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Parasites in Antarctic krill guts inferred from DNA sequences

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Abstract: The keystone role of Antarctic krill, *Euphausia superba* Dana, in Southern Ocean ecosystems, means it is essential to understand the factors controlling their abundance and secondary production. One such factor that remains poorly known is the role of parasites. A recent study of krill diet using DNA analysis of gut contents provided a snapshot of the parasites present within 170 *E. superba* guts in a small area along the West Antarctic Peninsula. These parasites included *Metschnikowia* spp. fungi, *Haptoglossa* sp. peronosporomycetes, *Lankesteria* and *Paralecudina* spp. apicomplexa, *Stegophorus* sp. nematodes, and *Pseudocollinia* spp. ciliates. Of these parasites, *Metschnikowia* spp. fungi and *Pseudocollinia* spp. ciliates had previously been observed in *E. superba*, as had other genera of apicomplexans, though not *Lankesteria* and *Paralecudina.* In contrast, nematodes had previously only been observed in eggs of *E. superba*, and there are no literature reports of peronosporomycetes in euphausiids. *Pseudocollinia* spp., parasitoids which obligately kill their host, were the most frequently observed infection, with a prevalence of 12%. The wide range of observed parasites and the relatively high frequency of infections suggest parasites may play a more important role than previously acknowledged in *E. superba* ecology and population dynamics.

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Introduction

Euphausia superba, Antarctic krill, are a key component of Southern Ocean ecosystems, serving as prey for most of the region's charismatic megafauna (Quetin & Ross 1991). These small pelagic crustaceans are also the target of a growing fishery (Nicol & Foster 2016). Because of these important roles as a prey item and as a harvestable resource, it essential to understand the factors controlling *E. superba* abundance and secondary production. One such factor that remains poorly understood is the role of parasites.

Globally, there is increasing recognition of the importance of parasites in marine ecosystems, and their potentially broad implications for carbon cycling, ecosystem structure and resiliency to environmental change (Kuris *et al.* 2008, Lima-Mendez *et al.* 2015, Cleary *et al.* 2016, Wallis *et al.* 2017). Euphausiids are thought to be particularly susceptible to parasites because their dense schooling behaviour facilitates parasite transmission (Gómez-Gutiérrez & Morales-Ávila 2016). Within the Euphausacea, 14 distinct parasite/parasitoid types have been identified, encompassing both internal and external parasites (Gómez-Gutiérrez *et al.* 2017). Antarctic krill are known hosts for four eukaryotic endoparasite types, namely, apicomplexans, fungi, nematodes, and *Pseudocollinia* spp. ciliates, as well as two types of epibiotic ciliates (Gómez-Gutiérrez & Morales-Ávila 2016). However, many of these parasites have been reported only a handful of times, some only in captivity, and the role of these parasites in euphausiid homeostasis and population dynamics remains very poorly known. Information is lacking on even their most basic aspects, such as taxonomic identity, distribution, prevalence, intensity and effects on secondary production.

Apicomplexa are the best-studied parasites in *E. superba*, with eight publications reporting on the prevalence of two different species within the Apicomplexan genus *Cephaloidophora* (Gómez-Gutiérrez & Morales-Ávila 2016). These *Cephaloidophora* spp. infest the digestive tract and hepatopancreas of *E. superba*, and are thought to reduce host fitness by decreasing nutrient uptake (Takahashi *et al.* 2011). For fungi, a handful of yeast-type fungi have been isolated from *E. superba* digestive tracts; however, their pathology and ecological function are "virtually unknown" (Donachie & Zdanowski 1998, Gómez-Gutiérrez & Morales-Ávila 2016). Nematodes have only been observed once in *E. superba*, in eggs reared under laboratory conditions (Gómez-Gutiérrez & Morales-Ávila 2016). *Pseudocollinia* spp. ciliates have also been observed in *E. superba* only once, where they were identified from photographs in a study near King George Island (Stankovic & Rakusa-Suszczewski 1996, Gómez-Gutiérrez & Kawaguchi 2017).

