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ORIGINAL PAPER

Endoparasite communities of New Zealand Penguins differ over time and among species

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Abstract
Parasites can provide valuable insights into the ecology and health of their hosts and the state of the surrounding ecosystem. In this study, we describe the helminth parasite communities infecting penguin species in Otago, New Zealand (little blue penguin, Fiordland crested penguin, Snares crested penguin, erect crested penguin and yellow-eyed penguin). We investigate differences in parasite communities among penguin species, and changes over time for little blue penguins. In total, 19 parasite species representing 8 families (Desmidocercidae, Anisakidae, Acuariidae, Capillariidae, Tetrabothriidae, Heterophyidae, Renicolidae and Polymorphidae) were recorded from 121 penguin individuals. Parasite assemblages differed among penguin species, likely reflective of their differences in diet and feeding strategies. We also observed significant changes in the composition of parasite communities of little blue penguins using samples from a 30-year timespan (1993–2023). There was an overall increase in parasite diversity over time, including some species of potential disease concern, which could reflect a shift in prey availability of fish in the area. Our findings contribute to the understanding of penguin ecology and emphasise the use of parasites as indicators of ecological change.

Keywords Penguin · Endoparasite · Community · Nematoda · Cestoda · Acanthocephala, *Renicola*

Introduction

Parasitic helminths are primarily known for their negative impacts on host health. However, they are increasingly recognized for their potential to provide insights into the structure, state, and stability of their surrounding ecosystems (Marcogliese 2005; Vidal-Martínez et al. 2010; Palm 2011; Gagne et al. 2022). For instance, parasites have been utilized as biomarkers of host population connectivity (Morales-Serna et al. 2024), environmental pollutant levels (Sures 2004) and as indicators of species presence within the surrounding community (Mastick et al. 2024).

Parasites provide insights into the feeding behaviour and ecology of their hosts (Santoro et al. 2012). Hosts typically become infected with endoparasites by consuming infected prey items. This means that the presence, abundance and diversity of most endoparasites is a consequence of specific prey species being consumed and reflects the relative contribution of different prey types or diet breadth of that host (Valtonen et al. 2010; Locke et al. 2014). For wildlife where basic dietary information is lacking, parasite data can therefore fill knowledge gaps for host species, especially in marine environments where direct observations are not always possible. Beyond the single host individual or species level, differences among parasite communities between multiple host individuals or species can also be explained

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by differential feeding habits among hosts (Leung and Koprivnikar 2016, 2019).

In the context of climate change, shifts in prey availability due to natural and anthropogenic pressures may be reflected in changes in parasite species and communities (Wood et al. 2010, 2014; Wood, Welicky, Wood et al. 2023a, b; Mastick et al. 2024). Parasites themselves will also respond to climate pressures, with varying effects across taxa (Lafferty 2012; Poulin et al. 2024). Our ability to observe and interpret changes in parasite communities over time is limited by the availability of historic records and natural history collections (Wood et al. 2010). The growing field of historic parasitology uses historic collections and more recent samples to assess changes in parasites and diseases over time (Harmon et al. 2019; Wood, Leslie, Wood et al. 2023a, b). Researchers are increasingly recognizing parasites as valuable tools for monitoring ecological communities over time (Wood and Vanhove 2023).

Penguins are among the world's most vulnerable bird groups, with almost half of penguin species listed as either Vulnerable or Endangered according to the International Union for the Conservation of Nature (IUCN) (HBW and BirdLife International 2024). A range of threats, from overfishing, fisheries bycatch, climate change, pollution, colony disturbance and disease are contributing to their decline (Trathan et al. 2015; Jaeger et al. 2018; Dias et al. 2019). Of the 19 species worldwide, 13 have been known to frequent New Zealand (NZ), nine species of which breed in the region (this includes the Ross Dependency governed by New Zealand). On NZ mainland, four species breed: yellow-eyed penguin/hoiho (YEP) *Megadyptes antipodes* (Hombron & Jacquinot, 1841), Fiordland crested penguin/tawaki (FCP) *Eudyptes pachyrhynchus* Gray, 1845, little blue penguins/kororā (LBP) *Eudyptula minor* (Forster, 1781) (NZ species) and *E. novaehollandiae* (Stephens, 1826) (Australian species, also found in the Otago region of New Zealand, (Grosser et al. 2015). Snares crested penguin/pokotiwha (SCP) *Eudyptes robustus* Oliver, 1953 and erect crested penguin/tawaki nana hī (ECP) *Eudyptes sclateri* Buller, 1888 are occasionally found on the mainland, but breed exclusively on the sub-Antarctic Islands. All of these species are at-risk of extinction according to the NZ Threat Classification System, apart from yellow-eyed penguin which is nationally endangered with fewer than 4000 individuals estimated to remain for the whole species (Robertson et al. 2021). Under the International Union for the Conservation of Nature (IUCN), yellow-eyed and erect crested are both classified as Endangered with decreasing population trends, Snares crested are listed as Vulnerable, Fiordland crested as Near Threatened, and little blue as Least Concern (note that the recent split in species *E. minor* and *E. novaehollandiae* has not yet been recognised (Grosser et al. 2015; IUCN 2024)).

