeding, schooling and molting. Science 220:433–435

Hamner WM, Hamner PP, Obst BS (1989) Field observations on the ontogeny of schooling of *Euphausia superba* furciliae and its relationship to ice in Antarctic waters. Limnol Oceanogr 34:451–456
Hebert PD, Cywinska A, Ball SL (2003) Biological identifications through DNA barcodes. Proc R Soc B 270(1512):313–321
Ikeda T, Nash GV, Thomas PG (1984) An observation of discarded stomach with exoskeleton moult from Antarctic krill *Euphausia superba* Dana. Polar Biol 3:241–244
Kagei N (1969) Life history of nematodes of the genus *Anisakis*. Saishin Igaku 24:389–400
Kagei N (1974) Studies on *Anisakid* Nematoda (Anisakinae) (IV). Survey of *Anisakis* larvae in the marine crustacea (Japanese). Bull Inst Publ Health 23(2):65–71
Kagei N (1979) Euphausiids and their parasites (I). Geiken Tsushin 328:53–62
Kagei N, Kureha K (1970) Studies on anisakid Nematoda (Anisakinae) I. Survey of *Anisakis* sp. on marine mammals collected in the Antarctic Ocean. Bull Inst Publ Health Tokyo 19(3):193–196
Kagei N, Asano K, Kihata M (1978) On the examination against the parasites of Antarctic krill, *Euphausia superba*. Sci Rep Whales Res Inst 30:311–313
Kawaguchi S, Toda T (1997) Discovery of ciliates reproducing in the gut of Antarctic krill. Polar Biol 18:158–160
Kawaguchi S, Hosie G, Nicol S et al (1999) Do gregarines cause damage to midgut gland and intestinal epithelium of Antarctic krill? Paper presented at the Second International Symposium of krill, Santa Barbara, CA August 22–26, 1999
Kawaguchi S, Candy S, King R et al (2006) Modelling growth of Antarctic krill. I. Growth trends with sex, length season, and region. Mar Ecol Prog Ser 306:1–15
Kelly MD, Lukaschewsky S, Anderson CG (1978) Bacterial flora of Antarctic krill (*Euphausia superba*) and some of their enzimatic properties. J Food Sci 43:1196–1197
Kittel W, Rakusa-Suszczewski S (1988) Biological characteristics of *Euphausia superba* Dana (BIOMASS III, November 1986–January 1987). Pol Polar Res 9:315–325
Klimpel S, Busch MW, Kuhn T et al (2010) The *Anisakis simplex* complex off the South Shetland Islands (Antarctica): endemic populations versus introduction through migratory hosts. Mar Ecol Prog Ser 403:1–11
Kulka DW, Corey S (1984) Incidence of parasitism and irregular development of gonads in *Thysanoessa inermis* (Kroeyer) in the Bay of Fundy (Euphausiacea). Crustaceana 46(1):87–94
Kuris AM, Blaustein AR, Alió JJ (1980) Hosts as islands. Am Nat 116:570–586
Kuris AM, Hechinger RF, Shaw JC et al (2008) Ecosystem energetic implications of parasite and free-living biomass in three estuaries. Nature 454:515–518
Lafferty KD (1999) The evolution of trophic transmission. Parasitol Today 15(3):111–115
Lafferty KD, Kuris AM (2002) Trophic strategies, animal diversity and body size. Trends Ecol Evol 17(11):507–513. doi:10.1016/S0169-5347(02)02615-0
Landers SC, Gómez-Gutiérrez J, Peterson WT (2006) *Gymnodinioides pacifica* n. sp., an exuviotrophic ciliated protozoan (Ciliophora, Apostomatida) from euphausiids of the Northeastern Pacific. Eur J Protistol 42:97–106
Landers SC, Gómez-Gutiérrez J, Peterson WT (2007) The fine structure of the phoront of *Gymnodinioides pacifica*, a ciliated protozoan (Ciliophora, Apostomatida) from euphausiids of the Northeastern Pacific. Eur J Protistol 43:239–249
Lear DW (1963) Occurrence and significance of chitinoclastic bacteria in pelagic waters and zooplankton. In: Oppenheimer CH (ed) Symposium on marine microbiology. CC Thomas, Publisher, Springfield, pp 594–610
Levine ND (1988) Progress in taxonomy of the Apicomplexan protozoa. J Protozool 35(4):518–520
Lindley JA (1978) Continuous plankton records: the occurrence of apostome ciliates (Protozoa) on Euphausiacea in the North Atlantic Ocean and North Sea. Mar Biol 46:131–136
Lynn DH, Gómez-Gutiérrez J, Strüder-Kypke MC et al (2014) Ciliate species diversity and host-parasitoid codiversification in the apostome genus *Pseudocollinia* (Ciliophora, Apostomatia,

