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REVIEW ARTICLE



# Biodiversity of marine helminth parasites in New Zealand: what don't we know?

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## ABSTRACT

A full account of the world's species is important for understanding how natural systems are structured, how they function and how they will respond to natural and anthropogenic pressures in the future. Despite the well-known importance of parasites in natural systems, they are too often underrepresented from studies on biodiversity and ecological functioning. In this review, we provide a quantitative synthesis of the current state of knowledge of helminth biodiversity within New Zealand's marine environment. We report that records of parasitic helminths within New Zealand marine animals are few and uneven across host taxa. A large proportion of parasite species are taxonomically unresolved, with some differences across parasite taxa. Few parasites have their whole life cycles resolved, and the majority are only reported from one host species at one life stage. Most endemic host species are yet to be investigated for helminths and there is likely an abundance of endemic parasite diversity yet to be discovered. Host species of greater conservation concern are being investigated for helminths less frequently than species of low conservation concern. We conclude that little is known about parasitic helminths in New Zealand's marine environment and make recommendations on how to improve this situation.

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## Introduction

A full account of the world's species is important for understanding how natural systems are characterised and how they function. Without such inventory, we are limited in our ability to predict how systems might change in response to natural and anthropogenic pressures. New Zealand (NZ) has a rich, diverse and unique marine environment. The nautical boundary or exclusive economic zone (EEZ) is 15 times larger than the land area, and one of the largest in the world (Ministry for the Environment & Statistics New Zealand 2016). There are currently around 10,000 marine metazoan species recorded in the NZ EEZ, accounting for almost 20% of the country's total biodiversity (Gordon et al. 2010). Almost 4,000 of these require further taxonomic resolution and, in addition, new species are discovered regularly. Some estimates suggest that there are up to 50,000 species yet to be discovered in NZ EEZ, five times the current known

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total (Gordon et al. 2010). Clearly, there is a substantial lack of basic knowledge regarding what species are present in New Zealand waters. Addressing this issue is important now more than ever, as addressing biodiversity loss is an urgent priority across the globe (Butchart et al. 2010). This raises an important question: how can researchers predict the way in which natural systems will respond to environmental change if they do not recognise which species exist at present?

Appropriate biodiversity estimates of NZ marine organisms are further complicated in problematic groups of organisms such as parasitic helminths, which are too often neglected in studies of biodiversity and ecosystem functioning (Marcogliese and Cone 1997; Lafferty et al. 2008). This is no surprise considering parasites are typically small in size, and often live within their host organisms and therefore out of sight to the naked eye. Parasites are ubiquitous, however, and make up a substantial proportion of total biodiversity within natural systems (Dobson et al. 2008). Parasites can have significant impacts on their host health and on the composition of surrounding communities and indirectly affect how natural systems respond to changing climates (Thompson et al. 2005; Wood et al. 2007; Selbach and Poulin 2020). They are therefore extremely important to consider for a full inventory of the world's species. Parasites are also recognised as important threats for commercially harvested species and aquaculture in NZ (Lane et al. 2021). Thus, it is essential to synthesise what is or is not known regarding parasitic helminth biodiversity in New Zealand's marine environment.

In this article, we provide a quantitative summary of what is currently known about aspects of helminth biodiversity in NZ's marine environment. We compiled data on helminth parasites from the literature and unpublished data to answer specific questions relating to our current state of knowledge of helminth biodiversity in the NZ marine environment. Our questions are as follows: (i) What proportion of host species have at least one record of parasitic helminths? (ii) How well resolved are the taxonomic identities of helminths previously reported? (iii) How do the average species richness and the relative contribution of the four major helminth taxa per host species compare to the worldwide data for some common host taxa? (iv) How well resolved are the life cycles of marine helminths in NZ? (v) What proportion of parasitic helminths are endemic to NZ, and how many species are potentially endemic and undiscovered? (vi) What proportion of host species from different threatened classifications has helminth records? This information provides a baseline for expanding the state of knowledge of marine helminth biodiversity in NZ. We also end with recommendations on how to improve parasite species discovery in NZ.

## Methods

We compiled data from existing and unpublished databases of free-living and parasite biodiversity inventories (Presswell, *in prep*; Gordon et al. 2010), host-parasite checklists (Hine et al. 2000; McKenna 2010, 2018; Lehnert et al. 2019), New Zealand Threat Classification System (accessed via <https://nztc.org.nz>) and other published datasets (Robertson and Heather 2005; Peoples et al. 2012; Roberts et al. 2015; Barker et al. 2019; Tedesco et al. 2020), as well as the primary literature, to explore aspects of marine helminth biodiversity in NZ. Parasites included are all complex-life cycle endohelminths: digenean trematodes (Platyhelminthes), cestodes (Platyhelminthes), zooparasitic nematodes (Nematoda), and

acanthocephalans (Acanthocephala). Monogeneans, ectoparasitic crustaceans, and protozoan parasites were not included in the dataset mainly because there are fewer reports for those taxa. Below are brief methods for each question we posed regarding marine parasite biodiversity.