Except for an investigation of parasite assemblages infecting little blue penguins (Bennett et al. 2021), and a few individual host-parasite reports in the literature (Crockett and Kearns 1975; Weekes 1982; Ranum and Wharton 1996; Hocken 2000; McKenna 2006, 2009; Presswell et al. 2018; Presswell and Bennett 2025), data are sparse on endoparasites infecting penguins in NZ, particularly at a community level. Currently, no records exist of helminth parasites of erect crested penguins, one species is documented for Snares crested, two from Fiordland crested, four from yellow-eyed, and 19 from little blue penguins (Fusaro et al. 2025). It is important to obtain baseline data on parasite infections in NZ penguins to understand the potential impacts of parasites on these birds, especially given the conservation concern for many species. Investigating parasite communities within and among penguin species may also provide insights into their ecological interactions, such as feeding habits, or prey availability. It is often difficult to determine if parasitic helminths are causative agents in wildlife mortality events, or what sub-lethal impacts they have on their host health. However, they can be implicated with mortality, especially when a host is already immunocompromised, stressed or co-infected with other symbionts (Bordes and Morand 2011; Shanebeck and Lagrue 2020; Shanebeck et al. 2022).

This study has three aims; (1) describe parasite communities infecting penguin species in NZ, (2) investigate differences in parasite communities among penguin species, and (3) investigate changes in parasite communities of little blue penguins over time, using samples from the past 30 years. The results are presented within the context of ecological insights that can be derived from examining parasite communities both within and across host species.

Materials and methods

Host and parasite sampling

Between 2018 and 2024, the Evolutionary and Ecological Parasitology Research Group at the University of Otago, New Zealand, have been involved in a multi-agency disease investigation pipeline aimed at creating baseline datasets of parasite infections in New Zealand's bird species. During this period, we obtained 121 penguin individuals representing five species: yellow-eyed (N= 26), little blue (N= 69), Fiordland crested (N= 17), erect crested (N= 5) and Snares crested (N= 4). Time of death spanned from 1993 to 2023 and birds were collected from various areas along Otago's coastal marine ecosystem. These deceased specimens were

kindly donated by Otago-based agencies, including Yellow-eyed Penguin Trust, Tūhura Otago Museum, the Department of Conservation, and the Wildlife Hospital, Dunedin.

Penguin specimens were received frozen and subsequently defrosted for dissection, at which point gastrointestinal tracts, kidneys, and lungs were removed for parasitological investigation using a dissecting microscope. Helminths recovered were preserved in 70% ethanol or 10% buffered formalin for whole-mount and 90–99% ethanol for genetic analysis. Morphological and molecular identification of parasite species was to the lowest taxonomic level. Morphological keys included Khalil et al. (1994) and Anderson et al. (2009) and original or re-descriptions (Hernández-Orts et al. 2017; Presswell et al. 2018; Bennett et al. 2021; Presswell and Bennett 2021, 2025). Molecular data supported our morphological identifications to identify parasites to the lowest taxonomic level possible. For cestodes, acanthocephalans and trematodes, partial 28S gene sequences were targeted, and for nematodes, the 18S gene was used to complement morphological identifications. DNA from selected parasites was extracted using DNeasy® Blood and Tissue kit (Qiagen, Hilden, Germany) and amplified using primers T16/T30 (Harper and Saunders 2001) (for cestodes, acanthocephalans and trematodes) and Nem18SF/Nem18SR (Wood et al. 2013) (nematodes). For the 28S gene, polymerase chain reactions consisted of 94 °C for 5 min, 38 cycles of 94 °C for 30 s, 45 °C for 30 s and 72 °C for 2 min, and 72 °C for 7 min. For the 18S gene amplification, conditions included consisting of 94 °C for 5 min, 35 cycles of 94 °C for 30 s, 54 °C for 30 s and 72 °C for 1 min, and 72 °C for 10 min. All positive sequences were cleaned using EXOSAP™ Express PCR Product Cleanup Reagent (USB Corporation, Cleveland, OH, USA) and sanger sequencing by capillary electrophoresis was performed by the Genetic Analysis Service, Department of Anatomy, University of Otago (Dunedin, New Zealand). Sequences were viewed and manually edited on Geneious Prime ® v11.0.20.1. To support morphological identifications, we used BLASTn searches (https://blast.ncbi.nlm.nih.gov/) to compare percentage identity relatives on GenBank. Voucher specimens of parasites have been deposited at the Museum of New Zealand Te Papa Tongarewa under accession numbers W.003980-88.

Characterizing parasite communities infecting Penguins

To address our first aim of characterising parasite communities infecting penguin species in New Zealand, we calculated the prevalence, mean abundance and mean intensity of each parasite species per penguin species (and over different time periods) after identification to the lowest taxonomic level possible. Prevalence was defined by the percentage of hosts infected with a parasite species, mean abundance was defined as the mean number of parasites per host (including all hosts investigated, whether infected or not), and mean intensity was defined as the mean number of parasites per infected hosts (Bush et al. 1997).

To achieve our second and third aims, we used two separate datasets to compare parasite assemblages among species ('among species') and over time for little blue penguins ('over time'). For the 'among species' dataset, infected erect crested penguins were omitted due to the low sample size of infected individuals (N = 2), however raw data are presented in Table 1. For the 'over time' dataset, only little blue penguins were considered (older specimens of other penguin species were not available), and these individuals were split into three periods, based on breaks in the years when specimens were collected. The 'pre-2000' period included 5 penguin individuals, ranging from 1993–1995. The '2005–2014' period included 16 penguin individuals, and the '2019–2023' period included 19 penguin individuals. All penguin digestive tracts from older specimens were adequately preserved to recover parasites. Little blue penguin individuals that were not infected with any helminths or had no date-associated metadata were excluded from the analysis.

