



Infestation dynamics between parasitic Antarctic fish leeches (Piscicolidae) and their crocodile icefish hosts (Channichthyidae)

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Received: 10 June 2019 / Revised: 6 April 2020 / Accepted: 8 April 2020 / Published online: 18 April 2020
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Abstract

An understanding of host–parasite interactions represents an important, but often overlooked, axis for predicting how polar marine biodiversity may be impacted by continued environmental change over the next century. Here, we survey three species of crocodile icefish (Notothenioidei: Channichthyidae) collected from two island archipelagos in the southern Scotia Arc region for evidence of leech infestations. Specifically, we report on infestation prevalence, intensity, spatial patterns of relative abundances, size distribution of parasitized fish, and patterns of host and attachment site specificity. Our results reveal high levels of attachment area fidelity for each leech species. These results suggest skin thickness and density of the vascular network constrain leech attachment sites and further suggest trophic (i.e., post-cyclic) transmission to be an important axis of parasitization. We also demonstrate that, while leech species appear to be clustered spatially, this clustering does not appear to be correlated with fish biomass. This study illuminates the complex interactions among fish hosts and leech parasites in the Southern Ocean and lays the groundwork for future studies of Antarctic marine leech ecology that can aid in forecasting how host–parasite interactions may shift in the face of ongoing climate change.

Keywords Parasite infestation and virulence · Leech ecology and specialization · Trophic transmission · Life history · Post-cyclic transmission

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00300-020-02670-x>) contains supplementary material, which is available to authorized users.

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Introduction

Over the past several decades, the Southern Ocean ecosystem has become increasingly threatened by climate change, fisheries interests, and a general increase in human traffic (Kennicutt et al. 2015). The impact of these changes on the future conservation status of wildlife is an area of intense research interest (Kock 2007; Raymond et al. 2014; Gutt et al. 2015; Krüger et al. 2017). However, lack of baseline data for Antarctica's parasite communities has challenged our ability to integrate these organisms into forecasts of Southern Ocean biodiversity over the next century (Bielecki et al. 2008). Differential responses to environmental stressors by hosts and their parasites can alter the balance of host–parasite interactions (Gehman et al. 2018), creating an urgent need for the quantification of baseline infestation parameters of ecologically or economically important host species (Palm 2011). Unfortunately, our knowledge of the ecology and dynamics of infestation for many groups of parasites in the Southern Ocean are restricted to few

studies, and many aspects of their biology remain virtually unexplored.

Across the world, marine fish leech (Piscicolidae) species are major pests for commercially important fisheries (Cruz-Lacierda et al. 2000; Marancik et al. 2012) and also epidemiologically important as vectors transmitting viruses and additional blood parasites (Khan 1980, 1984; Siddall and Desser 1993; Karlsbakk 2004). Although the few studies reporting leech abundances on fishes from the Southern Ocean have indicated a general low prevalence, leeches are spatially heterogeneous with high loads on individual fish (Bielecki et al. 2008; Kuhn et al. 2018). This distributional pattern is common for parasitic organisms in general (May 1978; Pacala et al. 1990) and suggests it is likely that Antarctic fishes face parasitic pressures similar to those of fishes in other parts of the world (Sawyer and Hammond 1973). However, the Southern Ocean is unusual in that the vast majority of marine teleost fish biomass, species abundance, and diversity is dominated by one clade: notothenioids (Eastman 2000). These fishes include species of high economic importance to fisheries (Kock 1992; Delord et al. 2009; Collins et al. 2010) and species that represent critical links in the Antarctic food web between lower trophic levels and higher-level consumers such as whales, seals, and penguins (Targett 1981; Smith et al. 2007). However, the impact of piscicolids on notothenioids remains unclear. As future ecological relationships of the Southern Ocean become increasingly uncertain, developing a basic understanding of marine leeches now is critical if we are to be able to detect changes in host–parasite interactions or disease transmission pathways in the future. How prevalent are leech infestations? Do leeches disproportionately parasitize one size class over another? Do sympatric species of leeches compete for the same host fish? Answering fundamental questions such as these is critical if we are to illuminate the role of leeches in the current and future ecology of the Southern Ocean.

Crocodile icefishes (Channichthyidae) are an exemplar lineage from which to investigate the dynamics of leech infestation in notothenioids. Globally renowned for their lack of hemoglobin (Sidell and O'Brien 2006), these scaleless fishes are among the most well-studied teleosts in polar latitudes (Ruud 1954; Cocca et al. 1995; Kock 2005; Near et al. 2012; Melillo et al. 2015; Giraldo et al. 2016) and include species such as mackerel icefish (*Champscephalus gunnari*) that are of high economic importance for fisheries (Williams et al. 1994; Duhamel et al. 1995; Everson et al. 1999; Everson 2015). Correspondingly, this is one of few clades in which leech occurrences and identifications are well documented by species (Bielecki et al. 2008; Oguz et al. 2012; Kuhn et al. 2018), providing the necessary taxonomic framework for ecological study.

Prior investigations of Antarctic leech parasitism have suggested three species to be particularly common across

a range of channichthyid host species: *Nototheniobdella sawyeri* A. Utevsky, 1993, *Trulliobdella bacilliformis* (Brinkmann, 1947), and *Trulliobdella capititis* Brinkmann, 1947. *Trulliobdella capititis* and *T. bacilliformis* were described from the dorsal region of the head of the blackfin icefish, *Chaenocephalus aceratus*, and from the oral cavity of the South Georgia icefish, *Pseudochaenichthys georgianus*, respectively (Brinkmann 1948). Since then, little data have been collected on the ecology of *T. bacilliformis*. While this species has also been discovered to infest at least four other species of icefish, prevalence and infection intensity of this leech have not been thoroughly investigated (Table 1). In contrast, *T. capititis* has been identified from eight additional channichthyid species, with patterns of infestation by *T. capititis* examined for five of these species (see citations in Table 1). These studies suggest a generally low prevalence (3–13%) across host species with a range of attachment sites including the head, body, mouth, and gills (Table 1). A notable exception for this pattern stems from Bielecki et al. (2008) who reported a prevalence of 45% for *T. capititis* on *Chionodraco rastrospinosus* with attachment sites concentrated in the cranial areas of the species (Table 1). However, absence of additional data from this host–parasite species pair precludes an understanding of whether the high prevalence of *T. capititis* on *C. rastrospinosus* reflects a generalizable pattern or whether it represents a unique phenomenon resulting from a localized concentration of parasite activity.