- i *What proportion of host species have at least one record of parasitic helminths?* We estimated for each host taxon the proportion of species that have at least one record of parasites. Host taxa included vertebrates (seabirds, elasmobranchs, teleost fish and marine mammals) and some invertebrates (Cephalopoda, Bivalvia, Gastropoda, Polychaeta, Maxillopoda, Amphipoda, Isopoda, Decapoda and Euphausiacea) that are known hosts for helminths either in NZ or worldwide.
- ii *How well resolved are the taxonomic identities of helminths previously reported?* We estimated for each helminth group present in the NZ marine ecosystem (acanthocephalans, cestodes, nematodes and trematodes) the proportion of records without species-level identification.
- iii *How do the average species richness and the relative contribution of the four major helminth taxa per host species compare to the worldwide data for some common host taxa?* We compared average helminth species richness per host species (i.e. number of species of parasite per species of host) and the relative contribution of the four major parasite taxa to the helminth fauna of various host taxa (Laridae; gulls, Spheniscidae; penguins, Phalacrocoracidae; shags, Rajidae; rays, Labridae; wrasse) between species present in NZ or worldwide; the five host taxa investigated were selected because species in the groups are common in New Zealand and worldwide. For worldwide data, Web of Science searches was employed for each host taxon with the 10 first articles sorted by relevance (excluding NZ species) selected to calculate indices (average parasite species richness per host species and relative contribution of the four major helminth taxa) (See Supplementary Material for search terms and list of articles). For each host taxon, we only retained search articles that had information regarding host species within marine environments and that included records of trematode, acanthocephalan, cestode and nematode species. We tested for differences between NZ and worldwide helminth species richness using Mann–Whitney tests.
- iv *How well resolved are the life cycles of marine helminths in NZ?* We estimated for each parasite taxon the proportion of adult species for which at least one other life stage has been discovered in addition to the adult stage.
- v *What proportion of parasitic helminths are endemic to NZ, and how many species are potentially endemic and undiscovered?* We estimated for each vertebrate host group (seabirds, elasmobranchs, teleost fish and marine mammals) the proportion of endemic parasites per endemic host species. We also estimated how many potentially endemic helminths are yet to be discovered from endemic hosts still to be investigated for helminths, simply by extrapolating from data on endemic host species that have already been studied for parasites. Helminths were classified as endemic if they are identified to species level and have only been reported in the New Zealand EEZ.
- vi *What proportion of host species from different threatened classifications has helminth records?* We estimated for each vertebrate group (elasmobranchs, marine mammals,

seabirds) the proportion of host species with helminth records per threatened status category. Threat status was categorised according to New Zealand Threat Classification System (NZTCS) into not threatened, at risk, threatened and data deficient. Teleost fish do not have threatened status classification so were excluded from this section.

### ***What proportion of host species have records of parasitic helminths?***

We would expect that most, if not all, animal species host at least one species of helminth parasite. In New Zealand, there are over 1400 vertebrate and at least 4500 invertebrate species in the marine realm that could potentially host helminth parasites (Table 1). At present, fewer than 5% of these have records of helminth parasites (Figure 1C). This suggests that parasites in New Zealand's marine environment are under-studied and remain largely unknown.

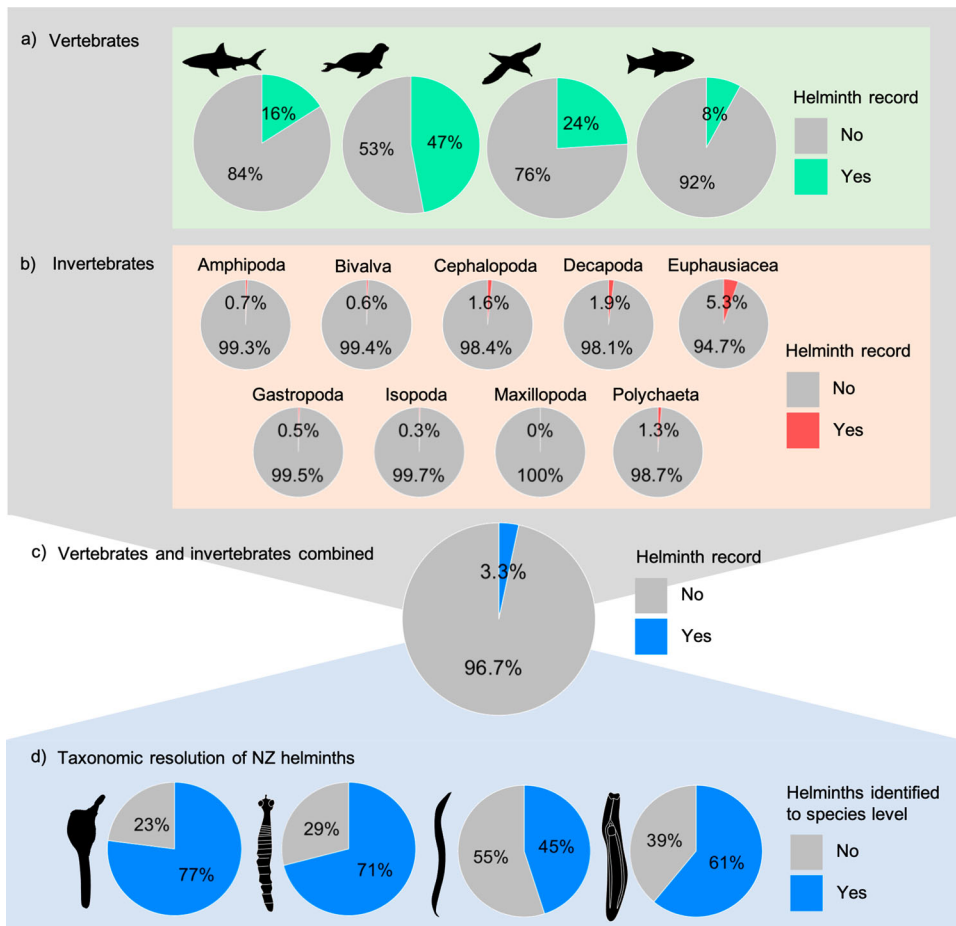
The best-studied vertebrate taxon is marine mammals, where 47% of species have helminth records (Figure 1A). This may, in part, be due to a generally mammal-centric bias in research (Fazey et al. 2005), and because they are frequently found washed up on shorelines.