All data conversions and analyses described below were performed in R v4.2.3 (R Core Team 2023) using packages vegan (Oksanen 2017) and ggplot2 (Wickham 2016). We calculated Jaccard and Bray Curtis dissimilarity indices from the presence/absence and abundance data of parasite infections from both 'among species' and 'over time' data (Bray and Curtis 1957; Chao et al. 2005). To visualize differences in parasite communities among species and over time, we used multidimensional scaling plots (MDS). Each point on the MDS plots represents a single parasite community of a host individual (infracommunity). The 95% covariance confidence intervals were plotted for each species and time period to illustrate the spread of parasite communities from the average community composition per species/time period.

Testing for differences in parasite communities among species and over time

We performed permutational multivariate analysis of variance (PERMANOVA) on diversity indices, for both 'among species' and 'over time' data, to test whether the parasite community composition varied significantly among penguin species and over time (over 999 permutations). A distance-based dispersion test, PERMDISP2 (Anderson 2006) was

Table 1 Mean intensity and prevalence (in parentheses) of various endoparasite species found infecting five penguin species in Otago, New Zealand. LBP = little blue penguin, FCP = Fiordland crested penguin, SCP = Snares crested penguin, ECP = erect crested penguin, and YEP = yellow-eyed penguin. A = mature adult, I = immature adult

	LBP	FCP	SCP	ECP	YEP
N dissected (N infected)	69 (61)	17 (12)	4 (3)	5 (2)	26 (16)
Nematoda					
Family Desmidocercidae					
Diomedenema dinarctos (A)	1 (1.4%)	2.3 (35.3%)	2 (25.0%)	1 (20.0%)	1 (3.8%)
Family Anisakidae					
Contracaecum rudolphii E (A)	7.1 (31.8%)	7.6 (35.3%)	–	–	8.25 (46.2%)
Contracaecum septentrionale (A)	1 (1.4%)	–	–	–	–
Anisakis pegreffi (I)	–	3 (5.8%)	–	3 (20.0%)	–
Anisakis simplex (I)	4 (1.4%)	–	–	–	–
Family Acuariidae					
Stegophorus macronectes (A)	4 (1.4%)	1 (5.8%)	–	–	–
Seuratia shipleyi (A)	–	1.5 (23.5%)	–	–	1 (3.8%)
Family Capillariidae					
Capillariidae gen. sp. 1 (A)	2.8 (5.8%)	–	–	–	–
Cestoda					
Family Tetrabothriidae					
Tetrabothrius lutzi (A)	26.6 (46.3%)	1 (5.8%)	6 (25.0%)	–	–
Tetrabothrius sp. 2 (A)	2 (1.4%)	–	–	–	–
Tetrabothrius sp. A (A)	–	–	–	11 (20.0%)	–
Tetrabothrius sp. B (A)	20.5 (2.9%)	–	–	–	–
Tetrabothrius sp. C (A)	15.1 (11.3%)	–	–	–	–
Trematoda					
Family Heterophyidae					
Galactosomum otepotiense (A)	26 (4.3%)	–	–	–	–
Family Renicolidae					
Renicola websterae (A)	24.8 (23.2%)	24 (11.7%)	–	–	–
Renicola sp. (A)	–	1 (5.8%)	–	–	–
Acanthocephala					
Family Polymorphidae					
Andracantha sigma (A)	3 (42.0%)	–	–	–	–
Corynosoma hannae (I)	–	–	–	–	37.3 (26.9%)
Bolbosoma balaenae (I)	1 (1.4%)	–	1 (25.0%)	–	–

also performed to test for homogeneity of variances in our data among penguin species and over time. Finally, pairwise comparisons were conducted using the Adonis2 Pairwise function to identify specifically which parasite assemblages differed among penguin species and over time periods.

Results

In total, 121 penguin individuals were dissected, and intestinal tract, lungs and kidneys investigated for parasitic helminths. Of those, 78% of individuals hosted internal helminth parasites, comprising 19 parasite species in total (Table 1). Of the infected penguins, 49% were infected with one parasite species, 29% with two species, 17% with three species and 4% with four parasite species. Only one parasite species *Diomedenema dinarctos*, a lung nematode, was recovered from all five penguin species. Eleven of the 19 parasites infected only one penguin species. Little blue penguins hosted 14 parasite species, while Fiordland crested penguins hosted eight species, yellow-eyed penguins hosted four, and erect crested and Snares crested penguins hosted three each (Table 1). Tetrabothriid cestodes (genus *Tetrabothrius*) were the most prevalent parasites infecting little blue penguins (90.2% of infected little blue penguins hosted at least one species of *Tetrabothrius*), while *Contracaecum rudolphii* E was the most prevalent parasite infecting yellow-eyed penguins. *Diomedenema dinarctos* and *C. rudolphii* were equally prevalent in Fiordland crested penguins (Table 1). Different parasite species were found in high numbers among penguin species. For little blue penguins, *Tetrabothrius lutzi* and *Renicola websterae* were found at the highest intensity and mean abundance, while *R. websterae* and *C. rudolphii* E had the highest abundance within Fiordland crested penguins. For yellow-eyed penguins, infected individuals hosted a mean intensity of 37 individual acanthocephalans *Corynosoma hannae* (Table 1).