Relative to either species of *Trulliobdella*, *N. sawyeri* has received more attention since its initial description (Utevsky 1993). *Nototheniobdella sawyeri* has been reported from the body surface, mouth, and gill cavity of eight channichthyid species (see Table 1), including infestation parameters for at least five channichthyid species (Table 1). Further contrasting observations of *T. capititis* with *N. sawyeri* suggests the latter to generally have higher prevalence (20–50%) than the former (8–13%) across the range of channichthyid hosts (Table 1). However, there are exceptions to the higher prevalence of *N. sawyeri* in channichthyids. For example, infestations of the commercially harvested mackerel icefish, *Champscephalus gunnari*, appear to be more restricted with a prevalence of only 5% (Bielecki et al. 2008). Lack of further investigation again stymies interpretation of whether this finding of lower prevalence is anomalous, or represents a general trend for this host species. More broadly, these knowledge gaps are unfortunate as channichthyids are widespread around the entire Antarctic, often occurring at extremely high biomass (Reid et al. 2007), with individual fishes harboring high infestation intensities of leeches (Bielecki et al. 2008; Kuhn et al. 2018). The limited number of investigations of infestation parameters not only creates a barrier to our understanding of leech–host ecology in the Antarctic, but also challenges our ability to establish general

Table 1 Summary of reported infection parameters for three Antarctic leech species and each of their notothenioid fish hosts. Crocodile icefish species are indicated in bold

Leech species				
	Hosts	Host feeding mode	Attachment sites	Reported prevalence
<i>Trulliobdella bacilliformis</i>	<i>Parachaenichthys georgianus</i> (Bathydraconidae)	Benthic (Targett 1981; Gon 1990)		
	<i>Chaenocephalus aceratus</i>	Benthic (Kock 2005)		
	<i>Champscephalus gunnari</i>	Pelagic (Iwami & Kock 1990)		
	<i>Channichthys rhinoceratus</i>	Benthic (Eastman 1993; Kock 2005)		
	<i>Chionodraco rastrospinosus</i>	Benthopelagic (Iwami & Kock 1990)		
	<i>Pseudochaenichthys georgianus</i>	Pelagic (Kock 2005)	Oral cavity (Brinkmann 1948)	
	<i>Notothenia coriiceps</i> (Nototheniidae)	Benthic (Dewitt et al. 1990)		
	<i>Lepidonotothen larseni</i> (Trematominae)	Pelagic (Targett 1981)		
<i>Trulliobdella capitata</i>	<i>Parachaenichthys georgianus</i> (Bathydraconidae)	Benthic (Targett 1981; Gon 1990)	Dorsal region of head (Brinkmann 1948)	
	<i>Chaenocephalus aceratus</i>	Benthic (Iwami & Kock 1990)	Dorsal region of head (Brinkmann 1948)	
	<i>Chaenodraco wilsoni</i>	Pelagic (Kock et al. 2008)	Stomach (Kuhn et al. 2018)	8% (Kuhn et al. 2018)
	<i>Champscephalus gunnari</i>	Pelagic (Iwami & Kock 1990)	Skin of head and mouth (Bielecki et al. 2008)	9% (Bielecki et al. 2008)
	<i>Channichthys rhinoceratus</i>	Benthic (Eastman 1993; Kock 2005)		
	<i>Chionodraco hamatus</i>	Epibenthic (La Mesa et al. 2004)	Skin (Santoro et al. 2014)	8% (Santoro et al. 2014)
	<i>Chionodraco rastrospinosus</i>	Benthopelagic (Iwami & Kock 1990)	Skin of head and mouth (Bielecki et al. 2008)	45% (Bielecki et al. 2008)
	<i>Cryodraco antarcticus</i>	Benthic (Kock 2005)		
	<i>Neopagetopsis ionah</i>	Pelagic (Kock 2005)		
	<i>Pseudochaenichthys georgianus</i>	Pelagic (Kock 2005)	Surface (Kuhn et al. 2018)	13.3% (Kuhn et al. 2018)
	<i>Notothenia coriiceps</i> (Nototheniidae)	Benthic (Dewitt et al. 1990)		
	<i>Notothenia rossi</i> (Nototheniidae)	Semipelagic (Dewitt et al. 1990)		
	<i>Trematomus bernacchii</i> (Trematominae)	Benthic (Dewitt et al. 1990)	Fin (Kmentová et al. 2016)	3% (Kmentová et al. 2016)

Table 1 (continued)

Leech species				
	Hosts	Host feeding mode	Attachment sites	Reported prevalence
<i>Nototheniobdella sawyeri</i>	<i>Parachaenichthys georgianus</i> (Bathydraconidae)	Benthic (Targett 1981; Gon 1990)	Body, mouth, and gill cavity (Utevsky 1993)	
	<i>Chaenodraco wilsoni</i>	Pelagic (Kock et al. 2008)	Body, mouth, and gill cavity (Utevsky 1993)	
			Mouth cavity and gills (Kuhn et al. 2018)	21.2% (Kuhn et al. 2018)
	<i>Champscephalus gunnari</i>	Pelagic (Iwami & Kock 1990)	Gill cavity (Bielecki et al. 2008)	5% (Bielecki et al. 2008)
	<i>Chionodraco hamatus</i>	Epibenthic (La Mesa et al. 2004)	Body, mouth, and gill cavity (Utevsky 1993)	
			Gill, skin, mouth (Santoro et al. 2014)	33% (Santoro et al. 2014)
	<i>Chionodraco rastrispinosus</i>	Benthopelagic (Iwami & Kock 1990)	Body, mouth, and gill cavity (Utevsky 1993)	
	<i>Cryodraco antarcticus</i>	Benthic (Kock 2005)	Body, mouth, and gill cavity (Utevsky 1993)	
	<i>Neopagetopsis ionah</i>	Pelagic (Kock 2005)	Body, mouth, and gill cavity (Utevsky 1993)	
	<i>Pagetopsis macropterus</i>	Pelagic (Daniels & Lipps 1982)	Mouth cavity and gills (Kuhn et al. 2018)	50% (Kuhn et al. 2018)
<i>Pseudochaenichthys georgianus</i>		Pelagic (Kock 2005)	Mouth cavity and gills (Kuhn et al. 2018)	26.7% (Kuhn et al. 2018)
	Harpagiferidae	Benthic (Hureau 1990)	Body, mouth, and gill cavity (Utevsky 1993)	
	<i>Trematomus bernacchii</i> (Trematominae)	Benthic (Dewitt et al. 1990)	Skin (Kmentová et al. 2016)	33% (Kmentová et al. 2016)

trends of infestation required for monitoring host fish stock health.