Of vertebrate host taxa, teleost fish have the lowest proportion of host species with helminth records at 8% (Figure 1A). There are over 1000 teleost species yet to have records of their respective helminth parasites. Fish are used by many helminths during their life cycles; therefore, this low proportion represents a major knowledge gap, and indicates a need for further research.

Only 9% of NZ fish species are commercially caught under the NZ governmental Quota Management System (QMS) (98 species out of 1144). Approximately 42% of commercially caught species have helminth records compared to only 4% of non-

**Table 1.** Various vertebrate and invertebrate taxa present in New Zealand's marine ecosystem and the proportion of species with helminth records.

	N present in NZ	N total helminth species	N of host spp. with helminth record
<b>Vertebrates</b>			
Seabird	107	124	27
Elasmobranch	112	72	19
Teleost	1144	326	94
Marine mammal	44	83	21
Combined vertebrate taxa	1413		161
<b>Invertebrates</b>			
Mollusca			
Cephalopoda	127	6	2
Bivalvia	450	10	3
Gastropoda	1718	28	9
Annelida			
Polychaeta	509	4	7
Arthropoda			
Maxillopoda	608	0	0
Malacostraca			
Amphipoda	346	5	2
Isopoda	269	1	1
Decapoda	477	9	9
Euphausiacea	19	3	1
Combined invertebrate taxa	4523		34



**Figure 1.** Schematic representation of the state of discovery and taxonomic resolution of parasites in New Zealand marine ecosystem, **A**, proportion of species in marine vertebrate taxa with and without parasite records; from left to right: elasmobranchs, marine mammals, seabirds, teleost fish, **B**, proportion of species of common invertebrate taxa with and without parasite records, **C**, percentage of all marine free-living species that have parasite records, **D**, Of the recorded parasites in NZ, proportions of each major parasite taxon with and without taxonomic resolution down to species level, from left to right: Acanthocephalans, Cestodes, Nematodes and Trematodes.

commercially caught fish species. Presumably, the percentage for commercial species is higher because they are examined more often, and any parasites would be recorded because they are of some importance to the fisheries management. In fact, helminth larval stages often occur in the muscle of commercial species and cause an immune response which leaves infected fillets undesirable for eating (Hine et al. 2000). Some helminths can also cause allergic reactions to human consumers and seafood workers (e.g. Anisakid larvae; Audicana et al. 2002), or result in zoonosis (Chai et al. 2005).

Helminths of invertebrates are much less known than those of vertebrates (Table 1). Almost all helminths with complex life cycles require both vertebrates and invertebrates to complete one generation so the lack of helminth records in invertebrates is likely reflective of a sampling bias between vertebrates and invertebrates (Titley et al. 2017).

The invertebrate host taxon with the highest proportion of helminth records is Euphausiacea (Krill), although over 94% of species still have no records (Figure 1B). The helminth parasites of all other invertebrate taxa are virtually unknown (<2%). With fewer than 1% of species having records of parasite infection in the literature, our knowledge of parasitism in this group of host taxa is virtually non-existent. A number of helminth larval stages undoubtedly occur in these invertebrates. Therefore, the lack of records reflects both our limited knowledge of these hosts, and an information gap on the life cycles of those helminths found as adults in vertebrate hosts.