Differences in helminth assemblages among Penguin species

We identified differences in parasite community composition among four penguin species in Otago, New Zealand (Fig. 1). First, when accounting for the presence/absence of parasite species among penguins, our PERMANOVA analyses highlighted overall differences in parasite community composition ($F_{1,3}$ = 8.95, R^2= 0.11, P< 0.001). A similar significant result was found based on abundances of parasite species among penguin species ($F_{1,3}$ = 8.95, R^2= 0.23, P< 0.001). For the presence/absence data, the PERMDISP analysis was also significant, indicating the spread of assemblages within each host species varied significantly among groups (ANOVA: $F_{1,2}$ = 3.53, P= 0.03; PERMUTEST: $F_{1,2}$ = 3.79, $P_{(perm)}$= 0.02). However, when considering parasite abundances, the variability of parasite communities within each host species was consistent across host species (ANOVA: $F_{1,2}$ = 1.61, P= 0.21; PERMUTEST: $F_{1,2}$ = 1.61, $P_{(perm)}$= 0.20). Pairwise-comparisons of parasite assemblages among host species showed that parasite communities infecting yellow-eyed penguins (whether using parasite abundance or presence/absence data) were different from all other penguin species investigated (Fig. 1; Table 2). Little blue penguin and Fiordland crested penguin parasite assemblages differed significantly from each other and from yellow-eyed penguins, but not from Snares crested penguins (Fig. 1; Table 2).

Changes in parasite assemblages of little blue Penguins over time

We identified changes in parasite communities of little blue penguins over time (Figs. 2 and 3; Table 2). Our PERMANOVA analyses for both presence/absence and abundance of parasites among each of the three time periods highlighted significant differences in composition (presence/absence: $F_{1,2}$ = 8.95, R^2= 0.11, P< 0.001; abundance: $F_{1,3}$ = 8.95, R^2= 0.23, P< 0.001). Pairwise comparisons of parasite community assemblages (for both presence/absence and abundance of parasites) for each time period revealed differences among each time period pair (Table 2). The largest change observed was an increase from two parasite species (recovered from the pre-2000 time period, i.e., Capillariidae gen. sp. 1 and *Andracantha sigma*), to nine species infecting little blue penguins from the more recent

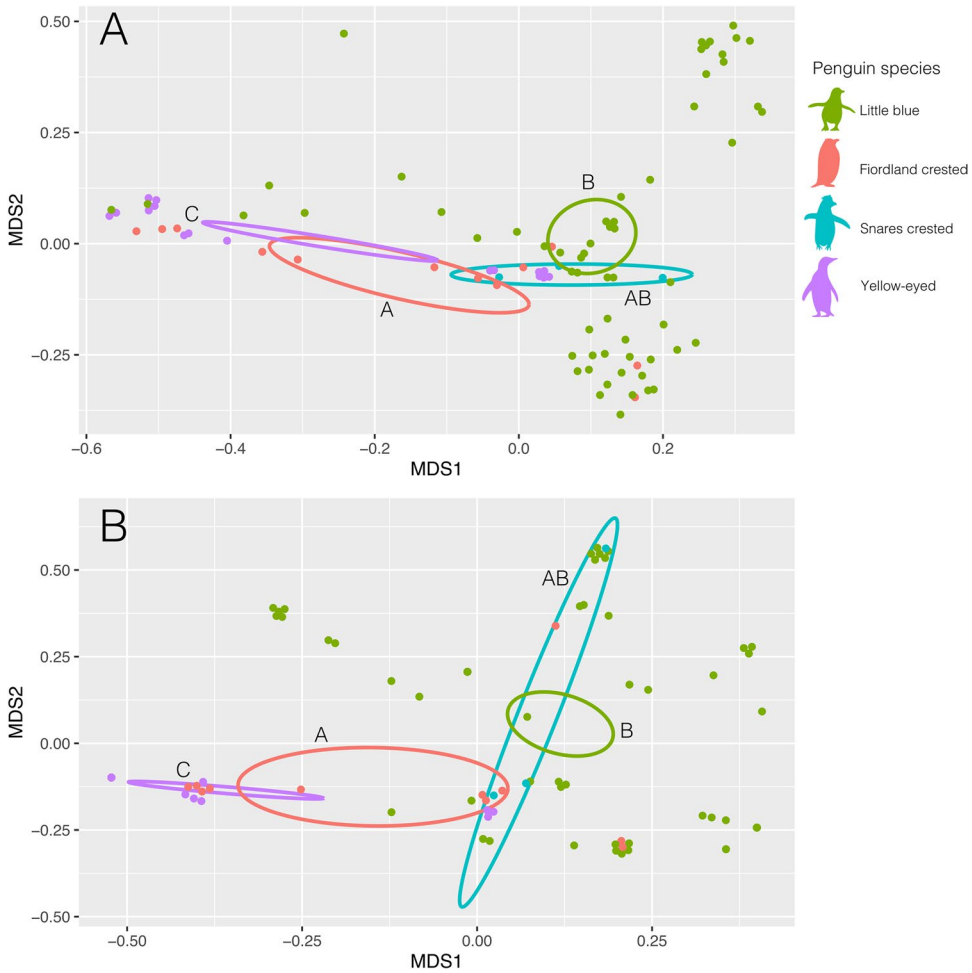

Fig. 1 Parasite communities infecting penguins (Fiordland crested, little, Snares crested and yellow-eyed) illustrated using multidimensional scaling (MDS) plots, (A) communities based on parasite presence/absence data, and (B) communities based on parasite abundance data. Each dot represents an individual host and each circle represents the 95% confidence intervals. Letters within plots denote significant differences among overall communities

Table 2 PERMANOVA Pariwise comparisons of parasite community assemblages between penguin species and over time for little blue penguins in Otago, New Zealand. FCP = Fiordland crested penguin, LBP = little blue penguin, SCP = Snares crested penguin, YEP = yellow-eyed penguin. * denotes statistical significance based on a 95% confidence interval