The purpose of this study was to characterize patterns of leech infestation on notothenioid fishes collected from two island archipelagos in the southern Scotia Arc. Here we report on various leech infestation parameters for three species of crocodile icefish (Notothenioidei: Channichthyidae) distributed around Elephant Island and the South Orkney Islands. Investigated infestation parameters included: (1) the proportion of infestations of each leech species found to parasitize crocodile icefish taxa; (2) the relative frequencies of each leech species at each collection site across the Elephant and South Orkney Islands; (3) the size distribution of parasitized fish relative to the size distribution of all fish collected; and (4) the prevalence and intensity of each leech species on each crocodile icefish species. We assess both global trends as well as differences in infestation parameters between Elephant Island and the South Orkney Islands, thereby revealing previously undocumented aspects of marine leech ecology in the Southern Ocean that include

infestation site fidelity between host–parasite species pairs and host size preferences.

Materials and methods

Sample acquisition

Sampling was conducted aboard the R/V Cabo de Hornos (Call Sign = CB7960) between 6 and 27 January, 2018, as part of a bottom trawl survey (Arana et al. 2020) of finfish around Elephant Island and the South Orkney Islands in the Southern Ocean. Trawling was conducted using a Hard Bottom Snapper Trawl (HBST; Net Systems, Inc., Bainbridge Island, WA). Thirty-five sampling sites were selected based on a random, depth stratified survey design that was primarily restricted to shelf regions (50–500 m). During trawl deployment, sensors monitored the geometry and seabed bottom contact of the trawl, ensuring that the trawl ground tackle was in contact with the seafloor for a 30-min tow.

All collected fish were surveyed for evidence of past and present leech infestation, yielding a total of 89 individual parasitized fishes representing three species and genera of crocodile icefishes (Channichthyidae). Locations of leech infestations were recorded and photographed for each parasitized fish. Identification and counts of leech specimens were conducted during the survey, and voucher photographs and specimens of both leeches and their host fish, were deposited in the North Carolina Museum of Natural Sciences (Supplemental materials). The total length and weights of all fishes captured were additionally recorded to enable quantification of leech abundances as they relate to fish size.

Leech infestation parameters

Several general parameters were examined to assess overall trends of leech infestation, with terminology following Bush et al. (1997). First, we calculated the relative proportions of infestation of each leech species that were found to parasitize each species of icefish in order to investigate patterns of host–parasite specificity. We also calculated the relative proportions of each leech species collected from each sampling site across the Elephant and South Orkney islands. Parasite infestation intensities per individual fish host were quantified and compared to the distribution of total fish caught (i.e., prevalence). Additionally, we explicitly tested the effect of body size on leech infestation using ANOVA in combination with a Tukey honest significance test. This allowed us to compare the distribution of total lengths of all parasitized fish to the distribution of total lengths of all non-parasitized fish to test for correlation between fish size class and frequency of parasitism. Tests were conducted for each icefish species, both across islands and for Elephant Island and the South Orkney Islands, individually.

We quantitatively assessed differences in leech occurrences between fish species by generating violin plots using the *vioplot* package in R (Adler 2005). These plots modify a traditional box plot by adding a rotated kernel density plot, thereby facilitating inspection of quartiles and the underlying probability distribution of the data (Hintze and Nelson 1998). We mapped distribution of leeches to specific body regions of the host, dividing the body into seven areas that included all areas leeches were encountered: dorsal surface of the head; lateral surfaces of the head; ventral surface of the head; inside of upper jaw; inside of lower jaw; ventral region of the body; and the pelvic fins. Although some Antarctic leech species are described as occurring on the gills of Antarctic fishes, no leeches recorded in this study were found on gills and therefore this region was not included in our division of host bodies.

To account for the potential impact of small sample sizes on the qualitative interpretation of patterns related to leech infestation, a number of simulations were performed to

test whether measures of infestation differed significantly from what might be expected based on random sampling alone. We investigated whether host fish species predicts relative proportion of leech species infestation. For this test, we simulated a dataset of 1000 individuals for each species of host fish, and each individual was randomly assigned to host one of the three species of leech. From this simulated dataset, we randomly sampled a subset of individuals, with subsample size mirroring the empirical sample sizes for each fish species in this study. Sampling was repeated 5000 times for each subsample size. For each host fish species, we then compared the simulated distribution of each leech species' percent frequencies to the empirically calculated relative frequencies of each leech species observed on each fish species to assess significance.

We also investigated whether particular leech species preferentially infest specific body regions on their host fish. To evaluate this, the host body was divided into discrete areas on which leeches were observed. We simulated a dataset of equal numbers (1000) of each host fish species collected for each of two focal leech species: (1) *T. capitatus* and (2) *T. bacilliformis*. To each of the individuals from each host fish species, we randomly assigned one of the seven body regions in which a leech was observed. From this simulated dataset, we randomly sampled a subset of individuals, with subsample size mirroring the empirical sample sizes for each fish species in this study. Sampling was repeated 5000 times for each subsample size. For each of the two focal leech species, we then compared the simulated distributions of infestations across body regions to the empirically calculated relative proportion of infestation to assess significance. All simulations were conducted in R.

Comparing estimates of fish and leech biomass

We tested whether leech abundance was correlated with fish abundance or biomass using two approaches. First, we tested if fish abundance predicted leech abundances in our samples using a simple linear regression model. We used the “linear model” (*lm*) function in R to calculate the correlation between the number of parasitized fish and the total number of fish collected at each station across both Elephant Island and the South Orkney Islands. This analysis was performed independently for each host fish species. Second, we estimated total standing biomass for each host fish and *T. bacilliformis* and *T. capitatus* over the total shelf area (50–500 m) of Elephant Island and the South Orkney Islands. For each haul, total count of individual leech specimens present for all finfish combined was summed and standardized to one square nautical mile of area swept using the average trawl mouth width and bottom distance covered at each station. Estimates of standing stock biomass were computed using a

Delta-lognormal maximum likelihood approach (Pennington 1985; De la Mare 1994), with overall biomass B as

$$B = \sum_{j=1}^k d_j A_j^2 \quad (1)$$

where the biomass is a product of the mean density of the sampling strata j and the area A_j of that strata. Similarly, the variance of the biomass estimates is given by

$$\hat{\sigma}_B^2 = \sum_{j=1}^k \hat{\sigma}_j^2 A_j^2 \quad (2)$$

where the variance of B is a product of the variance of the density of the sampling strata j and the strata area squared. Seabed areas for the Elephant Island shelf (50–500 m) were taken from Jones et al. (1999) and for the South Orkney Islands from Jones (2000). The above equations were again used to estimate fish biomass. This approach allowed us to both visualize areas of high leech or fish biomass, and incorporate trawl parameters into expectations of biomass when repeating the statistical tests outlined above.