Above we report on the proportion of host taxa with at least one record of helminths. Many of the records for each host species comprise a single parasite record, despite each host likely harbouring more than one helminth species. Therefore, our estimates might not reflect the proportion of host taxa with resolved helminth assemblages. In addition, research expertise can lead to bias in helminth groups that are reported for any host (Poulin and Jorge 2019). For instance, if over a period of time, parasite taxonomy in New Zealand is dominated by a trematode specialist it may be expected that trematodes would be reported more frequently than other helminth groups per host species.

### ***How well resolved are the taxonomic identities of parasites reported?***

Above we report that only about 4% of NZ marine animals likely to host helminth worms have records of helminths. Nearly 40% of those recorded helminth species require further study to confirm their taxonomic identity, i.e. they are recorded in the literature as ‘sp.’, ‘gen. sp.’ or ‘?’ (Table 2, Figure 1D). This further suggests our knowledge of helminth parasite biodiversity in the NZ marine environment is superficial.

The danger in a lack of taxonomic resolution should not be taken lightly. Accurate species identification underpins all studies of biodiversity, and poor resolution could mask total biodiversity. Incomplete identification also affects our ability to identify functional differences between closely related species or estimate host specificity.

Taxonomic resolution is not even across different helminth groups. Acanthocephalan species are relatively well resolved to species level compared to the other helminth groups. As varying life stages of acanthocephalans can be more easily identified to species level based on morphology than other helminth groups, this may explain why acanthocephalan identifications are better resolved in the literature. Additionally, the current known species richness of each helminth group may also reflect the proportion with taxonomic resolution. As acanthocephalans have the smallest number of species present in NZ, they are more likely to be better documented than groups.

**Table 2.** Number (N) of helminths (acanthocephalans, cestodes, nematodes, trematodes) present in NZ marine environment requiring further taxonomic resolution (Figure 1D).

	N resolved	N requiring resolution	N total
Acanthocephalan	20	6	26
Cestode	62	25	87
Nematode	45	54	99
Trematode	107	67	174
Total	234	152	386



Nematodes have particularly poor taxonomic resolution in the NZ literature, with more than 50% of species documented requiring more complete identification (Figure 1D). Many records are from commercial fish species and document larval nematode stages which were not necessarily investigated for taxonomic purposes. A PhD thesis by Brunson (1956) actually described morphologically and named 27 species of fish nematodes; however, this was never formally published and consequently these species are currently considered *Ascarophis* A to K, *Cucullanus* A to H, etc. (Hine et al. 2000). Similarly, a few nematode genera (e.g. *Anisakis*, *Capillaria*, *Contracaecum*) have representatives that require expert taxonomic knowledge to distinguish between species from different hosts and at different life stages. Due to their morphological similarity, identification of such species groups is increasingly reliant on additional molecular data, such as has been done for the *Anisakis simplex* species complex (Mattiucci et al. 2014). However, appropriate genetic markers are not yet available for many of these species complexes (e.g. *Capillaria* spp.).

Differences in taxonomic resolution between helminths also arise because taxonomists in NZ may be focusing on particular parasite taxa. Although NZ has relatively few taxonomists, their work has significantly contributed to the current knowledge of parasite biodiversity.

Globally, the number of well-trained parasite taxonomists and systematists is fast declining and this is identified as one of the greatest challenges for parasitological research (Brooks and Hoberg 2001; Poulin and Morand 2004). Having said that, it is interesting to note that the proportion of parasites without proper species-level identification is comparable to that for all free-living species in New Zealand's marine environment (Gordon et al. 2010).

### **How do the average species richness and the relative contribution of the four major helminth taxa per host species compare to the worldwide data for some common host taxa?**

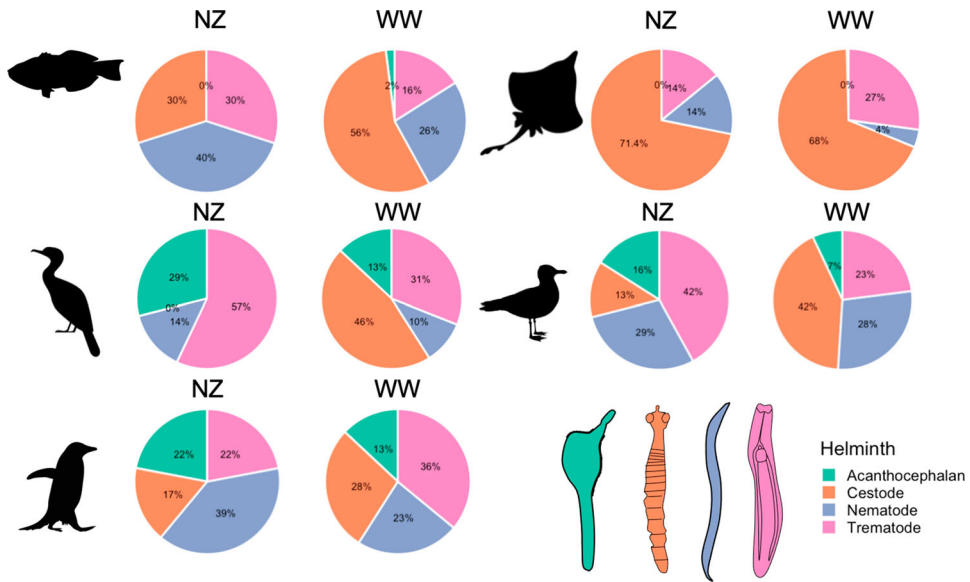
Overall, New Zealand helminth parasite biodiversity compares relatively well with what is reported worldwide in terms of species richness of parasites per host species and helminth taxonomic composition for most host taxa investigated (see Table 3, Figure 2). There were no significant differences in species richness between NZ host species and their relatives elsewhere in the world (all Mann–Whitney tests,  $p > 0.05$ ), although some differences were possibly not detected due to small sample sizes (e.g. Phalacrocoracidae).

