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Annotated checklist and genetic data for parasitic helminths infecting New Zealand marine invertebrates

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Abstract

Parasitic helminths with complex life cycles require multiple hosts in a particular order to complete their life cycles. Although almost all helminths infect invertebrates at some point in their life cycle, we know very little about which species of invertebrates harbor parasites compared with what is known for vertebrates. In New Zealand, <1% of marine invertebrates that may be expected to host parasites have records of parasite infections. This is a strong indication that our knowledge of invertebrate parasites within marine ecosystems is highly limited. Here, we provide the first comprehensive parasite–host checklist including data from the literature and newly discovered infections of parasitic helminths infecting marine invertebrates in New Zealand. Including both pre-existing and newly found data from our survey, we present data on 73 parasite taxa (five acanthocephalans, 13 cestodes, nine nematodes, and 46 trematodes) infecting 62 marine invertebrate species in New Zealand. In addition, we compile existing and new genetic data for many of these parasites, as a useful tool for future studies of parasite biodiversity and phylogenetics.

KEYWORDS
Acanthocephala, biodiversity, Cestoda, Nematoda, parasites, Trematoda

1 | INTRODUCTION

Parasitic helminths exhibit diverse and fascinating life histories. Most have complex life cycles, which require that parasites pass through multiple host species in a particular order to mature, reproduce, and complete one generation. The larval stages of such helminths are found in one or more intermediate hosts (typically invertebrates), and the adult stage, in which the worm matures and sexually reproduces, infects a definitive host (typically a vertebrate). Despite the fact that helminths with complex life cycles almost invariably use invertebrates at some point, our knowledge regarding parasites in invertebrates is largely unknown compared with that of vertebrates (Leung et al., 2015). In New Zealand, a recent review of marine parasites revealed that <1% of all invertebrate species that may be expected to host parasites actually have records of infection in the literature (Bennett, Presswell, et al., 2021). This is a strong indication that our knowledge of invertebrate parasites in New Zealand's marine ecosystem is extremely limited.

Although clearly overlooked and underrepresented in past studies, parasites that infect invertebrates are important for several reasons. First, parasites of invertebrates can significantly impact commercial fisheries and aquaculture (Shinn et al., 2015), and damage may include host castration and lowered growth and survival rates (e.g., Bower et al., 1994). Second, the matching of the identity of a larval parasite in an invertebrate intermediate host with its adult counterpart from a definitive host provides evidence for predator–prey interactions between the two hosts (e.g., Bennett et al., 2019). The marine realm is a notoriously difficult environment in which to study predator–prey interactions between animals, and helminth life cycle data can thus help, indirectly, to fill in the gaps in our knowledge of marine food webs. Third, knowledge of larval helminths within intermediate hosts has huge value to taxonomy. A species is characterized by its whole life cycle and not just its adult form; without identifying each life stage within each host, our knowledge of parasite biodiversity is incomplete (Blasco-Costa & Poulin, 2017). Last, in some marine ecosystems, the total biomass of larval parasites is comparable with that of top predators (Kuris et al., 2008). Some helminths such as trematodes have a free-living stage after emergence from their invertebrate hosts and constitute an important food source for animals that are not suitable hosts (e.g., Thieltges et al., 2013). Thus, parasites account for a significant portion of the overall biomass in a way that can affect the structure and functioning of whole ecosystems. Without a basic knowledge of which parasites are present within an ecosystem, our understanding of how natural systems are structured and how they function is limited.

The way forward to fully document parasite biodiversity in invertebrate hosts is seemingly straightforward: recover and identify parasites that infect marine macroinvertebrates. The main limitation here is that most larval parasites cannot be reliably identified to species, genus, or sometimes even family level using morphological characteristics alone. This also means that they usually cannot be matched to parasite species already known from their adult forms. Genetic tools are increasingly overcoming this limitation, allowing parasitologists to match larval forms from intermediate hosts with adult forms from definitive hosts (e.g., Bennett & Presswell, 2019; Presswell & Bennett, 2020). This is a crucial next step in the discovery of invertebrate parasite biodiversity, which will allow resolution of complete life cycles, provide appropriate taxonomic identifications, and compare between closely related species, geographic areas, and other life stages within multiple hosts (Blasco-Costa & Poulin, 2017). This can only be achieved through large-scale biodiversity surveys and through the use of integrative taxonomic methods that combine genetic and morphological data to form an overall picture of which invertebrates within a given ecosystem host particular parasite species.

Another important step to enhance our understanding of the parasites of invertebrates is to compile data on parasite infections within a given ecosystem. Synthetic checklists are essential tools to fully harness knowledge of host–parasite interactions and answer broader questions about biodiversity and ecosystem functioning. In New Zealand, readily available comprehensive parasite checklists are available for all vertebrate groups including birds (McKenna, 2010, 2018), mammals (Lehnert et al., 2019; McKenna, 2010, 2018), and fish (Hewitt & Hine, 1972; Hine et al., 2000). There are, however, no checklists for parasites of New Zealand invertebrates, despite there being more invertebrate species present in New Zealand's marine environment than all vertebrate species combined (Gordon, 2009; Gordon et al., 2010).

The objective of this study is to provide the first comprehensive checklist of parasitic helminths (acanthocephalans, cestodes, nematodes, and trematodes) currently known to infect New Zealand marine invertebrates. We focused on New Zealand marine invertebrates because the coast has been the focus of various parasitological surveys in the past two decades (e.g., Donald & Spencer, 2016; Koehler & Poulin, 2010; Leung, Donald, et al., 2009) but never have all published data been brought together in a succinct form. We also include new records of infections from a recent and extensive parasite biodiversity survey undertaken between June 2019 and August 2021 from the Otago Coast, South Island. In addition, we compile and present existing publicly available genetic data of these parasites and complement this by adding newly generated genetic data following our survey. Our study represents a one-stop repository of all available information on helminth parasites of New Zealand marine invertebrates.

2 | METHODS

For existing records of parasites infecting marine invertebrates in New Zealand, data were assembled from primary publications found on Google Scholar using combinations of relevant keywords, plus searches of the reference lists in those publications. In total, 138 relevant publications were found, each providing at least one record of a host–parasite association between a larval helminth and an invertebrate host.

With regard to new records, 6295 invertebrates from 87 invertebrate species were sampled from the Otago Harbour, South Island, New Zealand, between June 2019 and August 2021. Samples were opportunistically collected from a range of activities including hand sampling along the intertidal zone, plankton sampling on surface water, and box dredge on benthic substrates as part of a larger survey of parasites infecting marine animals in the Otago Harbour (unpubl. data). In addition, specimens of one cephalopod, *Moroteuthopsis ingens*, were provided from a recent trawl survey by the National Institute for Water and Atmospheric Research and collected from the Chatham Rise off the east coast of New Zealand in January 2020. Host species were identified to the lowest taxonomic level possible using invertebrate keys and guides such as Spencer et al. (2016) and Carson and Morris (2017). Upon necropsy of host individuals, parasites were recovered and stored in 70% EtOH for genetic and morphological analysis.