Pairwise comparisons	Model					
	Presence/absence			Abundance		
	F statistic	R^2	Adjusted p-value	F statistic	R^2	Adjusted p-value
Among penguin species						
FCP vs. LBP	**7.126**	**0.091**	**0.006***	**4.366**	**0.058**	**0.006***
FCP vs. SCP	1.369	0.095	1.000	1.232	0.086	1.00
FCP vs. YEP	**6.528**	**0.201**	**0.006***	**3.727**	**0.125**	**0.006***
LBP vs. SCP	1.921	0.030	0.468	1.295	0.021	1.000
LBP vs. YEP	**14.142**	**0.159**	**0.006***	**6.835**	**0.084**	**0.006***
SCP vs. YEP	**2.104**	**0.231**	**0.030***	**2.585**	**0.132**	**0.042***
LBP over time						
Pre-2000 vs. 2005–2014	**7.518**	**0.284**	**0.003***	**3.194**	**0.144**	**0.012***
Pre-2000 vs. 2019–2023	**4.505**	**0.169**	**0.006***	**3.562**	**0.139**	**0.006***
2005–2014 vs. 2019–2023	**7.409**	**0.183**	**0.003***	**4.141**	**0.112**	**0.006***

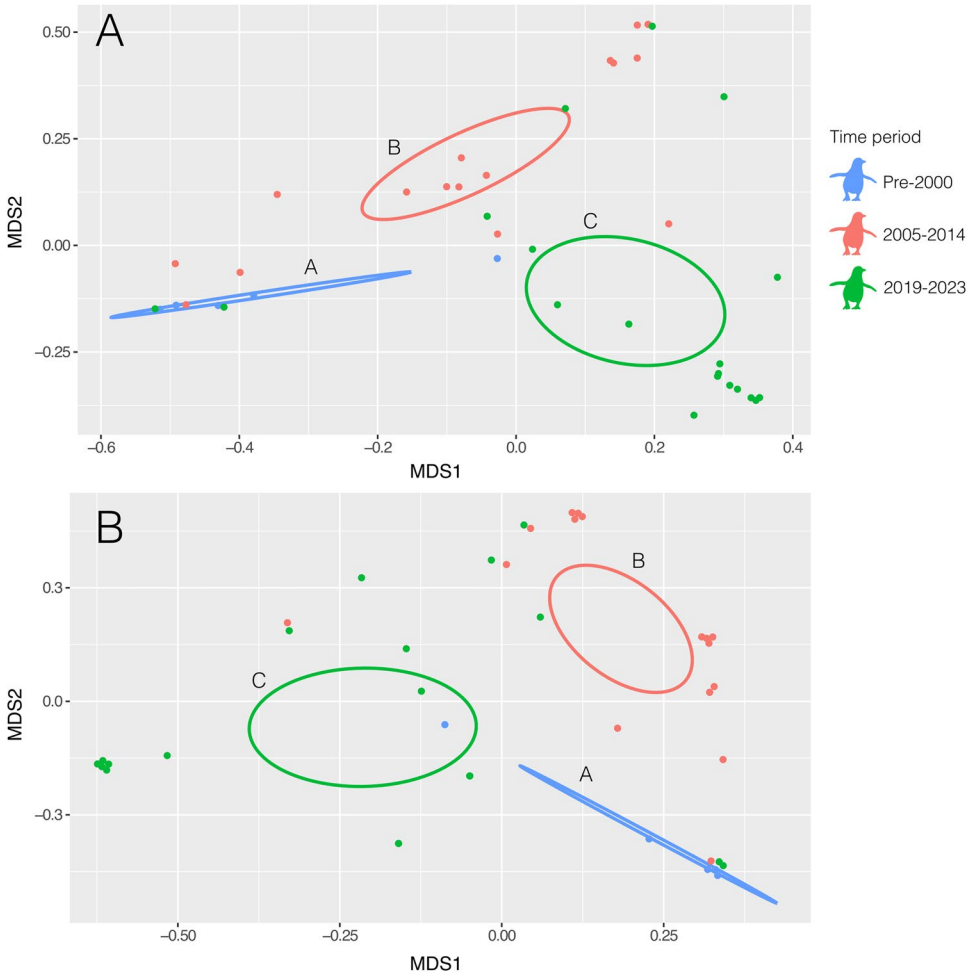

Fig. 2 Parasite communities infecting little blue penguins from three time periods (pre-2000, 2005–2014 and 2019–2023) illustrated using multidimensional scaling (MDS) plots, (**A**) communities using parasite presence/absence data, and (**B**) communities using parasite abundance. Each dot represents a host individual, and each circle represents the 95% confidence intervals. Capital letters within plots denote significant differences among overall communities

time period (Fig. 3). *Andracantha sigma* was found in the highest prevalence in the pre-2000 time period compared to 2005–2014 and 2019–2023 and was the only parasite species to occur across all time periods investigated (Fig. 3). Although cestodes within the genus *Tetrabothrius* are the most prevalent and abundant parasites infecting little blue penguins overall, none of the four species was recovered in the pre-2000 penguins. The trematode *Renicola websterae* appears to have increased in prevalence, intensity and abundance in penguins from 2005 to 2014 to 2019–2023,