**Table 3.** Average species richness of helminths per host species (including only those with helminth records) for New Zealand and rest of the world for some common host taxa.

Common taxa	Average NZ parasite species richness	Average worldwide parasite species richness
Labridae (wrasses)	2.25 (1–4) ( $N = 4$ )	6.3 (1–20) ( $N = 27$ )
Rajidae (skates)	10.5 (8–13) ( $N = 3$ )	2.0 (1–15) ( $N = 24$ )
Phalacrocoracidae (shags)	2.8 (1–5) ( $N = 5$ )	15.8 (2–35) ( $N = 6$ )
Laridae (gulls)	12 (11–13) ( $N = 2$ )	10.7 (1–61) ( $N = 22$ )
Spheniscidae (penguins)	5 (1–8) ( $N = 4$ )	7.2 (3–23) ( $N = 7$ )

Range of helminth species richness in parentheses.  $N$  denotes number of host species used to calculate average parasite species richness.





**Figure 2.** Relative contribution of the four main helminth groups to the parasite fauna of common host taxa for New Zealand (NZ) and worldwide (WW) regions. Host silhouettes top to bottom, left column first, represent Labridae, Phalacrocoracidae, Spheniscidae, Rajidae and Laridae, respectively.

The relative numbers of different helminth taxa recorded for each host group compare relatively well to what is known elsewhere in the world too. This is with the exception of cestodes from NZ Phalacrocoracidae, of which there are no records (Figure 2).

Additionally, for each of the five host groups investigated here, with the exception of Rajidae, cestodes contribute less to helminth assemblages in New Zealand compared to records outside NZ. This could be due to a lack of taxonomists with cestode expertise in New Zealand.

### **How well resolved are the life cycles of marine helminths in NZ?**

Most helminth parasites have complex life cycles; in other words, over one generation different life stages must infect different host species in a particular order to reach maturity and reproduce. The number of life stages and host species varies within and between helminth groups, with some groups requiring up to four host species in succession. In New Zealand, over 70% of reported helminth parasites are documented at only one

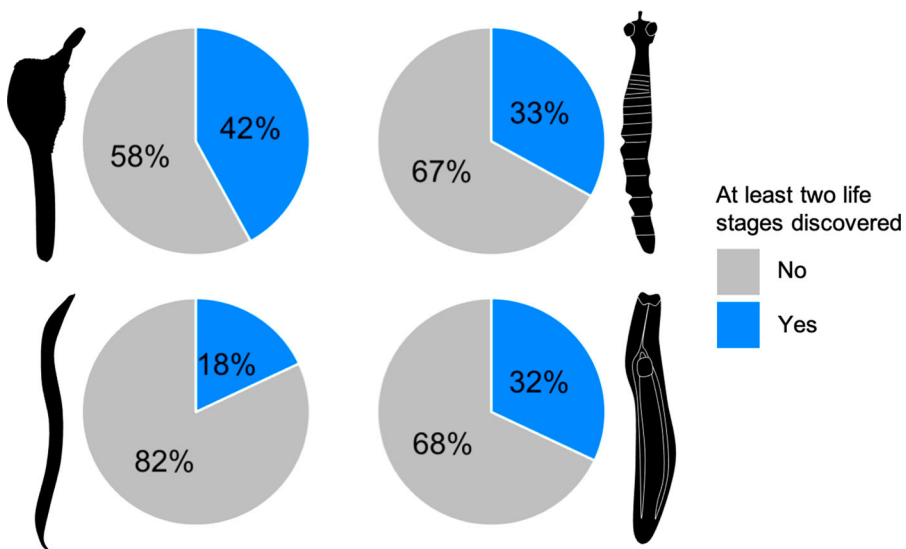
**Table 4.** Adult parasites described from New Zealand marine animals and proportion of life cycles partially or fully resolved.