Genomic DNA was extracted from parasites using DNeasy(R) Blood and Tissue Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol. For nematodes, the partial *18S* rRNA gene was amplified using primers Nem18SF and Nem18SR and conditions from Wood et al. (2013). For trematodes, cestodes, and acanthocephalans, a partial *28S* rRNA gene was targeted using primers T16 and T30 (Harper & Saunders, 2001) under conditions from Bennett et al. (2019). Additionally, *cox1* was targeted for some trematode and nematode taxa, using either primers JB3 (Bowles et al., 1993) and Trem. cox1.rrnl (Králová-Hromadová et al., 2008) or universal Folmer et al. (1994) primers LCO1490 and HCO2198, under PCR conditions described in Bennett and Presswell (2019). The resulting PCR product was cleaned using EXO-SAP™-Express PCR Product Cleanup Reagent (USB Corporation, Cleveland, OH, USA) following manufacturer's instructions. Sanger sequencing by capillary electrophoresis was performed by the Genetic Analysis Service, Department of Anatomy, University of Otago (Dunedin, New Zealand). Newly generated sequences were imported into Geneious Prime(R)v2021.1.1, trimmed using the trim function with default parameters, and manually edited for incorrect or ambiguous bases. The resulting sequences were submitted to GenBank under accession numbers ON661298-ON661331, ON661074-ON661076, and ON656399-ON656400. To achieve lowest taxonomic resolution possible, we used both BLASTn searches on GenBank to confirm species, identity if the sequences matched 100% with existing taxa, or to establish preliminary identification. Larval stages of some taxa (particularly trematodes) had morphological features that aided in identification, in which case extra specimens were stained or cleared for examination. Further taxonomic resolution was sought when number of individuals and preservation condition allowed, with the aid of morphological keys or original descriptions such as Schell (1970), Allison (1979), Brockerhoff and Smales (2002), Martorelli et al. (2004), Martorelli et al. (2006), and O'Dwyer, Blasco-Costa, et al. (2014). We acknowledge the importance of morphological vouchers for validation of the sources of DNA sequence data and have submitted morphological vouchers where possible. Unfortunately, most of the parasites found in this study were too small to be divided for molecular and morphological reference and were therefore sacrificed for DNA sequencing. Extra specimens were reserved for future study when genetically comparable adults become available.

Within the parasite–host list, each record contains information about the taxonomic authority, host species, and their common name (labeled A, B, C, and so on for more than one host), locality (either harbor, coastal city, or region within New Zealand), site of infection within host, life stage of parasite within host, and all bibliographical references associated with the parasite and host pair. Hosts within each parasite species record may have a "Remarks" subheading, under which are listed synonyms or notes pertaining to the specific host–parasite pair. Additionally, each parasite species may have an "Other remarks" subheading, which pertains to relevant information of interest, including definitive host species if known and location of type material for taxonomically described species. For host taxonomic names, we referred to WoRMS Editorial Board (2021) or the most up-to-date primary taxonomic literature (e.g., Caira & Jensen, 2017). The parasites are presented in alphabetical order by family within their relevant phylum, class, and order. Within families, species are listed in alphabetical order. Hosts of each parasite species are listed in alphabetical order by family and species. The host–parasite list is ordered alphabetically by host taxonomy.

3 | RESULTS

A majority of records of host–parasite associations in the literature come from the last 20 years of research in parasitology, although the first record was published in 1903 by Haswell (Figure 1B). In total, including both pre-existing records and those newly found in our survey, we present data on 73 parasite taxa (five acanthocephalans, 13 cestodes, nine nematodes, and 46 trematodes) infecting 62 invertebrate species (six polychaetes, five amphipods, 16 decapods, one chaetognath, one cnidarian, one euphausiid, three isopods, two stomatopods, one barnacle, six bivalves, four cephalopods, and 16 gastropods). Of the 73 parasite taxa, 20 obtained from our survey are reported for the first time in New Zealand marine invertebrates (one acanthocephalan, 10 cestodes, eight trematodes, and one nematode). Additionally, for 13 invertebrate host species, this is the first time they are reported as hosts to parasitic helminths. Of the parasite species, 80% (58/73) have associated genetic data, and of those, 40% (23/58) are newly produced from this study (Table 1). Most parasites are only known from one host, and most hosts are only known to be infected with one parasite species (Figure 1A). The host with the highest number of parasite records is *Zeacumantus subcarinatus* with 11 helminth species. The trematode *Maritrema novaezealandense* infects the highest number of different host species (14).

We also provide video data on three parasite species recovered in this survey as examples for nonparasitologists of what larval parasites within invertebrate hosts can look like. These include the trematode *Acanthoparyphium* sp. A from a chiton host (Supporting Information Video S1), cercariae of Schistosomatidae gen. sp. being shed from a limpet host (Video S2) and the trematode *Copiatestes thyrsitae* within a euphausiid host (Video S3) and ex situ (Video S4).

Below, we present the parasite–host checklist of helminth parasites recorded in invertebrate species in New Zealand, representing an up-to-date summary of the current knowledge. We also present a host–parasite list of helminth parasites reported in invertebrate species in New Zealand in Table 2.

3.1 | Family Plagiorhynchidae Golvan 1960 (Acanthocephala, Palaeacanthocephala, Polymorphida)

3.1.1 | *Plagiorhynchus allisonae* Smales, 2002

Host A

Transorchestia serrulata (Dana 1852). Talitridae, intertidal amphipod.

Localities. Lower Portobello, Otago Harbour.

Infection site. Body cavity.

Stage. Cystacanth.

References. Lagrue et al. (2016)

Other remarks

The adult stage of this species has been described from the variable oystercatcher, *Haematopus unicolor*, and from the South Island pied oystercatcher, *H. finschi* (Smales, 2002). This host species was originally identified as *Transorchestia chilensis* (MILNE-EDWARD 1840) but has recently been identified from molecular data as *T. serrulata* (J. MacDonald, unpubl. data). Type specimens are deposited at the South Australian Museum under accession numbers SAM 34170–34172.