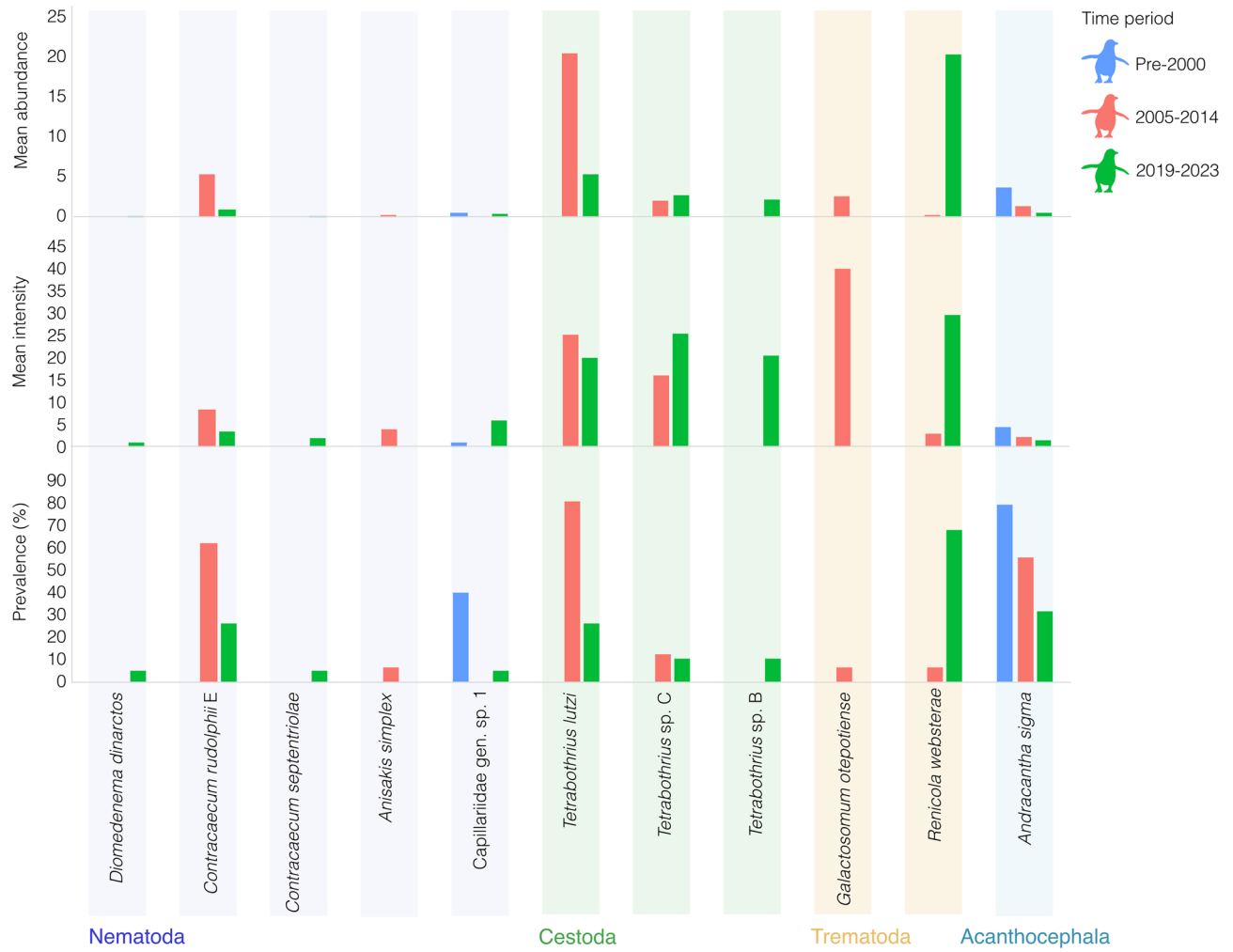

Fig. 3 Mean abundance, intensity and prevalence of parasite species infecting little penguins in Otago, New Zealand from three time periods from 1993–2023 (pre-2000, 2005–2014 and 2019–2023), grouped by parasite type

whereas the nematode *C. rudolphii* E, cestode *T. lutzi* and acanthocephalan *A. sigma* appear to have decreased over time (Fig. 3). Some parasites were recovered from only one time period, such as *Anisakis simplex* sensu lato and *Galactosomum otepotiense*, both recovered in the 2005–2014 time period only, and *D. dinarctos*, *Contracaecum septentrionale* and *Tetrabothrius* sp. B recovered only in the latter period (2019–2023). The dispersion of parasite communities (for both presence/absence and abundance data) within each time period was not significantly different (presence/absence: ANOVA: $F_{1,2} = 2.83$, $P = 0.07$; PERMUTEST: $F_{1,2} = 2.83$, $P_{(perm)} = 0.07$, abundance: ANOVA: $F_{1,2} = 2.27$, $P = 0.12$; PERMUTEST: $F_{1,2} = 2.27$, $P_{(perm)} = 0.12$).

Discussion

Parasite communities are prevalent and differed significantly among penguin species investigated in New Zealand, but the parasites recovered broadly reflect what has been found in penguins elsewhere (Brandão et al. 2014). Recent gastrointestinal investigations of penguin parasites, regardless of their distributions, tend to include some combinations of *Tetrabothrius* sp. cestodes, *Contracaecum* sp. and capillariid and acuariid nematodes (e.g. Vidal et al. 2012; Diaz et al. 2016; Vanhoni et al. 2018; Fusaro et al. 2025). Most studies also report a low diversity of gastrointestinal helminths and high prevalence of infection by at least one parasite species. For instance, gastrointestinal helminth diversity studies of Magellanic (Diaz et al. 2010; Vanhoni et al. 2018), Adélie (Diaz et al. 2016), king (Fonteneau et al. 2011), Humboldt (Fernandez et al. 2019) and chinstrap penguins (Vidal et al. 2012) all report between three and five

helminth species, and between 52 and 100% prevalence of infection with at least one parasite species.