Results

Patterns of host and site specificity

Out of all 1461 icefish specimens examined, we encountered 89 individuals with leech infestations, yielding a combined prevalence of 6.1%. Across both Elephant Island and the South Orkney Islands, we encountered 426 leeches on a total of 89 individual fish: 30 individuals of *C. aceratus*, 43 individuals of *C. gunnari*, and 16 individuals of *C. rastrospinosus*. Based on this pooled sampling of individuals from the two regions, we calculated the relative proportion of infestation (RPI) of all three leech species (*T. capititis*, *T. bacilliformis*, and *N. sawyeri*) that parasitized each host fish species (Table 2). These proportions are suggestive of patterns of a degree of host–parasite specificity across the Elephant and South Orkney islands, with *T. bacilliformis* appearing to preferentially infest *C. gunnari* (71% RPI; Table 2) and *T. capititis* appearing to preferentially infest *C. aceratus* (54%

RPI; Table 2). The results of our simulations demonstrate that for *C. aceratus*, the RPI by *T. capititis* is higher than would be expected under an assumption of random assortment (Online Resource 1 Fig. 1; RPI=0.54, $p=0.0084$). The same is true of the empirical RPI of *C. gunnari* by *T. bacilliformis* (Online Resource 1 Fig. 1, RPI=0.71, $p=0.000$), and the empirical RPI of *C. rastrospinosus* by *N. sawyeri* (Online Resource 1 Fig. 1; RPI=0.8, $p=0.000$).

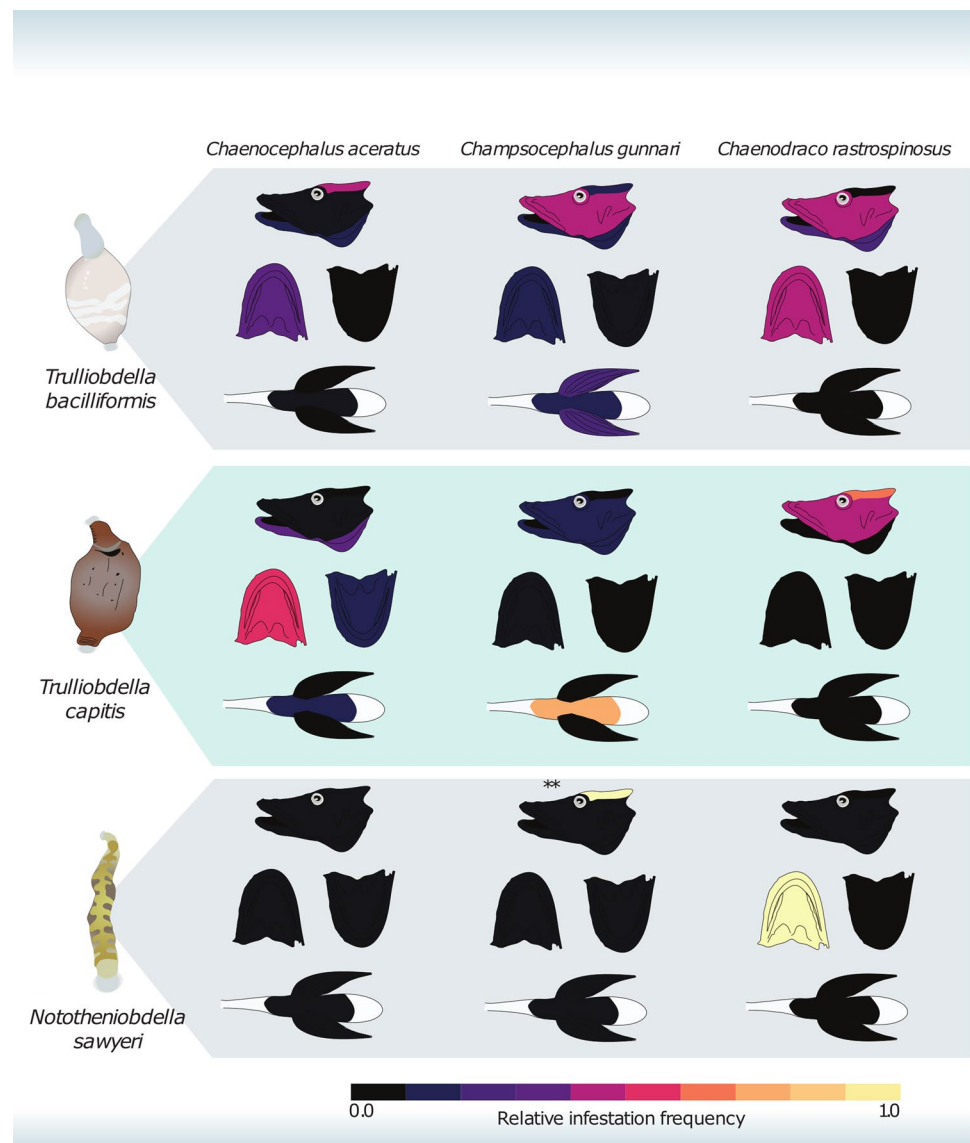
Quantifying the distribution of leeches on host fish additionally suggests site specificity of leech species on particular host fish species (Fig. 1). Our results demonstrate that the species *T. capititis* most frequently infests *C. aceratus* on the upper inner jaw [Relative infestation frequency (RFI)=0.52; Fig. 1], while on *C. gunnari*, it is most commonly encountered between the pelvic fins (RFI=0.8333; Fig. 1) and, on *C. rastrospinosus*, occurs most frequently on the dorsal surface of the head (RFI=0.6087; Fig. 1). *Trulliobdella bacilliformis* appears to preferentially infest the dorsal surface of the head on *C. aceratus* (RFI=0.667; Fig. 1), but on *C. gunnari* it is found predominantly on the lateral surfaces of the head (RFI=0.3898; Fig. 1). Simulation results demonstrate that for both *T. capititis* and *T. bacilliformis*, these empirical infestation frequencies on particular body regions of host fish species are higher than the frequencies that might be expected under an assumption of random assortment (Fig. 1 and Online Resource 1 Fig. 1).