The present authors recently conducted a study of krill feeding (Cleary *et al.* 2018). Although not the target of the

study, DNA sequences from a variety of parasite groups in krill gut contents were observed. The methods employed were optimized to study diet, rather than parasites; however, given the paucity of available data on krill parasites, the results provide useful confirmation of some parasite–krill interactions that have been only rarely reported, and give new indications of previously unknown parasite–*E. superba* interactions.

Materials and methods

Sampling and analytical methods for the present study are detailed in Cleary *et al.* (2018). In brief, adult krill were collected in the West Antarctic Peninsula region between Andvord Bay (64.83°S, 62.64°W) and the coast of Renaud Island (65.61°S, 66.44°W) during summer 2014 (10–21 December). Seven stations were sampled, from which a total of 170 krill individuals were analysed. Krill were collected in a 1 m² MOCNESS (Wiebe *et al.* 1985), outfitted with strobe lights to minimize krill net avoidance (Sameoto *et al.* 1993, Wiebe *et al.* 2004). No visible signs of parasite infection were noted in any of the collected krill, either at the time of collection, or during later dissection.

Krill were dissected and genomic DNA was extracted from isolated foreguts. The v7 region of the 18 S ribosomal DNA gene was amplified for all non-krill organisms in these extracts using a krill-blocking peptide nucleic acid polymerase chain reaction, and the resulting amplicons were sequenced on an Illumina MiSeq. Sequences were clustered into operational taxonomic units (OTUs) using minimum entropy decomposition (Eren *et al.* 2015), and taxonomy was assigned by BLAST searching against the SILVA database and NCBI GenBank (Altschul *et al.* 1990, Morgulis *et al.* 2008, Quast *et al.* 2013). Only OTUs containing a total of ≥500 reads were included in analyses, to minimize the effect of sequencing noise. Individual krill were considered to be "infected" by a specific parasite type if that individual contained at least 50 reads from that parasite. This threshold was chosen to minimize potential effects of miss-assignment of reads due to sequencing errors in the sample identification tags and of trace contamination, although preliminary investigations showed little difference in infection thresholds from 10 reads through 100 reads. These thresholds (≥500 total reads and ≥50 reads within an individual) provide only a conservative estimate of parasite prevalence, as incipient or very rare infections may not be detected. This approach detects any parasite in any krill individual; thus the prevalence of each parasite is equal to simply the number of parasitized individuals divided by 170, where 170 is the total number of krill analysed.

Results

Six taxonomic groups of parasites were observed in a total of 34 instances of infection (Table I). These parasites were *Pseudocollinia* sp. ciliates (21 infections), *Metschnikowia* sp. fungi (5 infections), *Haptoglossa* sp. peronosporomycetes (4 infections), *Stegophorus macronectes* (Johnston & Mawson) nematodes (2 infections), and *Lankesteria* and *Paralecudina* sp. apicomplexans (1 infection each).

Pseudocollinia ciliate sequences were found in 21 individual krill (12.4% prevalence) from across all but one of the sampled stations. These sequences grouped into ten OTUs (Fig. 1). Five of these OTUs differed from the most abundant OTU by only a single base, and were found at low abundance, suggesting that they reflect intraspecific diversity or sequencing artefacts. Thus these six OTUs (A–F in Fig. 1) are considered to represent together a single ecotype. The remaining four OTUs differed from each other by between two to six base positions, with variation in consistent areas of the amplicon, and are treated henceforth as each representing their own ecotype. These may represent distinct species, although it is impossible to determine species delimitation from sequence data alone. Each individual krill was infected (>50 reads) by only a single *Pseudocollinia* ecotype. One of the ecotypes (*Pseudocollinia* OTU J) was identical (100%) to reference sequences for the North Pacific ciliate spp. *Pseudocollinia beringensis* (Capriulo & Small), *Pseudocollinia brintoni* Gómez-Gutiérrez, Strüder-Kypke, Lynn, Shaw, Aguilar-Méndez, López-Cortés,

Table I. Parasite sequences from *E. superba*.