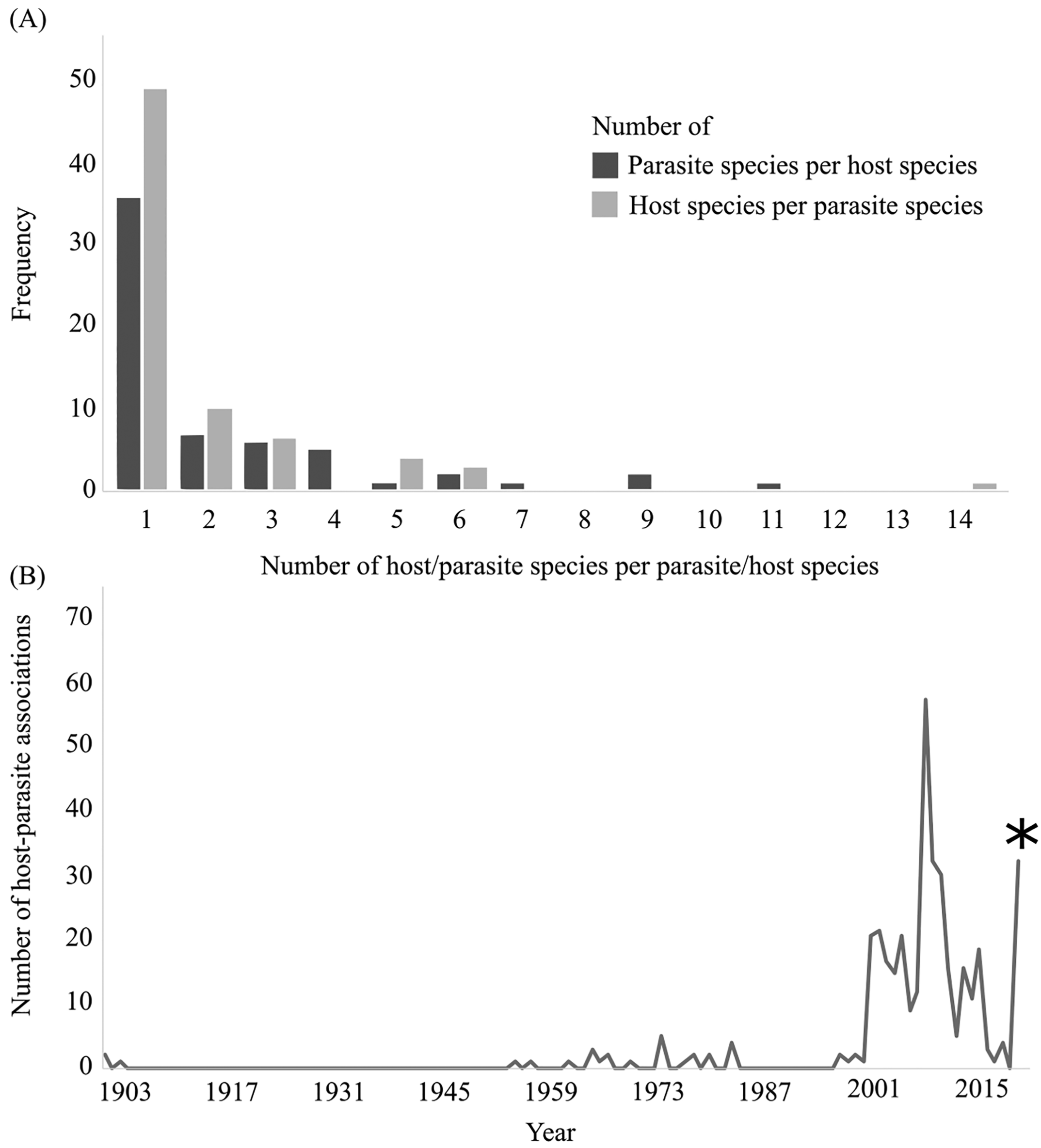

FIGURE 1 (A) Frequency distribution of number of parasites per host and number of hosts per parasite species. (B) Time series of total records in literature regarding individual parasite–host associations; asterisk denotes associations in 2021 from this survey

3.2 | Family Polymorphidae Meyer 1931 (Acanthocephala, Palaeacanthocephala, Polymorphida)

3.2.1 | *Bolbosoma balaenae* (Gmelin 1790) Porta 1908

Host A

Themisto sp. Hyperiidae, marine amphipod

Localities. Otago.

Infection site. Body cavity.

Stage. Cystacanth.

References. This study, new record.

Remarks. This is the first record of a cystacanth of *B. balaenae* in New Zealand.4

Other remarks

The only previous record of *B. balaenae* from New Zealand is of a subadult in an accidental host, little penguin (*Eudyptula novaehollandiae*) from Otago, New Zealand (Bennett, McPherson, et al., 2021). The definitive host is reported in the literature as humpback whale, *Megaptera novaeangliae* (Johnston & Deland, 1929; Lehnert et al., 2019).

3.2.2 | *Profilicollis antarcticus* Zdzitowiecki 1985

Host A

Austrohelice crassa (Dana 1851). Varunidae, tunnelling mud crab.

Localities. Avon-Heathcote Estuary.

TABLE 1 Publicly available genetic data for helminth parasites infecting New Zealand marine invertebrates, for different markers

Parasite ID	Host	*28S*	*cox1*	Other markers
Acanthocephala				
Plagiorhynchus allisonae	*Transorchestia serrulata*	KU922939 (Lagrue et al., 2016)		
Bolbosoma balaenae	*Themisto* sp.	ON661298 (this study)		
Profilicollis novaezelandensis	*Hemigrapsus crenulatus*	MG602357–MG602363 (Hay et al., 2018)	MG602424–MG602473 (Hay et al., 2018)	
Cestoda				
Eutetrarhynchidae gen. sp. 1	*Pagurus traversi*	ON661299 (this study)		
	Macroctopus maorum	ON661300 (this study)		
	Halicarcinus varius	ON661301 (this study)		
	Hemiplax hirtipes	ON661302 (this study)		
	Ovalipes catharus	ON661303 (this study)		
	Hippolyte sp.	ON661304 (this study)		
Acanthobothrium sp. 1	*Nectocarcinus antarcticus*	MH924014 (Bennett et al., 2019)		
Microsomacanthus sp. 1	*Themisto* sp.	ON661305 (this study)		
Anomotaenia sp. 1	*Transorchestia serrulata*	ON661306 (this study)		
Yamaguticestus sp. 1	*Nototodarus sloanii*	ON661307 (this study)		
Yamaguticestus squali	*Nototodarus sloanii*	ON661308 (this study)		
Clistobothrium sp. 1	*Nototodarus sloanii*	ON661309 (this study)		
Clistobothrium sp. 2	*Nototodarus sloanii*	ON661310 (this study)		
Nybelinia sp. 1	*Nototodarus sloanii*	ON661311 (this study)		
Tentaculariidae gen. sp. 1	*Nototodarus sloanii*	ON661312 (this study)		
Hepatoxylon trichiuri	*Nototodarus sloanii*	ON661313 (this study)		
Trilocularia sp. 1	*Nototodarus sloanii*	ON661314 (this study)		
Anthobothrium sp. 1	*Nototodarus sloanii*	ON661315 (this study)		
Nematoda				
Anisakis simplex sensu *lato*	*Moroteuthopsis ingens*		ON661074 (this study)	*18S*, ON656399 (this study)
	Nototodarus sloanii		ON661075 (this study)	*18S*, ON656400 (this study)
Thaumamermis zealandica	*Bellorchestia quoyana*	KY264165 (Tobias et al., 2017)	KY264161 (Tobias et al., 2017)	*cytB*, KY264163; *NADH*, KY264162; *18S*, KY264164 (Tobias et al., 2017)
Anisakidae gen. sp. 1	*Balanus* sp.	ON661316 (this study)		
Trematoda				
Gymnophallus sp.	*Austrovenus stutchburyi*		FJ765467–FJ765471 (Leung, Donald, et al., 2009)	
Neolebouria maorum	*Macroctopus maorum*	ON661317 (this study)		
Lecithochirium sp. 2	*Pterygosquilla armata*	ON661318 (this study)		
Galactosomum otepotiense	*Zeacumantus subcarinatus*	MN227729 (from definitive host; Presswell & Bennett, 2020)	FJ765489 (Leung, Donald, et al., 2009)	ITS2, MN227730 (from definitive host; Presswell & Bennett, 2020)
Acanthoparyphium sp. A	*Zeacumantus subcarinatus*	ON661319 (this study)	FJ765457–FJ765459 (Leung, Donald, et al., 2009), KJ956252–KJ956278 (Keeney et al., 2015)	*16S*, FJ396045–FJ396061, FJ396063–FJ396072, FJ396076–FJ396079, FJ396082–FJ396084,