There were only seven observations of *T. bacilliformis* on *C. rastrospinosus*, with 2 observations each on the lateral surfaces of the head, on the inner region of the lower jaw, and on the inner region of the upper jaw, but the empirical RFI values of these infestation parameters did not differ significantly from expectations of random assortment (Online Resource 1 Fig. 1). From our sample, we also observed five individuals of *C. gunnari* and two individuals of *C. aceratus* from the South Orkney Islands that were parasitized by both *T. capititis* and *T. bacilliformis* simultaneously (Online Resource 1 Table 1). On two individuals of *C. gunnari*, members of the two leech species were found together in the same body region (between the pelvic fins on one individual and on the dorsal surface of the head in the other), but on all other individuals parasitized by both species, members of

Table 2 Relative proportion of infestation of each leech species per host fish species across pooled samples from Elephant Island and the South Orkney Islands. Greatest relative proportion of each leech species is bolded

Fish species	Relative proportion of <i>Trulliobdella bacilliformis</i> (%)	Relative proportion of <i>Trulliobdella capititis</i> (%)	Relative proportion of <i>Nototheniobdella sawyeri</i> (%)
<i>Chaenocephalus aceratus</i>	22	54	0
<i>Champscephalus gunnari</i>	71	24	20
<i>Chionodraco rastrospinosus</i>	7	22	80

Fig. 1 Relative infestation frequency of the Antarctic fish leech species *Trulliobdella bacilliformis* (top); *Trulliobdella capitis* (middle); and *Nototheniobdella sawyeri* (bottom) on three species of crocodile icefishes. Brightness indicates relative frequency of infestation on body surfaces (dorsal, lateral, and ventral surfaces of the head; upper jaw; lower jaw; ventral surface of body between pelvic fins; and pelvic fins). ** Indicates single *N. sawyeri* found inside the braincase of a single *Champsocephalus gunnari*. Fish illustrations modified from public domain images with Creative Commons Licenses



the two leech species were each found segregated on different body regions (Online Resource 1 Table 2).

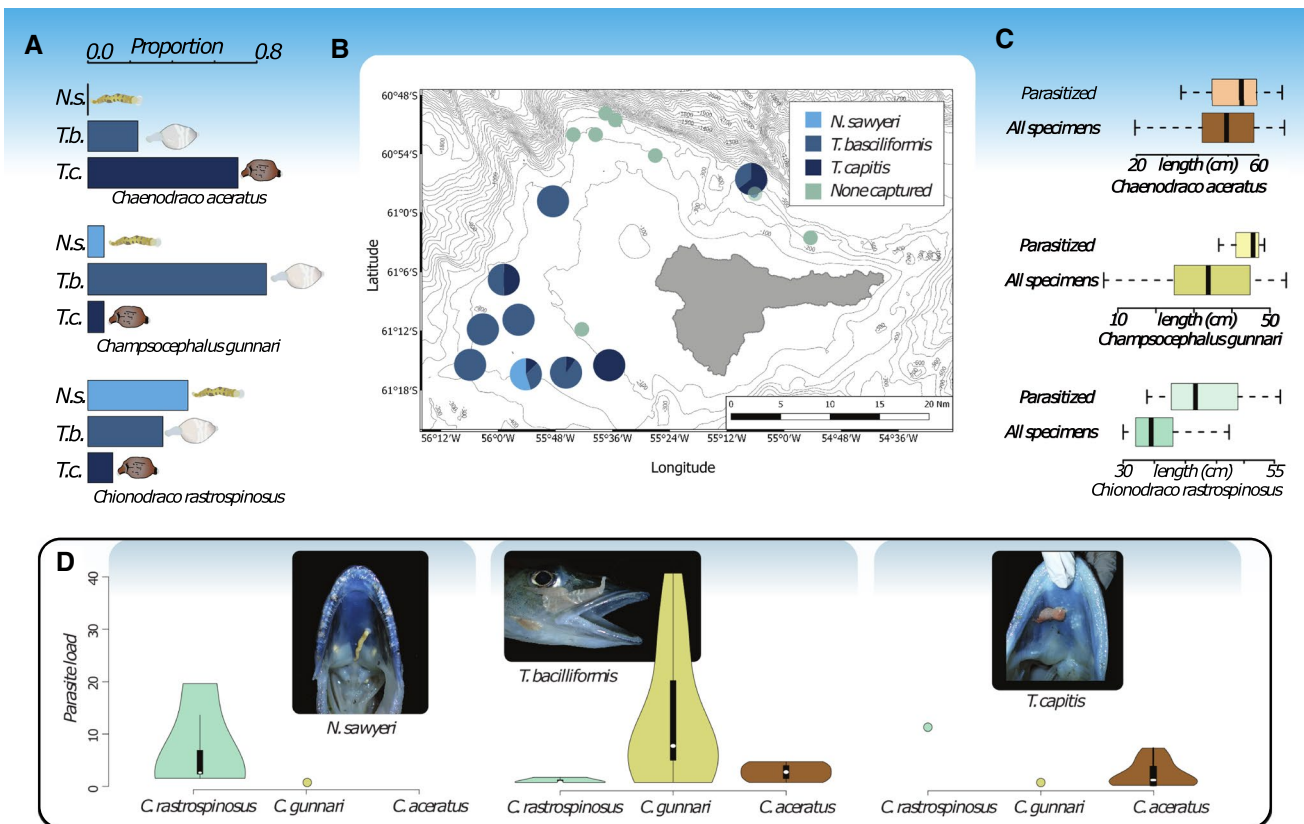
Patterns of infestation across Elephant Island

Across all Elephant Island stations, we inspected a total of 68 *C. aceratus*, 709 *C. gunnari*, and 13 *C. rastrospinosus* for the presence of leeches, generally finding relatively low prevalence of leech infestations (Table 3). For infested individuals, each fish species had a unique dominant leech; *T. capitis* was the commonly encountered leech on *C. aceratus* (75%) while *T. bacilliformis* was the most common leech on *C. gunnari* (87.5%). *Chionodraco rastrospinosus* was infested primarily by *N. sawyeri* (50%) (Fig. 2a and Online Resource 1 Table 3). Infested individuals displayed a heterogeneous spatial distribution, with most leeches found to the southwest of the Island (Fig. 2b).

Leech density was not correlated with fish abundance for the icefish hosts *C. aceratus* and *C. gunnari* across stations, although there was a significant correlation between abundance of parasitized fish and total abundance of fish for *C. rastrospinosus* (Table 4). Despite spatial heterogeneity, there was a clear trend of leeches preferentially infesting only larger adult fishes of all three species [*C. aceratus*: $R = 67\text{--}43$ cm total length (TL), $p = 0.067$; *C. gunnari*: $R = 49\text{--}34$ cm TL, $p = 0.000$; *C. rastrospinosus*: $R = 56\text{--}34$ cm TL, $p = 0.002$; Fig. 2c). Infestation intensity varied by leech species and host fish species. In *C. gunnari*, *T. bacilliformis* infestations ranged from few individuals to upwards of 20, with a remarkable individual covered by more than 40 leeches. In contrast, *T. capitis* always occurred in comparatively low (< 10 individuals) intensities (Fig. 2d).