Type	Stns	Indivs (Prevalance)	OTUs	Reads	M/F	Length (range)	Closest GenBank reference	Id	Ref.
Ciliate	6	21 (12%)	10	174313	7/13	44.5 ± 5.7 (33–53)	*Pseudocollinia* spp.	98	Lynn *et al.* 2014
Fungus	4	5 (3%)	1	1255	0/4	47 ± 4.2 (42–52)	*Metschnikowia bicuspidata*	99	Searle *et al.* 2015
Peronosporo-mycete	1	4 (2%)	3	4317	2/2	44.5 ± 2.6 (42–48)	*Haptoglossa* sp.	93	Hakariya *et al.* 2009
Nematode	2	2 (1%)	4	27607	1/1	49 ± 5.6 (45–53)	*Stegophorus macronectes*	100	Vidal *et al.* 2016
Apicomplexa	1	1 (0.6%)	1	901	0/1	36	*Lankesteria* sp.	98	Rueckert & Leander 2008
Apicomplexa	1	1 (0.6%)	1	569	0/1	46	*Paralecudina anankea*	92	Iritani *et al.* 2018

Stns = stations, out of seven, where parasite sequence was observed, Indivs = individual krill, out of 170, infected, % prevalence across all sampling stations combined, OTUs = count of distinct OTUs, Reads = total sequence reads, M/F = sex ratio of infected individuals (overall sex ratio: 32/130), Length = mean ± SD length of the infected individuals, with range in parentheses (overall mean length is 44.5 ± 6, range is 32–57), Id = % identity between OTU sequence and GenBank reference sequence. (n.b. a few individuals lack data for sex and length.)

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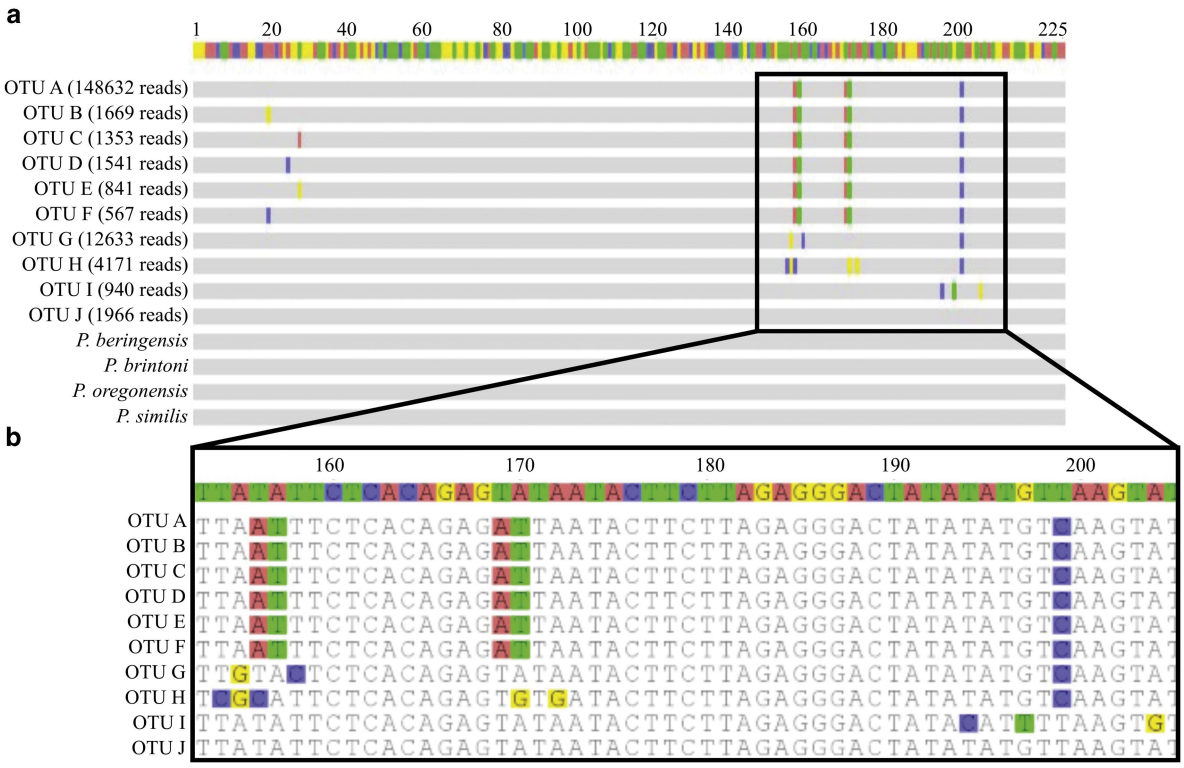