(Continues)

TABLE 1 (Continued)

Parasite ID	Host	28S	cox1	Other markers
				FJ396087–FJ396094, FJ396096–FJ396099, FJ396101, FJ396102 (Leung, Keeney, & Poulin, 2009); *ITS1*, FJ396143–FJ396145, FJ396150–FJ396152, FJ396155, KJ956376–KJ956378 (Leung, Keeney, & Poulin, 2009)
Acanthoparyphium sp. B	*Zeacumantus subcarinatus*		FJ765460–FJ765462 (Leung, Donald, et al., 2009)	*16S*, FJ396146, FJ396100 (Leung, Keeney, & Poulin, 2009); *ITS1*, FJ396146, FJ396147 (Leung, Keeney, & Poulin, 2009), KJ956379 (Keeney et al., 2015)
Acanthoparyphium sp. C	*Zeacumantus subcarinatus*		KJ956280–KJ956284 (Keeney et al., 2015), FJ765463, FJ765464 (Leung, Donald, et al., 2009)	*16S*, FJ396062, FJ396073–FJ396075, FJ396077, FJ396078, FJ396085, FJ396086, FJ396103 (Leung, Keeney, & Poulin, 2009); *ITS1*, FJ396148, FJ396149, FJ396153, FJ396154 (Leung, Keeney, & Poulin, 2009), KJ956380, KJ956381 (Keeney et al., 2015)
Acanthoparyphium sp. D	*Zeacumantus subcarinatus*		KJ956285–KJ956288 (Keeney et al., 2015), FJ765465, FJ765466 (Leung, Donald, et al., 2009)	*ITS1*, KJ956382, KJ956383 (Keeney et al., 2015)
Acanthoparyphium sp. E	*Zeacumantus lutulentus*		KJ956289–KJ956295 (Keeney et al., 2015)	*ITS1*, KJ956384, KJ956385 (Keeney et al., 2015)
Acanthoparyphium sp.	*Notoacmea scapha*	ON661320(this study)		
Himasthlidae gen. sp.	*Zeacumantus* sp.		KJ956296–KJ956375 (Keeney et al., 2015)	
Himasthla sp. 1	*Macomona liliana*	ON661321 (this study)		
	Mytilus edulis	ON661322 (this study)		
	Sigapatella novaezelandiae	ON661323 (this study)		
Curtuteria australis	*Cominella glandiformis*		FJ765453–FJ765455 (Leung, Donald, et al., 2009), KU748695–KU748697, KU748699–KU748705, KU748707 (Donald & Spencer, 2016)	Microsatellites, EU274473–EU274482 (Leung et al., 2008) *16S*, KU525065–KU525076 (Donald & Spencer, 2016), FJ396104–FJ396125, FJ396129, FJ396134 (Leung, Keeney, & Poulin, 2009); *ITS1*, KU695771–KU695783 (Donald & Spencer, 2016), FJ396158–FJ396161 (Leung, Keeney, & Poulin, 2009)

TABLE 1 (Continued)

Parasite ID	Host	28S	cox1	Other markers
Curtuteria sp. A	*Cominella glandiformis*		FJ765456 (Leung, Donald, et al., 2009), KU748690–KU748694 (Donald & Spencer, 2016)	*16S*, KU525061–KU525064 (Donald & Spencer, 2016), FJ396135–FJ396142, FJ396126–FJ396128, FJ396130–FJ396133 (Leung, Keeney, & Poulin, 2009); *ITS1* KU525066–KU525070 (Donald & Spencer, 2016), FJ396162–FJ396164 (Leung, Keeney, & Poulin, 2009)
Maritrema novaezealandense	*Zeacumantus subcarinatus*	ON661324 (this study)	FJ765472, FJ765473 (Leung, Donald, et al., 2009), FJ766537–FJ766563 (Molecular Ecology Resources Primer Development Consortium et al., 2009), GQ868102–GQ868242 (Keeney, Bryan-Walker, et al., 2009), KJ540203 (Born-Torrijos et al., 2014)	Microsatellite loci, DQ414412–DQ414418 (Keeney et al., 2006),
	Paridotea ungulata	ON661325 (this study)	FJ765474 (Leung, Donald, et al., 2009)	
	Paracalliope novizealandiae	ON661326 (this study)	FJ765475 (Leung, Donald, et al., 2009)	
	Heterosquilla tricarinata ("*Lysiosquilla spinosa*)		FJ765476 (Leung, Donald, et al., 2009)	
	Eurylana sp.	ON661327 (this study)		
Microphallidae gen. sp. 1	*Cominella glandiformis*		FJ765510 (Leung, Donald, et al., 2009), KU748725 (Donald & Spencer, 2016)	*ITS1*, KU695801, KU695802; *16S*, KU525077 (Donald & Spencer, 2016)
Microphallus sp. 1	*Zeacumantus subcarinatus*		FJ765477, FJ765479–FJ765482 (Leung, Donald, et al., 2009)	
	"Crabs"		FJ765478, FJ765483, FJ765484 (Leung, Donald, et al., 2009)	
Microphallus sp. NZ	*Austrolittorina cincta*	KJ868216, KJ868217 (O'Dwyer, Blasco-Costa, et al., 2014)	KJ868203, KJ868204 (O'Dwyer, Blasco-Costa, et al., 2014)	
Notocotylidae gen. sp. 1	*Austrolittorina antipodum*	KJ868210, KJ868212, KJ868213 (O'Dwyer, Blasco-Costa, et al., 2014)	KJ868198, KJ868200, KJ868201 (O'Dwyer, Blasco-Costa, et al., 2014)	
	Austrolittorina cincta	KJ868211 (O'Dwyer, Blasco-Costa, et al., 2014)	KJ868199 (O'Dwyer, Blasco-Costa, et al., 2014)	
Notocotylidae gen. sp. 2	*Austrolittorina antipodum*	KJ868214 (O'Dwyer, Blasco-Costa, et al., 2014)	KJ868202 (O'Dwyer, Blasco-Costa, et al., 2014)	
Opecoelidae gen. sp. A	*Diloma subrostratum*		FJ765496–FJ765500 (Leung, Donald, et al., 2009)	*16S*, AY494876–AY494878, AY494881–AY494884, AY494886, AY494891–AY494893; *ITS2*,