Our results highlight some outliers from this expected low richness. First, we recovered 14 species of helminths from little blue penguins, albeit from a broad range of time. Even considering only the most recent time period (2019–2023), there was still a high diversity of parasites reported (nine species in total). This increases the known parasite species of little blue penguins by three from the last investigation of the same population by Bennett et al. (2021). Little blue penguins (including both *E. novaehollandiae* and *E. minor*) are recognized for hosting one of the highest diversities of parasite species among penguins (Brandao et al. 2014, Fusaro et al. 2025). This diversity likely reflects (1) the study effort and sample size, as this penguin species is abundant and relatively easy to access for parasitological study compared to other rarer species, and (2) their broad and diverse diet (Fraser and Lalas 2004; Flemming et al. 2013; Brandão et al. 2014).

Secondly, while Fiordland crested penguins are less-studied than little blue penguins, they were also found to host a relatively high diversity of parasites, with eight species in total. Van Heezik (1990) found that little blue and Fiordland crested penguins have a higher degree of diet overlap (46%) and a shared pelagic foraging niche compared to yellow-eyed penguins from the same location (Whenua Hou, approximately 200 km south of the Otago region). This is consistent with what we know about yellow-eyed penguins as a predominantly benthic forager across the Otago region (Mattern et al. 2007). Despite the little blue and Fiordland crested penguins being phylogenetically distant, at least compared to the other crested penguins (Ksepka et al. 2006), they share some parasite species and both have high number of parasite species, as well as high dietary overlap. This suggests that in the context of Otago penguins, diet may potentially play a larger role in shaping parasite communities than host phylogeny (Marcogliese 2002).

We observed a high proportion of yellow-eyed penguins that were not infected with any helminth parasites (39%). Although some were hosted at a wildlife hospital before their death, these individuals were not dosed with anthelminthics (A Argilla pers. comm.). Not only were a lower percentage of individuals infected compared to other penguin species globally, but the parasite species were also not host-specific to yellow-eyed penguins. Yellow-eyed penguins shared all parasite species with at least one other penguin species. It is often assumed that every free-living species hosts at least one species of unique parasite (Poulin and Morand 2014), so it is surprising that no parasites were host-specific to yellow-eyed penguins. The only species infecting this penguin but not the other penguins was *C. hannae*, an acanthocephalan that infects marine mammals as mature adults (found as immature adults here), but is also found in its cystacanth stage in a diverse range of fish paratenic hosts, and as immature adults in fish-eating bird accidental hosts (Bennett et al. 2023b). Yellow-eyed penguins are Nationally Endangered (Robertson et al. 2021), and the latest population estimate for the New Zealand mainland (including Rakiura/Stewart Island) was approximately 160 breeding pairs. It is estimated that, despite considerable conservation effort, this population may be locally functionally extinct by 2043 or sooner (Mattern et al. 2017). Parasites are entirely dependent on their hosts for survival, making them more vulnerable to secondary extinctions than their hosts (Colwell et al. 2012). Furthermore, parasites with complex lifecycles– such as all species infecting yellow-eyed penguins recovered in this study– rely on a stable abundance of each host and life stage for long-term viability. Consequently, yellow-eyed penguin parasites may have experienced population bottlenecks due to the fluctuating mainland population, potentially rendering the current assemblage unrepresentative of their original parasite community. In addition to the mainland population, there are yellow-eyed penguins on the subantarctic Auckland and Campbell Islands. Any host-specific gastrointestinal parasites obtained from yellow-eyed penguins on the subantarctic islands could provide valuable insights into whether these parasites have undergone secondary extinctions in Otago, supporting or challenging the hypothesis.

Fernandez et al. (2019) suggested that lower diversity of parasite species in a host might reflect a low diversity of prey items in the diet. It is not possible to infer with the low sample sizes of Snares and erect crested penguins whether low parasite diversity is reflective of a relatively specialized diet, or if they are not compatible hosts for parasite species living around the Otago coastline. As both Snares and erect crested penguins primarily inhabit and breed on sub-Antarctic islands (Miskelly et al. 2001), and only occur on the mainland as vagrants, it is not surprising that only a limited number of specimens were available for this study. All parasite species infecting both species were also found in other penguins in Otago, except for *Tetrabothrius* sp. A which was only found in one erect crested individual. Potentially, this parasite species is restricted mainly to the subantarctic islands within erect crested penguin's typical home range (Marchant and Higgins 1990).

Our study provides insights into the importance of penguin prey species for parasite transmission. All parasite species recovered infecting New Zealand penguins, except *D. dinarctos* and potentially Capillariidae gen. sp., use fish as intermediate or paratenic hosts in their life cycles. No larval stages have been reported for any species within Desmidocercidae, and species within Capillariidae can have single-host life cycles (Anderson 2000). Blue cod *Parapercis colias* and sprat, *Sprattus antipodum* have been identified as

intermediate hosts for *C. rudolphii* E, and the presence of multiple adult *C. rudolphii* E in the proventriculus of little blue, Fiordland crested and yellow-eyed penguins suggests these penguins often consume one or both fish species (Bennett et al. 2022). Indeed, blue cod and/or sprat are important dietary components of all three species around New Zealand (Van Heezik 1990; Flemming et al. 2013; Young et al. 2020). Yellow-eyed penguins hosted a higher number of individual *C. rudolphii* E compared to Fiordland crested and little blue penguins suggesting that blue cod may play a more significant role in their diet than in those of the other penguin species (Van Heezik 1990). This is consistent with diet studies which suggest that yellow-eyed penguin diet has changed significantly since the 1980 s; now dominated by blue cod with reduced frequency of occurence of other prey species (e.g. red cod, ahuru) (Van Heezik 1990; Young et al. 2020). Additionally, while the adult stage of *Renicola* sp. has been documented infecting Fiordland crested penguins, the metacercarial larval stage was recently recovered from anchovy *Engraulis australis* in Otago (Bennett et al. 2023b). This provides further evidence of the predator-prey interaction between Fiordland crested penguins and anchovies, as indicated by the observed parasite associations.