	Total N adult helminths	N helminths with only adult stage identified	N helminths with 2 or more life stages resolved
Acanthocephalan	26	15	11
Cestode	83	56	27
Nematode	96	79	17
Trematode	149	101	48
Total	354	251	103

life stage (generally the adult stage) within one host (Table 4). As it stands, we know very little regarding marine helminth life cycles in NZ (Figure 3). This is not restricted to NZ, as worldwide, it is estimated that less than 5% of all helminth life cycles have been resolved (Blasco-Costa and Poulin 2017).

Greater effort at resolving helminth life cycles will have implications extending beyond species identification at different life stages (Blasco-Costa and Poulin 2017) and would be extremely beneficial for our understanding of parasite transmission in NZ marine systems. Life cycles can inform taxonomy as larval stages within intermediate hosts can exhibit morphological features useful for delineation of species going beyond morphology of the adult form (e.g. trematode cercariae have morphological features unique to cercarial life stage and to family (Schell 1970)). Resolution of helminth life cycles can provide insight into expected hosts of closely related species. This is because closely related parasites typically share similar host taxa requirements and number of life stages. For example, trematodes from the Heterophyidae family all follow a three-stage life cycle, including a gastropod first intermediate host, fish second intermediate host and bird definitive host. Life cycles can also give insight into evolutionary history of helminths (Pearson 1972). Lastly, completing life cycles reveals trophic interactions between different hosts, which can be used in analyses of food web structure and dynamics to explore ecosystem stability and response to natural and anthropogenic stressors (Dunne et al. 2013).

Approximately 8% of helminth species recorded in NZ are known only as larval stages within the respective intermediate hosts. Typically, formal descriptions require at least the adult stage, these records will likely remain incomplete until further effort is aimed at confirming their identities.



**Figure 3.** Proportion of parasite species in New Zealand marine ecosystem with 2 or more life stages identified. Parasite silhouettes represent helminth group: left to right acanthocephalans, nematodes, cestodes and trematodes.

A higher proportion of acanthocephalan life cycles are partially or fully resolved compared to other helminth groups. This may be partly due to morphological features (i.e. proboscis hooks) being retained throughout much of the life cycle, making it easy to match up different life stages in different hosts. This could also be due to a concentrated taxonomic effort by local researchers focusing on acanthocephalan life cycles. Conversely, nematode and cestode life cycles can be difficult or often impossible to match using morphological features alone, a fact reflected in the low proportion of NZ species with partially or fully resolved life cycles.

Although parasitologists have been slow to incorporate them (Selbach et al. 2019), molecular tools can overcome some of the challenges associated with tracking helminth life cycles (Poulin and Keeney 2008). Recent research in NZ has succeeded in genetically matching larval forms with their adult counterparts (e.g. Randhawa 2011; Bennett et al. 2019; Presswell and Bennett 2019). In addition to resolving some life cycles (Jensen and Bullard 2010), the increasing availability of genetic sequences has paved the way for our understanding of the classification, evolution and host associations of helminths (e.g. Waeschenbach et al. 2007).

### ***What proportion of parasitic helminths are endemic to NZ, and how many species are potentially endemic and undiscovered?***

Worldwide, endemic species are valued by both general and scientific communities, both for their uniqueness and their likelihood of being endangered or threatened. Endemic species can play unique roles in the local biodiversity and ecological functioning of a natural system, making it important to characterise endemic species biodiversity (Gorman et al. 2014).

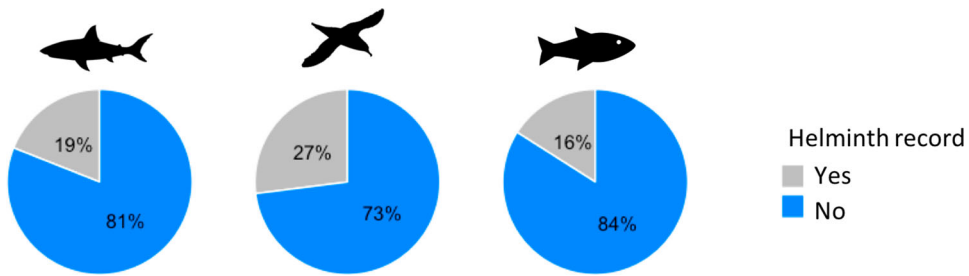
For NZ marine vertebrates, approximately 16% are currently considered endemic, in that they only occur naturally within NZ's EEZ. Of these, only 20% have records of helminths, including 33 unique endemic parasite species (Table 5).

The NZ marine environment is potentially sitting on a gold mine of undiscovered endemic helminth species (Figure 4). By a rough extrapolation based on species already studied for parasites, we estimate that there are probably over 130 undiscovered

**Table 5.** Endemic marine vertebrates in New Zealand, proportion with parasite records and how many potentially endemic helminth species are yet to be discovered.