(Continues)

TABLE 1 (Continued)

Parasite ID	Host	28S	cox1	Other markers
				AY494908–AY494919 (Donald et al., 2004)
Opecoelidae gen. sp. B	*Diloma subrostratum*			*16S*, AY494880, AY494885, AY494887–AY494890; *ITS2*, AY494922–AY494925 (Donald et al., 2004)
Opecoelidae gen. sp. C	*Diloma aethiops*		FJ765494, FJ765495 (Leung, Donald, et al., 2009)	*16S*, AY494894–AY494901; *ITS2*, AY494926, AY494929–AY494935 (Donald et al., 2004)
	Diloma aridum			*16S*, AY494903; *ITS2*, AY494928
	Diloma nigerrimum			*16S*, AY494903; *ITS2*, AY494927 (Donald et al., 2004)
Opecoelidae gen. sp. D	*Cominella glandiformis*		FJ765501–FJ765503 (Leung, Donald, et al., 2009), KU748678, KU748680–KU748682, KU748684, KU748686, KU748687, KU748713 (Donald & Spencer, 2016)	*16S*, KU525054–KU525056, KU525059, KU525060; *ITS1*, KU695753, KU695755–KU695757, KU695759, KU695761, KU695762, KU695780 (Donald and Spencer (2016)
	Cominella adspersa		KU748679, KU748683 (Donald & Spencer, 2016)	*16S*, KU525058; *ITS1*, KY695754, KY695758, KY695763 (Donald & Spencer, 2016)
	Cominella virgata		KU748057 (Donald & Spencer, 2016)	*16S*, KU525057; *ITS1*, KU695760 (Donald & Spencer, 2016)
Opecoelidae gen. sp. E	Capitellidae gen. Spp.		FJ765504–FJ765508 (Leung, Donald, et al., 2009)	
Opecoelidae gen. sp. F	*Trizocheles spinosus*	ON661328 (this study)		
Opecoelus sp. 1	*Nyctiphanes australis*	ON661329 (this study)	ON661076 (this study)	
Philophthalmus attenuatus	*Zeacumantus subcarinatus*		FJ765485–FJ765488 (Leung, Donald, et al., 2009), GQ868079–GQ868101 (Keeney, Bryan-Walker, et al., 2009), MK482102, MK482103 (From definitive hosts; Bennett & Presswell, 2019)	*ITS2*, KJ540204 (Born-Torrijos et al., 2014)
Parorchis sp. NZ	*Austrolittorina antipodum*	KJ868208, KJ868209 (O'Dwyer, Blasco-Costa, et al., 2014)	KJ868194–KJ868197 (O'Dwyer, Blasco-Costa, et al., 2014)	
	Austrolittorina cincta	KJ868206, KJ868207 (O'Dwyer, Blasco-Costa, et al., 2014)	KJ868192, KJ868193 (O'Dwyer, Blasco-Costa, et al., 2014)	
Renicola sp. NZ	*Austrolittorina antipodum*	KJ868215 (O'Dwyer, Blasco-Costa, et al., 2014)	KJ868205 (O'Dwyer, Blasco-Costa, et al., 2014)	
Renicola sp.	*Zeacumantus subcarinatus*		FJ765490–FJ765493 (Leung, Donald, et al., 2009)	
Copiatestes thyrsitae	*Nyctiphanes australis*	ON661330 (this study)		
Schistosomatidae gen. sp. 1	*Patelloida corticata*	ON661331 (this study)		

TABLE 1 (Continued)

Parasite ID	Host	28S	cox1	Other markers
Strigeidae gen. sp. 1	*Cominella glandiformis*		FJ765510 (Leung, Donald, et al., 2009)	
Trematoda sp.	*Amphibola crenata*		FJ765511 (Leung, Donald, et al., 2009)	
Family A	*Cominella maculosa*		KU748715, KU748716, KU748718, KU748720 (Donald & Spencer, 2016)	*16S*, KU525043–KU525045; *ITS1*, KU695792, KU695795, KU695796, KU695798 (Donald & Spencer, 2016)
	Cominella virgata		KU748714, KU748717, KU748719 (Donald & Spencer, 2016)	*16S*, KU525046–KU525048; *ITS1*, KU695793, KU695794, KU695797 (Donald & Spencer, 2016)
Family B	*Cominella glandiformis*		KU748708–KU748712 (Donald & Spencer, 2016)	*16S*, KU525049–KU525053; *ITS1*, KU695799, KU695800 (Donald & Spencer, 2016)
Family C	*Cominella virgata*		KU748688, KU748689 (Donald & Spencer, 2016)	*ITS1*, KU695764, KU695765 (Donald & Spencer, 2016)

Note: GenBank accession numbers and references are provided for each marker.

Infection site. Body cavity.

Stage. Cystacanth.

References. Brockerhoff and Smales (2002).

Remarks. Brockerhoff and Smales (2002) used host name *Helice crassa*.

Host B

Hemigrapsus crenulatus (H. Milne-Edwards 1837). Varunidae, hairy-handed crab.

Localities. Governors Bay, Lyttleton Harbour; Blueskin Bay, Otago; Company Bay, Otago Harbour; Lower Portobello, Otago Harbour.

Infection site. Body cavity.

Stage. Cystacanth.

References. Brockerhoff and Smales (2002); Dittmer et al. (2011); Koehler and Poulin (2010); Latham and Poulin (2002a, 2002b); Poulin et al. (2003).

Host C

Hemiplax hirtipes (Hombron & Jacquinot 1846). Macrophthalmidae, stalk-eyed mud crab.

Localities. Governors Bay, Lyttleton Harbour; Papanui, Aramoana, and Waipuna, Otago; Blueskin Bay, Otago; Lower Portobello, Otago Harbour; Taieri Mouth, Otago.

Infection site. Body cavity.

Stage. Cystacanth.

References. Brockerhoff and Smales (2002); Dittmer et al. (2011); Fredensborg and Poulin (2005a); Koehler and Poulin (2010); Latham and Poulin (2002a, 2002b, 2003); Poulin et al. (2003).

Remarks. All of the above authors used host name *Macrophthalmus hirtipes*.

Host D

Halicarcinus varius (Dana 1851). Hymenosomatidae, pillbox crab.

Localities. Lower Portobello, Otago Harbour.

Infection site. Body cavity.

Stage. Cystacanth.

References. Koehler and Poulin (2010).

Host E

Hemigrapsus sexdentatus (H. Milne-Edwards 1837). Varunidae, purple shore crab.

Localities. Aramoana, Dowling Bay, Portobello, and Blueskin Bay, Otago.

Infection site. Body cavity.

Stage. Cystacanth.

References. Koehler and Poulin (2010); Latham and Poulin (2002a).

Remarks. Latham and Poulin (2002a) used host name *Hemigrapsus edwardsi*.