Fig. 1. *Pseudocollinia* OTU sequences from *E. superba* guts and known reference sequences (Lynn *et al*. 2014). Bases that differ from the described species are coloured. The total number of sequence reads for each OTU is given in parentheses. **a.** Full amplicon for OTUs and known species – note that all described species are identical over the sequenced amplicon. **b.** Closer view of the most variable part of the amplicon for krill gut OTUs. OTUs A–F are discussed in the text as a single "ecotype" because they differ by only a single base position.

Martínez-Gómez & Robinson, *Pseudocollinia oregonesis* Gómez-Gutiérrez, Peterson & Morado and *Pseudocollinia similis* Lynn, Gómez-Gutiérrez, Strüder-Kypke & Shaw (which are themselves all identical over the sequenced 18 S v7 amplicon) (Gómez-Gutiérrez *et al*. 2012, Lynn *et al*. 2014). This "known" *Pseudocollinia* OTU was found exclusively from krill within fjords ($n = 4$ krill). Similarly, one of the "new" ecotypes (OTU I) was found in a single fjord krill ($n = 1$ krill). The two most abundant ecotypes in terms of total sequence reads (OTUs A–F and OTU G), which differ from the "known" type by five and six base positions (over the 225 base pair amplicon), were found exclusively further offshore in open water areas ($n = 9$ krill, $n = 2$ krill), and the fifth ecotype (OTU H) was found in krill across both areas ($n = 5$ krill).

Metschnikowia sp. fungi sequences were found in five individual krill (2.9% prevalence) from across four sampling stations. These sequences grouped into a single OTU, which was 99% identical to the sequence from Searle *et al*. (2015) for *Metschnikowia bicuspidata* (Metschnikoff) Kamienski.

Haptoglossa sp. peronosporomycetes were found in four individuals (2.3% prevalence), all sampled from a single station in the Bismarck Strait, near Cape Lancaster (Anvers Island). These sequences grouped into three different OTUs, the most abundant of which was 93% identical to a sequence from Hakariya *et al*. (2009).

Stegophorus macronectes nematode sequences clustered into four OTUs. All four of these OTUs were each found at over 100 reads in each of two individual krill, one collected in Flandres Bay, and the other collected between Anvers and Tangent islands. The most abundant of these OTUs, making up over 90% of the observed nematode sequences, was found to be 100% identical to a *S. macronectes* sequence isolated from penguin intestines (Vidal *et al*. 2016).

The *Lankesteria* and *Paralecudina* sp. apicomplexans were only observed as a single OTU in a single krill individual each. Both of the krill individuals infected by apicomplexa were collected in the same sampling station near Cape Lancaster.

No clear patterns were observed with regard to krill host sex or length for any of the parasite types (Fig. 2, Table I), although this may be partially a result of the relatively low numbers of infected individuals.

Discussion

The parasites observed here include 1) taxonomic groups already known to infect *E. superba* adults (*Metschnikowia* sp., apicomplexa, *Pseudocollinia* sp.), 2) a group suspected to infect *E. superba* adults, but which has only been

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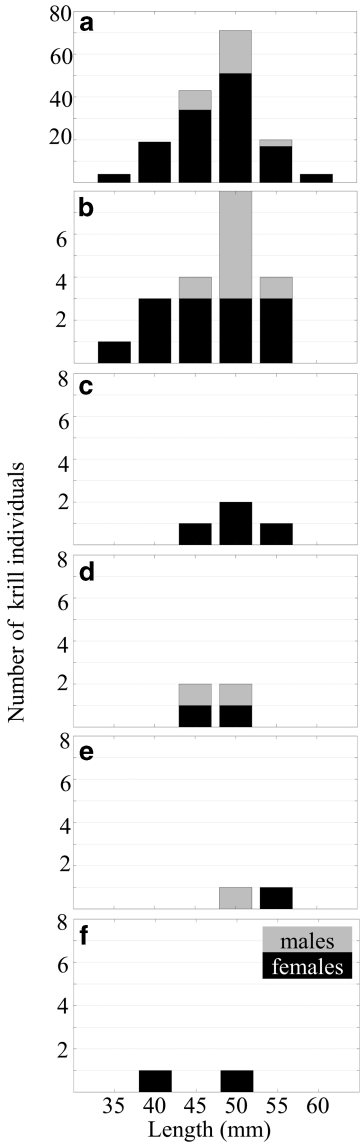