	N spp	N endemic (%)	N endemic host species w/ helminth records	Ratio of non-/endemic parasites <sup>a</sup>	N unique endemic parasites reported in endemic hosts	Average endemic helminth species richness per endemic host	Endemic parasites yet to be discovered from endemic host
Seabird	107	36 (33.6%)	10	3:1	8	1.1	20.8
Elasmobranch	118	26 (22.0%)	5	2:1	9	1.8	37.8
Teleost fish	1144	160 (13.9%)	27	0.5:1	16	0.85	78.8
Marine mammal	44	3 (6.8%)	2	–	0	–	0 <sup>a</sup>
<b>Total</b>	<b>1413</b>	<b>225 (15.9%)</b>	<b>44 (19.5%)</b>		<b>33</b>		

<sup>a</sup>Note that although there are no endemic parasites described from NZ endemic marine mammals, some are likely endemic. However, there is little taxonomic resolution of these parasites (12/18 total species records for endemic marine mammals are only identified to genus level).



**Figure 4.** Proportion of NZ endemic host species with at least one parasite record. Silhouettes denote vertebrate host groups, left to right – elasmobranchs, seabirds and teleost fish.

helminth species infecting endemic vertebrates that are yet to be subject to parasite studies. This is comparable to the total number of endemic vertebrate host species present in NZ marine ecosystems. If these endemic species do exist, their presence is worth recording for a full understanding of biodiversity, their likelihood of being endangered, and their uniqueness to New Zealand.

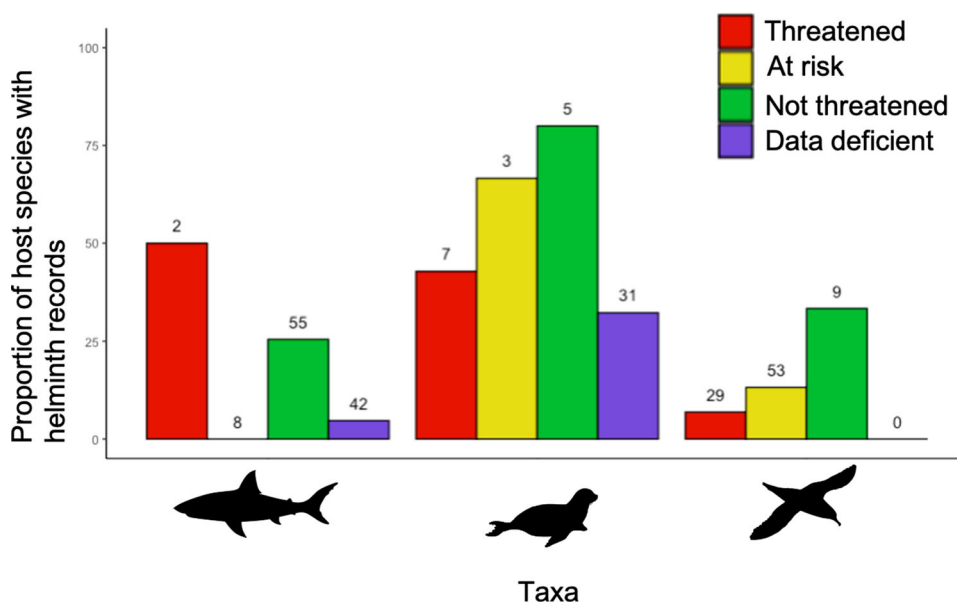
On average, elasmobranchs have more endemic species per endemic host than other vertebrates (Table 5). This could be due to the high host specificity of many elasmobranch helminths, such as cestodes, and the fact that these communities often include many closely related species (Benz and Bullard 2004).

Marine mammals currently have no recorded endemic helminths in NZ (Table 5). However, the endemism of their helminths may be masked by lack of taxonomic resolution, as 12 of the 18 species infecting endemic marine mammals are not identified to species level, and therefore cannot be classified as endemic. These species will require further investigation by a taxonomic expert.

### ***What proportion of host species from different threatened classifications has parasite records?***

Our results do not paint a clear picture on the overall status of helminth records as a function of different host threat classifications. A high proportion of elasmobranch and marine mammal species are currently considered ‘data deficient’, meaning there are insufficient data to categorise their species to a threat status (Figure 5). Teleost fish are also not included here because there is currently no system for classifying the threat status of NZ marine fish. This should be revisited when better threat classification of host groups is established, to determine whether host threat status relates to our knowledge of their helminths.

Seabirds are the only host group in which all species have been categorised as either ‘not threatened’, ‘at risk’ or ‘threatened’. A lower proportion of threatened seabird species have records of helminths compared to seabird species in other categories (Figure 5). This is probably due to limited access to specimens of threatened species for parasitologists intending to investigate helminth burdens. Helminths, however, have been associated with mass mortalities of some seabird populations (Randall and Bray 1983) and in future, opportunistic samples of deceased specimens of threatened species should be analysed for their parasite infection. Increased effort to identify



**Figure 5.** Proportion of host species with parasite records within each of the vertebrate taxa considered here, shown separately for different threat status categories (threatened, at risk, not threatened or data deficient). Numbers on each column indicate the number of host species in each category. Host silhouettes from left to right represent elasmobranchs, marine mammals and seabirds, respectively.

parasites with the potential to indirectly or directly cause mortality in threatened hosts that are already deceased could greatly aid conservation efforts.