Other remarks

In New Zealand, adults of *P. antarcticus* are found in bar-tailed godwit, *Limosa lapponica*, and in South Island pied oystercatcher, *Haematopus finschi* (Brockerhoff & Smales, 2002), as well as in kelp gull, *Larus dominicanus* (Latham & Poulin, 2002c; these authors used the vernacular name "southern black-backed gull"). There is genetic sequence available for this species (from off the coast of Chile from *Hemigrapsus*

TABLE 2 Host–parasite list of helminth parasites (A, acanthocephalan, C, cestode, N, nematode, T, trematode) infecting New Zealand marine invertebrates

*Phylum clas (order)	Family	Host species	Parasite species
*Annelida			
Polychaeta			
(Phyllodocida)	Nereididae	*Perinereis* sp.	Acanthoparyphium sp. B (T)
(Terebellida)	Ampharetidae	Ampharetidae gen. sp.	*Curtuteria australis* (T)
	Terebellidae	*Streblosoma toddae*	Strigeidae gen. sp. 2 (T)
(Unassigned order)	Arenicolidae	*Abarenicola affinis*	Opecoelidae gen. sp. E (T)
	Capitellidae	*Capitella* sp.	Opecoelidae gen. sp. E (T)
		Heteromastus filiformis	Opecoelidae gen. sp. E (T)
*Arthropoda			
Malacostraca			
(Amphipoda)	Hyperiidae	*Themisto* sp.	*Bolbosoma balaenae* (A)
			Microsomacanthus sp. 1 (C)
	Paracalliopiidae	*Paracalliope novizealandiae*	*Maritrema novaezealandense* (T)
	Phoxocephalidae	*Proharpinia stephenseni*	*Maritrema novaezealandense* (T)
	Talitridae	*Bellorchestia quoyana*	*Maritrema novaezealandense* (T)
		Transorchestia serrulata	*Plagiorhynchus allisonae* (A)
			Anomotaenia sp. 1 (C)
			Maritrema novaezealandense (T)
(Decapoda)	Hymenosomatidae	*Halicarcinus varius*	*Profilicollis antarcticus* (A)
			Profilicollis novaezelandensis (A)
			Eutetrarhynchidae gen. sp. (C)
			Maritrema novaezealandense (T)
		Halicarcinus whitei	*Maritrema novaezealandense* (T)
	Hippolytidae	*Hippolyte* sp.	Eutetrarhynchidae gen. sp. 1 (C)
	Macrophthalmidae	*Hemiplax hirtipes*	*Profilicollis antarcticus* (A)
			Profilicollis novaezelandensis (A)
			Eutetrarhynchidae gen. sp. (C)
			Maritrema novaezealandense (T)
			Microphallus sp. 1 (T)
			Acuariidae gen. sp. 1 (N)
			Ascarophis sp. 1 (N)
	Ovalipidae	*Nectocarcinus antarcticus*	*Acanthobothrium* sp. 1 (C)
		Ovalipes catharus	Eutetrarhynchidae gen. sp. 1 (C)
			Ascaridoidea gen. sp. 1 (N)
	Paguridae	*Pagurus traversi*	Eutetrarhynchidae gen. sp. 1 (C)
	Portunidae	*Charybdis japonica*	Ascaridoidea gen. sp. 2 (N)
	Pylochelidae	*Trizocheles spinosus*	Opecoelidae gen. sp. 2 (T)
	Varunidae	*Austrohelice crassa*	*Profilicollis antarcticus* (A)
			Profilicollis novaezelandensis (A)
			Microphallus sp. 1 (T)
			Ascarophis sp. 1 (N)
		Cyclograpsus lavauxi	*Maritrema novaezealandense* (T)
			Microphallus sp. 1 (T)
			Ascarophis sp. 1 (N)

TABLE 2 (Continued)

*Phylum clas (order)	Family	Host species	Parasite species
		Hemigrapsus crenulatus	*Profilicollis antarcticus* (A)
			Profilicollis novaezelandensis (A)
			Microphallus sp. 1 (T)
			Ascarophis sp. 1 (N)
			Acuariidae gen. sp. 1 (N)
		Hemigrapsus sexdentatus	*Profilicollis antarcticus* (A)
			Profilicollis novaezelandensis (A)
			Maritrema novaezealandense (T)
			Microphallus sp. 1 (T)
			Ascarophis sp. 1 (N)
			Acuariidae gen. sp. 1 (N)
	Unknown	Decapoda sp.	*Hysterothylacium aduncum* (N)
(Euphausiacea)	Euphausiidae	*Nyctiphanes australis*	*Anisakis simplex* (N)
			Copiatestes thyrsitae (T)
			Opecoelus sp. 1 (T)
(Isopoda)	Cirolanidae	*Eurylana* sp.	*Maritrema novaezealandense* (T)
	Idoteidae	*Batedotea elongata*	*Maritrema novaezealandense* (T)
		Paridotea ungulata	*Maritrema novaezealandense* (T)
(Stomatopoda)	Squillidae	*Heterosquilla tricarinata*	*Maritrema novaezealandense* (T)
		Pterygosquilla armata	*Lecithochirium* sp. 2 (T)
Thecostraca			
(Balanomorpha)	Balanidae	*Balanus* sp.	Anisakidae gen. sp. 1 (N)
*Chaetognatha			
Sagittoidea			
(Aphragmophora)	Sagittidae	*Serratosagitta tasmanica*	*Hysterothylacium aduncum* (N)
*Cnidaria	Unknown	Cnidaria sp.	*Hysterothylacium aduncum* (N)
*Mollusca			
Bivalvia			
(Cardiida)	Tellinidae	*Macomona liliana*	*Himasthla* sp. 1 (T)
			Curtuteria australis (T)
			Acanthoparyphium sp. A (T)
			Gymnophallus sp. 1 (T)
(Mytilida)	Mytilidae	*Mytilus edulis*	*Himasthla* sp. 1 (T)
			Gymnophallus sp. 1 (T)
		Mytilus galloprovincialis	*Tergestia agnostomi* (T)
		Perna canaliculus	*Tergestia agnostomi* (T)
			Alcicornis longicornutus (T)
(Ostreida)	Ostreidae	*Ostrea chilensis*	*Alcicornis longicornutus* (T)
(Venerida)	Veneridae	*Austrovenus stutchburyi*	*Gymnophallus* sp. 1 (T)
			Acanthoparyphium sp. A (T)
			Curtuteria sp. A (T)
			Curtuteria australis (T)
			Faustulidae gen. sp. 1 (T)
Cephalopoda			
(Octopoda)	Octopodidae	*Macroctopus maorum*	Eutetrarhynchidae gen. sp. 1 (C)

(Continues)

TABLE 2 (Continued)