Temporal shifts observed in parasite communities of little blue penguins highlight the dynamic nature of host-parasite interactions over time. Although our sample size for pre-2000 penguins ($n = 5$) was limited, it likely reflects the conditions of that period, as the low diversity and intensity of infections are consistent with previous findings from a necropsy study conducted in Otago between 1994 and 1998 that reported a questionable absence of any endoparasitic helminths from over 80 little blue penguins in the Otago population (Hocken 2000). Perhaps the most significant observation in this study is therefore the substantial increase in species diversity infecting little blue penguins, rising from 2 to 11 species over 30 years (14 species found overall, but without dates for some specimens, only 11 parasite species can be confirmed for the most recent time period). While it is well documented that little blue penguins can be dietary generalists, with significant variation depending on season, reproductive periods, and distribution (Fraser and Lalas 2004; Flemming et al. 2013), determining the drivers of this increased parasite diversity is complex and challenging.

Of the parasite species that exhibited large changes over time, the kidney trematode *Renicola websterae* appears to have increased in prevalence, mean intensity and abundance. *Renicola* spp. are known to infect little blue penguins in other areas of NZ (Crockett and Kearns 1975), and parasites of penguins are thought to accentuate the impact of starvation (Duignan 2001). As such, it is important to ascertain whether this species has any pathogenic impacts on little blue and Fiordland crested penguins in Otago that may inform conservation of both species. Other renicolids have been associated with necrosis and renal inflamation in their hosts (Timon-David 1953; Mahdy and Shaheed 2001; Jerdy et al. 2016; Cardoso et al. 2021). To explain this change in infection parameters of *Renicola websterae* we may look towards the second intermediate host, likely a small fish, based on knowledge of intermediate hosts in sister species, such as anchovy, which acts as intermediate host for *Renicola* sp. infecting Fiordland crested penguins (Bennett et al. 2023a, b). In North Otago (Oamaru), slender sprat *Sprattus antipodum* and Graham's gudgeon *Grahamichthys radiata*, are the two most important fish species in the diet of little blue penguins. Based on two diet studies of little blue penguins in Oamaru between 1994 and 5 (Fraser and Lalas 2004) and 2010 (Flemming et al. 2013), the contribution of Graham's gudgeon has increased from less than 10% prey biomass to over 50% prey biomass. Identification of *R. websterae* metacercariae in Graham's gudgeon in future would provide insights into whether this shift in prey consumption can explain the increase in *Renciola* infection over time.

While parasites are usually not directly implicated as the cause of death for wildlife, they are often overlooked for their potential to cause disease or sub-lethal impacts on their hosts (Shanebeck et al. 2022). Additionally, parasites can exacerbate or cause disease when hosts are already under stress or are immuno-compromised (Petney and Andrews 1998; Jolles et al. 2008; Ezenwa 2016). Disease has the potential to become more of an issue in the future, as the climate warms, food abundance is reduced and human disturbance and stress on penguin populations' increase. Additionally, if a population is already in decline, such as yellow-eyed penguins, then they may also have lower resilience to disease spread when outbreaks occur (King and Lively 2012).

Both little blue and yellow-eyed penguins in Otago have suffered from starvation events and cumulative stress in recent years. We identified parasites from penguins in Otago that have the potential to cause disease, or should be taken into account in future mortality events or monitored for an assessment of their impacts on host health. The nematode *Diomedenema dinarctos* was found in the lung and air sacs of all five penguin species (Presswell and Bennett 2021). A conspecific *D. diomedeae* has previously been associated with the death of albatross off the coast of Brazil (Vanstreels et al. 2018). Although infection loads in the penguins examined here are relatively low, with a maximum average of 2.3 individuals per infected host, increasing disease outbreaks affecting yellow-eyed chicks (e.g. Wierenga et al. 2023) highlights the need for closer monitoring of this parasite. Understanding its potential role in compromising penguin health is essential future work.

Additionally, other parasite species recovered here have implications for the welfare of the penguins. *Contracaecum* spp. were commonly recovered from the stomachs of Otago penguins. Between 2011 and 2016, approximately 5% of all little blue penguin deaths in Western Australia were attributed to heavy gastrointestinal burdens of *Contracaecum* (Cannell et al. 2016). To our best knowledge, no data currently exist on the health impact, lethal or sub-lethal, of *Tetrabothrius* infections. In little blue penguins, the average burden of *Tetrabothrius* was about 26 individual worms per infected host. Given that each worm can reach lengths of 15 cm, it is important to establish the health impacts, both lethal and sublethal, for this genus of cestodes.

Overall, our study underscores the valuable insights that parasitological investigations can provide regarding the health, feeding habits and ecology of hosts, both within and among species, and the spatial and temporal variation in parasite diversity and abundance.

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Data availability Voucher specimens have been deposited in the Museum of New Zealand Te Papa Tongarewa under accession numbers W.003980-88.

Declarations

Competing Interests Authors declare no conflicts of interest.

Ethics approval Authors hold a Department of Conservation permit to hold and dissect deceased birds in New Zealand.

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