Fig. 2. *E. superba* length frequencies and sexes. Length is standard 1 total length (Mauchline 1980) in 5 mm bins, with the top of the bin labelled on the graph. Females are shown in black, males in grey. **a.** All individuals. Remaining panels, krill individuals infested with each parasite type: **b.** *Pseudocollinia* spp. ciliates, **c.** *Metschnikowia* spp. fungi, **d.** Peronosporomycetes, **e.** *Stegophorus* sp. nematodes, **f.** Apicomplexa. Note the different y-axis scale for panel **a**.

observed previously in their eggs (*S. macronectes*), and 3) a group known only from other crustaceans (*Haptoglossa* sp.).

The molecular methods applied offer high sensitivity and can detect the full range of known parasite species. However, there are some caveats to bear in mind in considering the results. As with all net-catch based studies, there is a possibility that parasitized individuals have been disproportionately sampled, as these krill have reduced swimming capacity (Hamner 1984, Gómez-Gutiérrez *et al*. 2017) and may thus have reduced ability to avoid the sampling gear. However, conversely, parasitized krill individuals may have been under-sampled if their reduced swimming capacity caused them to fall behind the school, as net catches were targeted on acoustically identified krill aggregations. Secondly, the distinction between "prey" which had been consumed, and "parasites" infesting the krill was based mainly on literature information on the lifestyles and trophic strategies of the prey/parasite organisms. Thus, it is possible that some true parasites were erroneously classified as prey if they had not previously been described as parasitic. Conversely, some of the identified parasites may not have been actively infecting the krill, but could simply have been recently consumed, and would potentially have been digested or destroyed by the krill's immune system rather than completing their parasitic lifecycle. However, the observed patterns of sequence read abundance suggest this is not a major complicating factor. Parasites tended to be found in relatively few individual krill, but within each infected individual had very high abundance. This pattern would be consistent with actively growing parasites and was not observed for prey species. In future work, krill should be held in filtered seawater for several hours to empty their guts of prey, if feasible, to minimize this potential confounding factor. Lastly, molecular data provides no information on the life stage of the parasite, and only semi-quantitative results on the intensity of the infection within each individual host. Future work could benefit from combining molecular detection with microscopy, as these two approaches provide complementary information.

Unlike most investigations of parasitism, which typically focus on the intestines, hemocoel and/or hepatopancreas this study analysed the stomach (sometimes referred to as the foregut) of the krill. Krill stomachs are a fairly inhospitable environment for parasites, as they are lined with armoured plates used for crushing prey (Suh & Nemoto 1988). This choice of tissue may have led to underestimation of the prevalence of some parasite taxonomic groups - and future studies should consider analysing a range of tissues - but it also provided indications of the transmission pathway of the detected parasites. The most parsimonious transmission pathway for parasites found in the stomach is through ingestion, although it is of course also possible that parasites migrated through the krill body cavity to the stomach. Trophic transmission is known to be the general infection pathway in euphausiids for apicomplexa (Takahashi *et al*. 2003), and has been suggested to be the infection pathway for *Pseudocollinia* spp. (Gómez-Gutiérrez *et al*. 2015), and nematodes (Gómez-Gutiérrez *et al*. 2017). Little is known of the transmission pathways of parasitic fungi and peronosporomycetes (Gómez-Gutiérrez *et al*. 2017). The results presented here support these suggestions of trophic transmission as an infection pathway in krill for *Pseudocollinia* spp. and nematodes, and suggest trophic

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transmission as a pathway for the poorly known fungi and peronosporomycetes.