*Phylum clas (order)	Family	Host species	Parasite species
			Neolebouria maorum (T)
			Lecithochirium sp. 1 (T)
		Octopus australis	*Neolebouria maorum* (T)
(Oegopsida)	Ommastrephidae	*Nototodarus sloanii*	*Nybelinia* sp. 1 (C)
			Anthobothrium sp. 1 (C)
			Hepatoxylon trichiuri (C)
			Tentaculariidae gen. sp. 1 (C)
			Trilocularia sp. 1 (C)
			Yamaguticestus sp. 1 (C)
			Yamaguticestus squali (C)
			Contracaecum sp. 1 (N)
			Anisakis simplex s.l. (N)
	Onychoteuthidae	*Moroteuthopsis ingens*	*Clistobothrium* sp. 1 (C)
			Clistobothrium sp. 2 (C)
			Anisakis simplex s.l. (N)
Gastropoda			
(Littorinimorpha)	Littorinidae	*Austrolittorina antipodum*	*Renicola* sp. NZ (T)
			Parorchis sp. NZ (T)
			Notocotylidae gen. sp. 1 NZ (T)
			Notocotylidae gen. sp. 2 NZ (T)
		Austrolittorina cincta	*Parorchis* sp. NZ (T)
			Notocotylidae gen. sp. 1 NZ (T)
			Microphallus sp. NZ (T)
(Neogastropoda)	Cominellidae	*Cominella adspersa*	Opecoelidae gen. sp. d (T)
		Cominella glandiformis	*Profilicollis* sp. (A)
			Trematoda Family B (T)
			Strigeidae gen sp. 1 (T)
			Opecoelidae gen. sp. d (T)
			Microphallidae gen. sp. 1 (T)
			Maritrema sp. 1 (T)
			Curtuteria australis (T)
			Curtuteria sp. A (T)
			Acuariidae gen. sp. 1 (N)
		Cominella maculosa	Trematoda Family A (T)
		Cominella virgata	Trematoda Family A (T)
			Trematoda Family C (T)
			Opecoelidae gen. sp. d (T)
(Unassigned)	Batillariidae	*Zeacumantus lutulentus*	*Acanthoparyphium* sp. E (T)
			Himasthlidae gen. sp. (T)
			Acanthoparyphium sp. A (T)
			Acanthoparyphium sp. A (T)
			Acanthoparyphium sp. A (T)
			Acanthoparyphium sp. A (T)
			Galactosomum otepotiense (T)
			Himasthlidae gen. sp. (T)

TABLE 2 (Continued)

*Phylum clas (order)	Family	Host species	Parasite species
			Microphallus sp. 1 (T)
			Microphallidae gen. sp. 2 (T)
			Maritrema novaezealandense (T)
			Philophthalmus attenuatus (T)
			Renicola sp. 1 (T)
	Amphibolidae	*Amphibola crenata*	Trematoda sp. (T)
		Sigapatella novaezelandiae	*Himasthla* sp. 1 (T)
		Notoacmea scapha	Opecoelidae gen. sp. A (T)
			Curtuteria australis (T)
			Acanthoparyphium sp. A (T)
			Acanthoparyphium sp. (T)
		Patelloida corticata	Schistosomatidae gen. sp. 1 (T)
(Trochida)	Trochidae	*Diloma aethiops*	Opecoelidae gen. sp. b (T)
		Diloma aridum	Opecoelidae gen. sp. b (T)
		Diloma nigerrimum	Opecoelidae gen. sp. b (T)
		Diloma subrostratum	Opecoelidae gen. sp. A (T)
			Opecoelidae gen. sp. b (T)
			Opecoelidae gen. sp. c (T)
Polyplacophora			
(Chitonida)	Chitonidae	*Chiton glaucus*	*Acanthoparyphium* sp. A (T)
		Sypharochiton pelliserpentis	*Acanthoparyphium* sp. A (T)

crenulatus; Rodríguez et al., 2017), but not from New Zealand. The type specimens for this species are probably kept at the Research Centre for Parasitology, Polish Academy of Sciences, Warsaw.

3.2.3 | *Profilicollis novaezelandensis* Brockerhoff & Smales, 2002

Host A

Austrohelice crassa. Varunidae, tunnelling mud crab.
Localities. Avon-Heathcote Estuary; Governors Bay, Littleton Harbour.
Infection site. Body cavity.
Stage. Cystacanth.
References. Brockerhoff and Smales (2002).
Remarks. Brockerhoff and Smales (2002) used host name *Helice crassa*.

Host B

Hemigrapsus crenulatus. Varunidae, hairy-handed crab.
Localities. Avon-Heathcote Estuary; Governers Bay, Littleton Harbour; Blueskin Bay, Otago; Company Bay, Otago Harbour; Lower Portobello, Otago Harbour; Christchurch, Kakanui, Aramoana, Taieri Mouth, Papatowai and Invercargill.
Infection site. Body cavity.
Stage. Cystacanth.
References. Brockerhoff and Smales (2002); Dittmer et al. (2011); Hay et al. (2018); Koehler and Poulin (2010); Latham and Poulin (2002a, 2002b); Poulin et al. (2003).

Host C

Hemiplax hirtipes. Macrophthalmidae, stalk-eyed mud crab.
Localities. Avon-Heathcote Estuary; Governors Bay, Littleton Harbour; Papanui, Aramoana and Waipuna, Otago; Blueskin Bay, Otago; Lower Portobello, Otago Harbour; Taieri Mouth, Otago.
Infection site. Body cavity.
Stage. Cystacanth.
References. Brockerhoff and Smales (2002); Dittmer et al. (2011); Fredensborg and Poulin (2005b); Koehler and Poulin (2010); Latham and Poulin (2002a, 2002b, 2003); Poulin et al. (2003).
Remarks. All of the above authors used host name *Macrophthalmus hirtipes*.

Host D

Halicarcinus varius. Hymenosomatidae, pillbox crab.
Localities. Lower Portobello, Otago Harbour.
Infection site. Body cavity.
Stage. Cystacanth.
References. Koehler and Poulin (2010).

Host E

Hemigrapsus sexdentatus. Varunidae, purple shore crab.

Localities. Aramoana, Dowling Bay, Portobello, and Blueskin Bay, Otago.

Infection site. Body cavity.

Stage. Cystacanth.

References. Koehler and Poulin (2010); Latham and Poulin (2002a).

Remarks. Latham and Poulin (2002a) used host name *Hemigrapsus edwardsi*.

Other remarks

In New Zealand, adults of *P. antarcticus* are found in bar-tailed godwit, *Limosa lapponica*, and in South Island pied oystercatcher, *Haematopus finschi* (Brockerhoff & Smales, 2002), as well as in kelp gull, *Larus dominicanus* (Latham & Poulin, 2002c; these authors used the vernacular name "southern black-backed gull"). Type specimens are deposited as NMNZ ZW 1497 at National Museum, Wellington, New Zealand (NMNZ).

3.2.4 | *Profilicollis* sp.

Host A (experimentally infected)

Cominella glandiformis (Reeve 1847). Cominellidae, mudflat whelk.

Localities. Waipuna Bay, Otago Harbour.

Infection site. Digestive tract.

Stage. Cystacanth.

References. Latham et al. (2003).