Historically, parasite biodiversity is not considered a conservation priority, even though the overall goal of conservation is to maintain biodiversity (Dunn et al. 2009). For parasite species that are highly host specific, threatened hosts also mean threatened parasites. Adding to this, parasites could be considered more threatened than their hosts, because parasites depend completely on hosts for survival and can require up to four host species to complete one generation. If one or more of the hosts for a multi-host helminth life cycle is threatened and undergoes population decline, this will significantly affect the probability of a parasite completing its life cycle. This is exacerbated for helminths that are highly host specific at any stage in their life cycle. At present, the key limitation to conserving biological diversity within NZ marine ecosystems is that we simply do not have basic knowledge regarding which helminth species are present in most threatened or at risk vertebrates; it is therefore challenging to even consider their conservation.

## Summary

This study synthesised the current state of knowledge regarding several aspects of helminth parasite biodiversity within New Zealand's marine environment. We report that records of parasitic helminths within New Zealand marine animals are sporadic and uneven across host taxa. Teleost fish and invertebrates are particularly understudied. A large proportion of reported helminth species are taxonomically unresolved, i.e. not

identified to species level, and this is also uneven across different parasite taxa. Few have their whole life cycles resolved, and the majority are only reported from one host species at one life stage. Helminths with larval and adult stages that are not morphologically comparable are particularly lacking in life cycle resolution. Most endemic host species are yet to be investigated for helminths and there is likely an abundance of endemic parasite diversity yet to be discovered. Host species of greater conservation concern are being investigated for parasites less frequently than species of low conservation concern.

To date, there have been no large-scale surveys exploring New Zealand marine helminth biodiversity. Data compiled here come from previous opportunistic descriptions by the few parasite taxonomists active in New Zealand, occasional reports of helminths without proper taxonomic identification, or early surveys from the mid-twentieth century (e.g. Grabda and Slosarczyk 1981; Bowie 1984) in which species probably require further examination using modern integrative taxonomic techniques to be comparable to modern day descriptions. Therefore, we have only obtained a glimpse of the full extent of diversity of the NZ marine helminth fauna.

There are many ways to improve this situation. Firstly, there is a need for a few coordinated surveys of a wide range of free-living animals along different sections of the NZ coastline, with careful necropsy for parasite recovery followed by detailed morphological and genetic study of all extracted parasites. There are a few instances of researchers contributing to knowledge of larval and adult helminth biodiversity from relatively large-scale localised ecosystems (e.g. Jensen and Bullard 2010; Justine et al. 2010).

Secondly, increased collaborative effort between parasitologists in New Zealand and researchers from other disciplines would maximise parasite discovery. Marine ecologists sample a wide variety of animals; by sharing those specimens with parasitologists, information on parasitic helminths could be maximised without the need to euthanise further animals. Similarly, access to fish obtained by recreational and commercial fishermen could also facilitate parasite discovery without killing additional animals; fish are very understudied compared to other vertebrates. We are privileged in New Zealand to have a number of research institutes dedicated to the health and conservation of our ecosystems (e.g. Cawthron, National Institute of Water and Atmospheric Research and the Department of Conservation). Efficient communication and sharing of knowledge and physical specimens between these institutes and parasitologists working in NZ could yield enormously increased opportunities for study, and maximise the data extracted from individual samples.

Thirdly, parasitologists should more readily integrate new technologies. Scanning electron microscopy and genetic sequencing are now the expected norm for taxonomists producing new species descriptions, and are also invaluable for the resolution of lifecycles and evolutionary histories. For example, some diagnostic features on notocotylid trematodes are only visible under scanning electron microscopy. Genetic techniques overcome identification errors associated with cryptic species that are indistinguishable using morphological features alone (e.g. Herrmann et al. 2014). Some techniques (such as environmental DNA) have overcome challenges associated with traditional parasitological survey methods which are often labour- and time-intensive and invasive for host species (Huver et al. 2015). Ideally, parasitologists will integrate a range of different techniques and methods into their research for a more comprehensive understanding of parasitic helminth biodiversity within the NZ marine ecosystem.

We need to understand parasite biodiversity within NZ's marine environment for various reasons. Parasites make up a large proportion of the world's biodiversity and understanding how natural systems operate is not possible without a full account of parasite biodiversity present. Helminths can be problematic disease-causing agents that come at a large cost to fisheries management and conservation efforts for a variety of host species (Huston et al. 2020). Knowledge of parasites present in host species of commercial interest provides us with a list of potential disease risks in the face of environmental change. With increased effort toward parasite biodiversity discovery in NZ, parasitologists can identify potential disease agents before they become problematic.

We hope this review will serve as a baseline from which to begin resolving some of the knowledge gaps presented. We highlighted some host taxa particularly lacking in parasitological investigations, as well as parasite taxa lacking in resolution. The above recommendations are necessary first steps to improve the current situation.

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