Pseudocolliniidae) that infect krill, with description of *Pseudocollinia similis* n. sp., a parasitoid of the krill *Thysanoessa spinifera*. Dis Aquat Organ 112(2):89–102
Macaulay MC, English ST, Mathisen OA (1984) Acoustic characterization of swarms of Antarctic krill (*Euphausia superba*) from Elephant Islands and Bransfield Strait. J Crust Biol 4(spec. No. 1):16–44
Mauchline J (1980) The biology of mysids and euphausiids. In: Blaxter JHS, Russell FS, Younge M (eds) Adv Mar Biol 18:1–681
Mauchline J, Fisher LR (1969) The biology of the euphausiids. In: Russell FS, Younge M (eds) Adv Mar Biol 7:1–454
Miwa S, Kamaishi T, Matzuyama T et al (2008) Histopathology of Antarctic krill, *Euphausia superba*, bearing black spots. J Invert Pathol 98:280–286
Mooney JR, Shirley TC (2000) New hosts, prevalence, and density of the ellobiopsid parasite *Thalassomyces fagei* on euphausiids in Prince William Sound, Alaska. J Crust Biol 20:320–325
Nash SMB, Poulsen AH, Kawaguchi S et al (2008) Persistent organohalogen contaminant burdens in Antarctic krill (*Euphausia superba*) from the eastern Antarctic sector: a baseline study. Sci Total Environ 407(1):304–314
Nicol S (1984) *Ephelota* sp. a suctorian found on the euphausiids *Meganyctiphanes norvegica*. Can J Zool 62:744–746
Nowacek DP, Friedlaender AS, Halpin PN et al (2011) Super-aggregations of krill and humpback whales in Wilhelmina Bay, Antarctic Peninsula. PLoS ONE 6(4):e19173. doi:10.1371/journal.pone.0019173
Patarnello T, Bargelloni L, Varotto V et al (1996) Krill evolution and the Antarctic Ocean currents: evidence of speciation as inferred by molecular data. Mar Biol 126:603–608
Permitin YY, Traverdiyeva MJ (1972) The food of some Antarctic fishes in the South Georgia area. J Ichthyol 12:104–114
Poulsen AH, Kawaguchi S, Kukkonen JV et al (2012) Aqueous uptake and sublethal toxicity of p, p′-DDE in non-feeding larval stages of Antarctic krill (*Euphausia superba*). Environ Pollut 160:185–191
Rakusa-Suszczewski S, Filcek K (1988) Protozoa on the body of *Euphausia superba* Dana from Admiralty Bay (the South Shetland Island). Acta Protozool 27:21–30
Rakusa-Suszczewski S, Nemoto T (1989) Ciliates associations on the body of krill (*Euphausia superba* Dana). Acta Protozool 28:77–86
Rakusa-Suszczewski S, Zdanowski MK (1989) Bacteria in krill (*Euphausia superba* Dana) stomach. Acta Protozool 28:87–90
Ritz DA (1994) Social aggregation in pelagic invertebrates. Adv Mar Biol 30:156–156
Ritz DA, Hobday AJ, Montgomery JC et al (2011) Social aggregation in the pelagic zone with special reference to fish and invertebrates. Adv Mar Biol 60:1–161
Rocka A (2006) Helminths of Antarctic fishes: life cycle biology, specificity and geographical distribution. Acta Parasitol 51:26–35
Schmidt K, Atkinson A, Petzke K-J et al (2006) Protozoans as a food source for Antarctic krill, *Euphausia superba*: complementary insights from stomach content, fatty acids, and stable isotopes. Limnol Oceanogr 51:2409–2427
Seear PJ, Goodall-Copestake WP, Fleming AH et al (2012) Seasonal and spatial influences on gene expression in Antarctic krill *Euphausia superba*. Mar Ecol Prog Ser 467:61–75
Siegel V (1980a) Parasite tags for some Antarctic channichthyid fish. Arch Fischereiwissenschaft 31(2):97–103
Siegel V (1980b) Quantitative investigations on parasites of Antarctic channichthyid and nototheniid fishes. Meeresforschung 28(2/3):146–156
Spiridonov VA (1996) A scenario of the late-pleistocene-holocene changes in the distributional range of Antarctic krill (*Euphausia superba*). Mar Ecol 17:519–541
Stankovic A, Rakusa-Suszczewski S (1996) Parasitic protozoa on appendages and inside the body of *Euphausia superba* Dana. Polish Polar Res 17(3–4):169–171