Table 3 Prevalence of infestation of each leech species on each host fish species in the vicinity of Elephant Island and the South Orkney Islands

Species	Elephant Island			South Orkneys		
	<i>Trulliobdella bacilliformis</i>	<i>Trulliobdella capititis</i>	<i>Nototheniobdella sawyeri</i>	<i>Trulliobdella bacilliformis</i>	<i>Trulliobdella capititis</i>	<i>Nototheniobdella sawyeri</i>
	Number infested/ total catch (% prevalence)	Number infested/ total catch (% prevalence)	Number infested/ total catch (% prevalence)	Number infested/ total catch (% prevalence)	Number infested/ total catch (% prevalence)	Number infested/ total catch (% prevalence)
<i>Chaenocephalus aceratus</i>	4/68 (5.88%)	12/68 (17.65%)	0/68 (0%)	8/234 (3.42%)	8/234 (3.42%)	0/234 (0%)
<i>Champocephalus gunnari</i>	14/709 (1.97%)	1/709 (0.14%)	1/709 (0.14%)	25/333 (7.51%)	8/333 (2.40%)	0/333 (0%)
<i>Chionodraco rastrospinosus</i>	3/13 (23.08%)	1/13 (7.69%)	4/13 (30.77%)	1/104 (0.96%)	7/104 (6.73%)	0/104 (0%)

**Fig. 2** Summary of Antarctic fish leech infestation parameters around Elephant Island. **a** Relative proportions of leech taxa found across species of crocodile icefish. **b** Map of stations with pie charts indicating frequencies of leech species found per station. Shadings correspond to leech species. **c** Comparison of body size (TL) frequen-

cies of total parasitized individuals to all crocodile icefishes captured. **d** Violin plots depicting the infestation intensities by leech species. Embedded boxplots represent the quartiles of the parasite intensities per host–parasite species pair

Patterns of infestation across the South Orkney Islands

Across the South Orkney Island stations, we inspected a total of 234 *C. aceratus*, 333 *C. gunnari*, and 104 *C. rastrospinosus* for the presence of leeches, and again we observed

relatively low prevalence of leech infestations (Table 3). In the South Orkneys, only *T. capititis* and *T. bacilliformis* were encountered on all three fish species. *Trulliobdella capititis* and *T. bacilliformis* were encountered with equal frequency on *C. aceratus* (50% each). Similar to patterns observed at Elephant Island, *T. bacilliformis* was the most common

Table 4 Results of tests for correlation between abundance of parasitized fish and total abundance of fish for each species across stations (at both Elephant Island and South Orkney Islands). Bolded *p* values indicate statistically significant correlations ($p < 0.05$)

Species	Adjusted R^2	<i>F</i> -statistic	<i>t</i> value	<i>p</i> value
<i>Chaenocephalus aceratus</i>	-0.02431	0.07424	-0.272	0.7867
<i>Champocephalus gunnari</i>	0.001808	1.071	1.035	0.3073
<i>Chionodraco rastrospinosus</i>	0.2409	13.38	3.657	0.000769

leech on *C. gunnari* (75.8%) (Fig. 3a). Infested individuals again displayed a heterogeneous spatial distribution, with few leeches found in the eastern portions of the Islands (Fig. 3b). Despite spatial heterogeneity, there was a clear trend of leeches preferentially infesting only larger fishes for all three species (*C. aceratus*: $R=64-38$ cm TL, $p=0.018$; *C. gunnari*: $R=52-32$ cm TL, $p=0.002$; *C. rastrospinosus*:

$R=42-32$ cm TL, $p=0.239$; Fig. 3c). Parasite intensities varied by leech species and host fish species. In *C. aceratus* and *C. gunnari*, *T. bacilliformis* infestations ranged from few individuals up to 14, while only one *T. bacilliformis* individual was observed on a single *C. rastrospinosus*. *Trulliobdella capitis* always occurred in low intensities (< 5 individuals) on individual fish across all species (Fig. 3d).

Discussion

Patterns of host–parasite specificity have been commonly observed in marine ecosystems (Adamson and Cairra 1994; Whittington et al. 2000; Muñoz and Cortés 2009); however, our results coupled with prior investigations suggest that the Southern Ocean leech species in this study may be better characterized as opportunistic parasites that can utilize a range of host species. While all leech–host pairs demonstrated a preference for large-bodied hosts, we did observe asymmetric patterns of parasitism. *Trulliobdella capitis* was