Metschnikowia sp. fungi have been observed in *E. superba*, with three publications to date reporting its presence, but little is known about this taxonomic group (Gómez-Gutiérrez & Morales-Ávila 2016). The results given here add to these observations, but with no information on the impact of fungi on krill, it is difficult to assess what, if any, effect these interactions have.

Apicomplexa are also known to infest *E. superba*, although the specific genera observed here, *Lankesteria* and *Paralecudina*, have not previously been reported in *E. superba* or in other euphausiid spp. (Gómez-Gutiérrez & Morales-Ávila 2016, Gómez-Gutiérrez *et al.* 2017). The relative rarity of apicomplexan infections observed here is perhaps surprising, given that they have previously been found at high prevalence (2–96%) (Takahashi *et al.* 2003, 2011). This may be due to the tissue analysed, as gregarines are generally much more frequent in the intestine as compared to the stomach (Takahashi *et al.* 2003). Apicomplexa reduce host fitness by decreasing nutrient uptake in the gut (Takahashi *et al.* 2011), probably reducing the resources available to krill individuals for growth and reproduction. The observed infections by these two apicomplexa genera, though low in prevalence, may suggest reductions in *E. superba* secondary production in this region, which has implications for higher predators.

Holocarpic endoparasitic peronosporomycetes are known to infect marine crustaceans (Hakariya *et al.* 2009), but to date, there are no published observations of peronosporomycetes in euphausiids. Little is known about this group, and its phylogeny remains unclear. The finding of these sequences within *E. superba* suggests a potential interaction, but further studies will be needed to confirm if this is indeed parasitism, or simply reflects taxonomic confusion between parasitic and related free-living organisms.

The *Pseudocollinia* spp. ciliate sequences observed here include sequences identical to those of the North Pacific, as well as closely related, but clearly distinct sequences. All existing *Pseudocollinia* spp. 18 S sequences are identical over the sequenced v7 amplicon discussed here. This is a highly variable region of eukaryote genomes, but with a length of only 225–250 base pairs, it is not surprising to see identical sequences in closely related organisms. Because of this, it is not possible to distinguish which of the four described *Pseudocollinia* spp. the "known" OTU sequence represents, or if it represents a species that is closely related, but to date undescribed. The other *Pseudocollinia* OTU sequences which are distinct from the known *Pseudocollinia* spp., with 97–98% sequence identity, remain much more closely related to *Pseudocollinia* spp. than to any other described organism, suggesting a similar parasitoid lifestyle. These sequences may represent as yet undescribed species belonging to this still poorly known genus, although morphological investigations will be necessary to confirm or refute this possibility. Previous work (Gómez-Gutiérrez *et al.* 2015) has suggested *Pseudocollinia* spp. preferentially infect adult female krill. The present study did not find this to be the case; roughly one third of krill individuals infected with *Pseudocollinia* were male, leading to a male/female ratio of *Pseudocollinia*-infected krill over twice the overall male/female ratio of analysed krill.

Pseudocollinia ciliates are parasitoids, generally causing the death of their host within days (Gómez-Gutiérrez *et al.* 2003, 2015, 2017). These parasitoids have only previously been reported once in the Southern Ocean, from *E. superba* near King George Island (Stankovic & Rakusa-Suszczewski 1996, Gómez-Gutiérrez & Kawaguchi 2017). *Pseudocollinia* spp. ciliate infections have been observed in a variety of other krill species (*Euphausia pacifica* Hansen, *Euphausia similis* Sars, *Nyctiphanes simplex* Hansen, *Thysanoessa gregaria* G.O. Sars, *Thysanoessa inermis* Krøyer, *Thysanoessa longipes* Hansen, *Thysanoessa raschii* M. Sars, *Thysanoessa spinifera* G.O. Sars), including observations of high infection rates, and a mass mortality event off the Oregon coast (Gómez-Gutiérrez *et al.* 2003, Lynn *et al.* 2014, Gómez-Gutiérrez & Morales-Ávila 2016, Gómez-Gutiérrez & Kawaguchi 2017, Gómez-Gutierrez *et al.* 2017). Mass mortality events, a "dead body rain", have been suggested to occur in *E. superba* based on the occasional high prevalence of these krill in the guts of benthic deposit feeders (Sokolova 1994). No cause has been identified for mass mortality events in Antarctic krill; but it is not unreasonable to suggest *Pseudocollinia* sp. infections could be a contributing factor, as hypothesized by Gómez-Gutiérrez & Kawaguchi (2017). Given that these *Pseudocollinia* spp. parasitoids lead to fairly rapid death in euphausiids, their infections have important implications both for krill population dynamics as well as for the fluxes of organic carbon to the benthos. The finding, described here, of 21 infected individuals out of a sample of 170, a 12% prevalence, and the finding of these parasitoids across all but one of the sampling stations, suggests they may have significant impacts on *E. superba* population dynamics.