Stankovic A, Borsuk P, Koper M et al (2002) Studies on *Ephelota* sp., an epizoic suctorian found on Antarctic krill. Polar Biol 21:827–832

Stawiszyńska-Janas M, Kittel W (1982) Epizoiczne sysydlaczki (Protozoa, Suctorida) na *Euphausia superba* Dana i *Euphausia crystallorophias* Holt et Tattersal. Polskie Badania Polarne 1970–1982 Toruń, pp 239–248

Takahashi KT, Kawaguchi S, Kobayashi M et al (2003) Parasitic eugregarines change their spatial distribution within the host digestive tract of Antarctic krill, *Euphausia superba*. Polar Biol 26:468–473

Takahashi KT, Kawaguchi S, Kobayashi M et al (2004) The variability in abundance of eugregarines living in the Antarctic krill. Polar Biosci 17:16–25

Takahashi KT, Kobayashi M, Kawaguchi S et al (2008) Circumpolar occurrence of eugregarinid protozoan *Cephaloidophora pacifica* associated with the Antarctic krill, *Euphausia superba*. Antarct Sci 20:437–440

Takahashi KT, Kawaguchi S, Toda T (2009) Observation by electron microscopy of a gregarine parasite of Antarctic krill: its histological aspects and ecological explanations. Polar Biol 32(4):637–644

Takahashi KT, Kawaguchi S, Kobayashi M et al (2011) Eugregarinid infection within the digestive tract of larval Antarctic krill, *Euphausia superba*. Polar Biol 34:1167–1174

Tarling GA, Cuzin-Roudy J (2008) External parasite infestation depends on moult-frequency and age in Antarctic krill (*Euphausia superba*). Polar Biol 31:121–130

Tarling GA, Shreeve RS, Hirst AG et al (2006) Natural growth rates in Antarctic krill (*Euphausia superba*): I. Improving methodology and predicting intermolt period. Limnol Oceanogr 51:959–972

Théodoridès J (1989) Parasitology of marine zooplankton. Adv Mar Biol 25:117–177

Théodoridès J, Desportes O (1975) Sporozoaires d'Invertébrés pélagiques de Villefrenche-sur-mer (étude descriptive et faunistique). Protistologica 11:205–220

Timofeev SF (2001) Quantitative indices of the infection with gregarinids (Sporozoa: Gregarinina) in the euphausiid *Thysanoessa raschii* (Crustacea: Euphausiacea) from the Barents Sea. Parazitol 35(3):235–240 (in Russian)

Trathan PN, Hill SL (2016) Chapter 9, The importance of krill predation in the Southern Ocean. In: Siegel V (ed) The biology of Antarctic krill: *Euphausia superba* Dana 1850, Advances in Polar Ecology, Springer, Cham, pp 321–350

Turkiewicz M, Galas E, Kalinowska H (1982) Microflora of Antarctic krill (*Euphausia superba*). Acta Microbiol Polonic 31:175–184

Watkins J (2000) Aggregation and vertical migration, Chapter 4. In: Everson I (ed) Krill biology, ecology and fisheries, Fish and aquatic resources, series 6. Blackwell Science, Oxford, pp 80–102

Yamamoto Y, Honda K, Tatsukawa R (1987) Heavy metal accumulation in Antarctic krill *Euphausia superba*. Paper presented at the Proceedings of the NIPR Symposium on Polar Biology, Tokyo, pp 198−204

Zhao L, Yin B, Liu Q et al (2013) Purification of antimicrobial peptide from Antarctic Krill (*Euphausia superba*) and its function mechanism. J Ocean Univ China 12(3):484–490

Zoetendal EG, Chen B, Koike S et al (2004) Molecular microbial ecology of the gastrointestinal tract: from phylogeny to function. Curr Iss Intest Microbiol 5:31–48