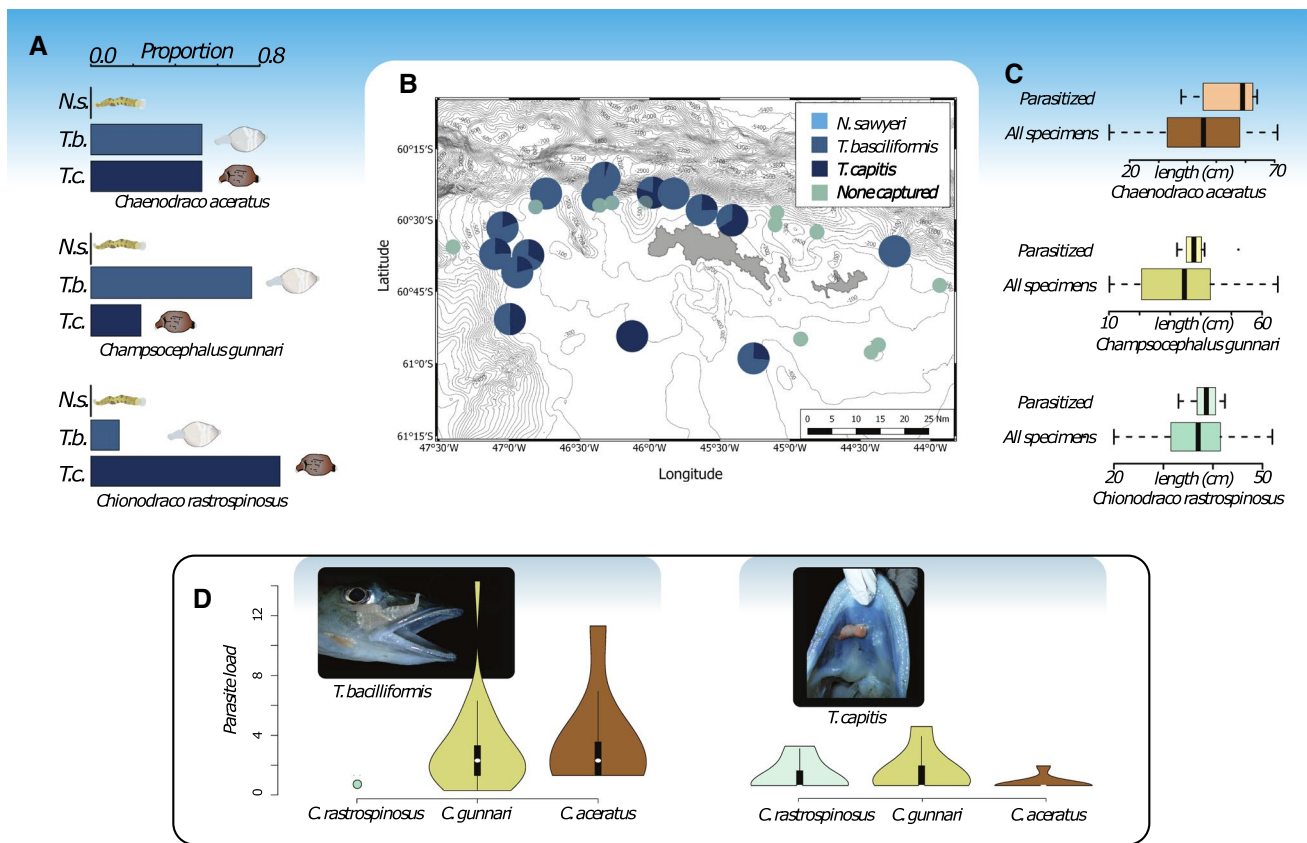


Fig. 3 Summary of Antarctic fish leech infestation parameters around the South Orkney Islands. **a** Relative proportions of leech taxa found across species of crocodile icefish. **b** Map of stations with pie charts indicating frequencies of leech species found per station. Shadings correspond to leech species. **c** Comparison of body size (TL) fre-

quencies of total parasitized fish to all crocodile icefishes captured. **d** Violin plots depicting the infestation intensities by leech species. Embedded boxplots represent the quartiles of the parasite intensities per host–parasite species pair

observed in relatively high intensities on the host *C. aceratus*, *T. bacilliformis* was encountered in high intensities on *C. gunnari*, and *N. sawyeri* was observed in high intensity on *C. rastrospinosus*. Our results further revealed non-random patterns of infestation sites on host bodies. Across all host and parasite species studied, these attachment sites appear restricted to regions of host fishes that exhibit the highest levels of vascularization and thinnest skin. However, attachment site fidelity varied between host–parasite species pairs. This variation suggests two additional drivers of leech parasitism. First, our findings suggest the potential for different leech species to be dominant at different habitats along the benthopelagic axis of the water column, yet utilize host fish to passively migrate between habitats, and thereby opportunistically encounter additional potential notothenioid hosts. Second, the occurrence of leeches inside the jaws of fish predators suggests the possibility that leeches are passively co-opting the food web to utilize smaller hosts as transmission vectors to reach larger piscivorous icefishes, a behavior that has been previously described from other parasite taxa (Richardson and Abdo 2011; Rauque et al. 2002). In total, our findings offer critically needed baseline data for Antarctic fish leech ecology and offer a wide range of novel hypotheses that can be tested as more data on these fascinating organisms becomes available.

Host preference in Antarctic leeches?

Previous work has suggested other species of piscicolids to go through boom and bust cycles of population growth, and therefore that parasite infestation prevalence may not be correlated with host abundance (Sawyer and Hammond 1973). This hypothesis provides a possible explanation for the results of our study, which demonstrate that leech infestation intensity in Elephant and the South Orkney Islands is not correlated with host fish abundance (Table 4; Online Resource 1 Tables 4 and 5). Instead, leech abundance at each island tends to be partitioned between host species. This raises the question of how differences between host fish species in terms of habitat and resource use can limit opportunities for between-host transmission that can ultimately promote the evolution of both host-switching and parasite host specificity (Poulin 1992). For example, *C. gunnari* undergoes diel vertical migrations to forage primarily in the water column from close to or in benthic habitats (Kock and Everson 1997). Occurrences of *T. bacilliformis* have been observed on eight other notothenioid species known to feed in the water column, including *Lepidonotothen larseni* (Lönnerberg 1905), *Pseudochaenichthys georgianus* Norman 1937, and *Channichthys rhinoceratus* Richardson 1844 (Table 1), suggesting this leech species to be a common parasite for pelagic Antarctic fishes (Utevsky 2007). The occurrence of *T. bacilliformis* infestations on pelagic

notothenioids suggests diel vertical migrations expose *C. gunnari* to *T. bacilliformis* at a higher frequency than benthic species. Additionally, *C. gunnari* is also commonly infested by *T. capitata* along the ventral surface of the body, largely between the pelvic fins. *Trulliobdella capitata* has been found on a mixture of pelagic and benthic notothenioids (Table 1), however, there is not enough data available to determine if these leeches are encountered in benthic habitats during vertical migrations of fish hosts, or if these are water column generalists. Given the predominantly ventral attachment, we favor the former hypothesis; however, more investigations are needed.

Our results demonstrate that infestation of *C. aceratus* with both species of *Trulliobdella* occurs at highest frequencies on the dorsal surface of the head and inner region of the upper jaw. Several previous studies of the diet of notothenioid fishes have shown that *C. gunnari* is commonly eaten by *C. aceratus* (Flores et al. 2004), in some cases representing the greatest proportion of the prey items observed in stomach content analysis (Reid et al. 2007). This suggests that predation on *C. gunnari* by *C. aceratus* provides both species of *Trulliobdella* with a transmission pathway to an alternate host. Such a hypothesis would be consistent with the high frequency of parasites found inside the upper jaw of this piscivore. This mode of transmission is unusual, as parasite transmission through food webs is often associated with parasites co-opting intermediate hosts as transmission vectors to definitive hosts when the density of the latter is lower than the former (Choisy et al. 2003). However, this is unlikely to be the case here. While the inclusion of intermediate hosts is common for a wide range of both terrestrial and aquatic parasites with complex life cycles (Brown et al. 2001; Iglesias-Piñeiro et al. 2016; Dornburg et al. 2019), all leeches have a direct life cycle. Further, post-cyclic transmission has been documented in other parasites (Richardson and Abdo 2011; Rauque et al. 2002; Kennedy 1999), and our findings further raise the possibility of such a phenomenon in some species of fish leeches. Although it is possible that benthic predators act as aggregators and potential mating sites of both *Trulliobdella* species, this is unlikely as platybelline leeches cannot swim (Sawyer 1986). It is therefore more likely that *Trulliobdella* species can opportunistically expand their host range. Our finding of *T. bacilliformis* on *C. rastrospinosus* suggests the additional potential for opportunistic host colonization. *Chionodraco rastrospinosus* feeds primarily on krill (*Euphausia superba* Dana 1850), with other fish representing a very small percentage of their diet (Takahashi 1983), making transmission of *T. bacilliformis* by predation less likely.