Sequences of the nematode *S. macronectes*, were found in two krill individuals, each collected in a different sampling station. The presence of four distinct OTUs, all four of which were present in each krill individual, probably reflects variation between the many copies of the 18 S gene within the nematode's genome. One of the nematode-parasitized krill did not contain any mesozooplankton sequences, indicating this nematode is highly unlikely to have been derived from consuming infected prey. *S. macronectes* is a parasite of Antarctic seabirds, which has been found in a variety of penguins, as well as albatrosses, petrels and sheathbills (Vidal *et al.* 2016). The sequence from the present work is 100%

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identical to that obtained from this species of nematodes in penguin intestines (Vidal *et al*. 2016). Since some of the infected bird species feed almost exclusively on *E. superba*, it has been suggested that *E. superba* are the likely intermediate hosts for this parasite (Diaz *et al*. 2016). However, no helminths of any kind have ever been observed in adult *E. superba*, although unidentified nematode larvae have been observed in *E. superba* eggs raised in aquaria, and various nematode species have been observed in adults of other krill species (Gómez-Gutiérrez & Morales-Ávila 2016, Gómez-Gutiérrez *et al*. 2017). The observation in the present work of the DNA sequence for *S. macronectes* within *E. superba* guts indicates that either *E. superba* are indeed an intermediate host for this common Antarctic avian parasite, or that *E. superba* feed at least occasionally on material derived from seabird faeces. Both of these explanations have interesting implications, such as for seabird health and for ecosystem carbon flows, and thus future research to clarify the nature of the interactions between *E. superba* and *S. macronectes* would be beneficial.

Conclusions

This study is the first to detect several parasite taxonomic groups within *E. superba*, providing the first suggestion of interactions between these krill and peronosporomycetes as well as the apicomplexan genera *Lankesteria* and *Paralecudina*. This study also provides the first genetic confirmation of *Pseudocollinia* spp. ciliates in *E. superba*, and the first observation of nematodes in adult *E. superba*. The large diversity of parasite types detected with this molecular approach, and the relatively high prevalence of some parasite types, suggest parasitism may be playing a more important role in *E. superba* population dynamics and ecology than has previously been generally acknowledged.

Parasites reduce host fitness, with effects ranging from reduced nutrient uptake in the case of apicomplexan parasites, through to death in the case of *Pseudocollinia* spp. parasitoids. Because of the keystone role of *E. superba*, these reductions in fitness have potentially important implications for Southern Ocean ecosystems. Increases in krill mortality, or reductions in growth or egg production could have negative cascading effects on the many megafaunal predators which rely upon *E. superba*. It is thus essential to increase what is known of the prevalence of these various parasite types across *E. superba*'s wide range, of how parasite load changes with spatial and temporal variations in environmental conditions, and of what effects parasites have on *E. superba* growth, reproduction, and mortality. Future work on krill parasites, ideally combining molecular detection approaches, with microscopic observations and experimental measures of parasite impact, may help to elucidate energy flows through the Southern Ocean, to predict responses to changing environmental conditions, and to sustainably manage the growing fishery for *E. superba*.

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Author contribution

ACC, MC and EGD planned the project and conducted field and lab work. ACC analysed the data and prepared the manuscript with help from EGD and JGG.

Details of data deposit

Representative sequences for each OTU are available in GenBank (MH259892-MH259911), and raw sequence reads are available in the Short Read Archive (SRP131159).

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