In addition to host selection, apparent site fidelity of leech species to particular body regions on their fish hosts represents an additional axis of leech ecology that has received little attention in the literature. The results of our study

demonstrate that each leech species preferentially infests different body regions on different host fish species. This pattern was not random, and portions of the host body that exhibit low levels of vascularization and increased skin thickness were conspicuously absent from the list of infested locations. Skin thickness has previously been invoked as an explanation for attachment site choice in leeches that parasitize salamanders, as thinner skin provides easier access to a host's vascular network (Pough 1971; Phillips et al. 2010). Additionally, areas of the host body with dense and shallow vascular networks should be preferred as these would naturally represent the highest ratio of energy return for investment in foraging effort for sanguivorous feeders. Our results fit both of these criteria. Skin in some species of notothenioids has been found to be thinner in the cranium relative to the post-cranium, with skin in the oral cavity being particularly thin (Eastman and Hikida 1991). Correspondingly, the cranium is also highly vascularized relative to the trunk (Eastman and Hikida 1991; Egginton and Rankin 1998), with an additional array of blood vessels providing blood to the pelvic fins (Eastman and Hikida 1991), possibly to keep the fins extended during perching.

The hypothesis that skin thickness and density of the underlying vascular network drive patterns of site attachment is also supported by prior studies documenting areas of leech infestation on crocodile icefishes (Brinkmann 1948; Bielecki et al. 2008; Santoro et al. 2014; Table 1), all of which reported predominantly external areas of the cranium as attachment sites. While leech attachments are temporary, we found high levels of scarring indicative of prior leech attachment on the surfaces of the cranium in numerous individuals (Fig. 4). This provides evidence that the same surfaces are repeatedly used as feeding sites during the lifespan of individual fishes. Previous studies have also included the gill cavity as an attachment point; however, despite investigation of 1461 individual fishes, we

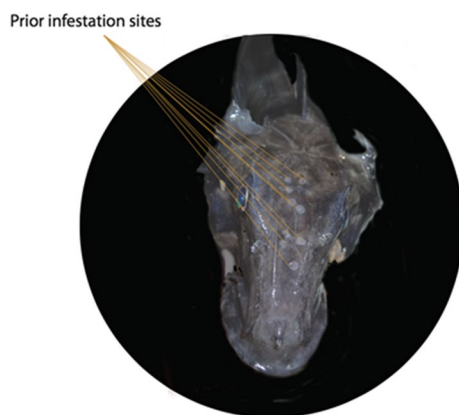


Fig. 4 Example of scarring from prior leech infestations on an icefish encountered during the course of this study

did not observe leeches on the gills or in the gill cavity of any host species. However, additional findings of leeches on gills or in the gill cavity would only further support vascularization and skin thickness of attachment sites to be a limiting factor in the attachment ability of Antarctic marine leeches.

Additionally, our results show that when leeches do occur on the same host, they may be partitioning attachment points in a manner analogous to sympatric species partitioning a landscape (Holmes 1961; Ramasamy et al. 1985; Fuselier and Edds 1994; Arlettaz 1999; Poulin 2001; Humphries et al. 2016). This is especially evident in two *C. aceratus* and five *C. gunnari* individuals that were parasitized by both *T. capitatus* and *T. bacilliformis*. In only two individuals of *C. gunnari* were the two leech species found to have infected the same body region (between the pelvic fins on one individual and on the dorsal surface of the head on the other individual). Otherwise, whether or not they are observed on the same individual host fish, leech species occupy different body regions of their host, suggesting that leech species may prefer to infest particular body regions. This preference may be a result of variation in host vascularization and skin thickness and how this relates to the ability of the leech to attach to particular body regions or be indicative of competitive interactions (Bashey 2015). However, the low prevalence of leech infestations renders sample sizes too small for further testing expectations of competitive interactions.

Conclusion

Understanding the relationship between hosts and parasites represents an important, but often neglected, axis when considering forecasts of marine biodiversity under the looming threat of continued environmental change and increased anthropogenic impacts. Our results provide new baseline data into the ecology and interactions of three species of Antarctic piscicolids with their host fish species. We show these parasites to be highly clustered spatially, but not in a manner that correlates with fish abundance. Instead, we demonstrate low levels of infestation, with high levels of fidelity to select host attachment areas, as well as the potential for trophic, post-cyclic, transmission between host species. These results reveal an under-appreciated complexity of interactions between this community of hosts and parasites and offer exciting avenues of further investigations that can illuminate the factors that underlie the abundance and persistence of Antarctic leech parasites. Such studies not only have the potential to further our understanding of host–parasite evolution, but also to provide essential context for understanding future changes of Antarctic host–parasite interactions.

Acknowledgements We thank the captain and crew of the R/V Cabo de Hornos for their excellent company and assistance during the course of this fieldwork and also thank Deris S.A. for providing the ship to carry out the work at sea, and Mr. Enrique Gutiérrez F., general manager of said company, for his permanent support in materializing these tasks. We would additionally like to thank Dieter Piepenburg, Florian Reyda, Aleksander Bielecki, Mario La Mesa, and two anonymous reviewers for providing helpful comments and suggestions on earlier versions of this manuscript. We are particularly grateful for the hypothesis proposed by one of the anonymous reviewers that skin thickness and vascularization are driving the site attachment patterns we observed.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Ethical approval The authors have followed all applicable national and institutional guidelines for the collection, care, and ethical use of research organisms and material in the conduct of the research, in strict accordance with NOAA Antarctic Ecosystem Research Division policies under ACA Permit #2017-012. Animal collection was approved by the Yale University Institutional Animal Care and Use Committee (Protocol 10681) and adheres to the AFS guidelines for Use of Fishes in Research (<https://fisheries.org/docs/wp/Guidelines-for-Use-of-Fishes.s.pdf>).

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