Remarks. Latham et al. (2003) state that the cystacanths are ingested by scavenging freshly dead crabs (*H. hirtipes*, *H. crenulatus*, and *H. sexdentatus*) infected with *Profilicollis* spp. and that the whelk is a temporary paratenic host. They do not say which of the *Profilicollis* species is implicated.

3.3 | Family Dilepididae Railliet & Henry 1909 (Platyhelminthes, Cestoda, Cyclophyllidea)

3.3.1 | *Anomotaenia* sp. 1

Host A

Transorchestia serrulata. Talitridae, intertidal amphipod.

Localities. Lower Portobello, Otago Harbour.

Infection site. Body cavity.

Stage. Metacestode, cysticercoid type.

References. Lagrue et al. (2016).

3.4 | Family Hymenolepididae Perrier 1897 (Platyhelminthes, Cestoda, Cyclophyllidea)

3.4.1 | *Microsomacanthus* sp. 1

Host A

Themisto sp. Hyperiidae, marine amphipod.

Localities. Otago Harbour.

Infection site. Body cavity.

Stage. Metacestode, cysticercoid type.

References. This study, new record.

3.5 | Family Onchobothriidae Braun 1900 (Platyhelminthes, Cestoda, Onchoproteocephalidea)

3.5.1 | *Acanthobothrium* sp. 1

Host A

Nectocarcinus antarcticus (Hombron & Jacquinot 1846). Ovalipidae, red swimming crab.

Localities. Otago coast.

Infection site. Body cavity.

Stage. Metacestode, plerocercoid type.

References. Bennett et al. (2019).

Other remarks. Adults are found in rough skate, *Zearaja nasuta* (Bennett et al., 2019).

3.6 | Family Phyllobothriidae Braun 1900 (Platyhelminthes, Cestoda, Phyllobothriidea)

3.6.1 | *Yamaguticestus* sp. 1

Host A

Nototodarus sloanii (Gray 1849). Ommastrephidae, arrow squid.

Localities. Otago.

Infection site. Visceral cavity.

Stage. Metacestode, plerocercoid type.

References. This study, new record.

3.6.2 | *Yamaguticestus squali* (Yamaguti 1952) Caira, Bueno & Jensen 2021

Host A

Nototodarus sloanii. Ommastrephidae, arrow squid.

Localities. Otago.

Infection site. Visceral cavity.

Stage. Metacestode, plerocercoid type.

References. This study, new record.

Other remarks. Type specimens are held at Meguro Parasitological Museum, Tokyo, under collection number 22778.

3.6.3 | *Clistobothrium* sp. 1

Host A

Moroteuthopsis ingens (E. A. Smith 1881). Onychoteuthidae, greater hooked squid.

Localities. Chatham Rise.
Infection site. Visceral cavity.
Stage. Metacestode, plerocercoid type.
References. This study, new record.

3.6.4 | *Clistobothrium* sp. 2

Host A
Moroteuthopsis ingens. Onychoteuthidae, greater hooked squid.
Localities. Chatham Rise.
Infection site. Visceral cavity.
Stage. Metacestode, plerocercoid type.
References. This study, new record.

3.7 | Family Eutetrarhynchidae Guiart 1927 (Platyhelminthes, Cestoda, Trypanorhyncha)

3.7.1 | Eutetrarhynchidae gen. sp. 1

Host A
Pagurus traversi (Filhol 1885). Paguridae, hermit crab.
Localities. Otago.
Infection site. Body cavity.
Stage. Metacestode; plerocercus type.
References. This study, new record.

Host B
Macroctopus maorum (Hutton 1880). Octopodidae, New Zealand octopus.
Localities. Otago.
Infection site. Body cavity.
Stage. Metacestode; plerocercus type.
References. This study, new record.

Host C
Halicarcinus varius. Hymenosomatidae, pillbox crab.
Localities. Otago.
Infection site. Body cavity.
Stage. Metacestode; plerocercus type.
References. This study, new record.

Host D
Hemiplax hirtipes. Macrophthalmidae, stalk-eyed mud crab.
Localities. Otago.
Infection site. Body cavity.
Stage. Metacestode; plerocercus type.
References. This study, new record.

Host E
Ovalipes catharus (White in White & Doubleday 1843). Ovalipidae, paddle crab.
Localities. Otago.
Infection site. Body cavity.
Stage. Metacestode; plerocercus type.
References. This study, new record.

Host F
Hippolyte sp. Hippolytidae, chameleon shrimp.
Localities. Otago.
Infection site. Body cavity.
Stage. Metacestode; plerocercus type.
References. This study, new record.

3.8 | Family Tentaculariidae Poche 1926 (Platyhelminthes, Cestoda, Trypanorhyncha)

3.8.1 | *Nybelinia* sp. 1

Host A
Nototodarus sloanii. Ommastrephidae, arrow squid.
Localities. Karamea Bight, Tasman Bay and Cape Egmont, Taranaki.
Infection site. Visceral cavity and muscle.
Stage. Metacestode, plerocercoid type.
References. Smith et al. (1981).
Remarks. Smith et al. (1981) reported *Nototodarus sloanii* as *N. sloani*.

Other remarks
We have since recovered *Nybelinia* sp. from arrow squid and assume that our specimens and those of Smith et al. (1981) represent the same species.

3.8.2 | Tentaculariidae gen. sp. 1

Host A
Nototodarus sloanii. Ommastrephidae, arrow squid.
Localities. Otago.
Infection site. Visceral cavity.
Stage. Metacestode, plerocercoid type.
References. This study, new record.

3.9 | Family Sphyriocephalidae Pintner 1913 (Platyhelminthes, Cestoda, Trypanorhyncha)

3.9.1 | *Hepatoxylon trichiuri* (Holten 1802) Bosc 1811

Host A
Nototodarus sloanii. Ommastrephidae, arrow squid.
Localities. Otago.
Infection site. Visceral cavity.
Stage. Metacestode, plerocercoid type.
References. This study, new record.

3.10 | Family Tetraphyllidea *incertae sedis* (Platyhelminthes, Cestoda, "Tetraphyllidea")

3.10.1 | *Trilocularia* sp. 1

Host A

Nototodarus sloanii. Ommastrephidae, arrow squid.
Localities. Otago.
Infection site. Visceral cavity.
Stage. Metacestode, plerocercoid type.
References. This study, new record.

3.10.2 | *Anthobothrium* sp. 1

Host A

Nototodarus sloanii. Ommastrephidae, arrow squid.
Localities. Otago.
Infection site. Visceral cavity.
Stage. Metacestode, plerocercoid type.
References. This study, new record.

3.11 | Family Bucephalidae Poche 1907 (Platyhelminthes, Trematoda, Plagiorchiida)

3.11.1 | *Alcicornis longicornutus* Manter 1954

Host A

Ostrea chilensis Küster 1844. Ostreidae, dredge oyster.
Localities. Foveaux Strait; Wellington Harbour, Tasman Bay, Timaru, and Hauraki Gulf; Marlborough Sounds.
Infection site. Gonad.
Stage. Redia and sporocyst.
References. Howell (1966, 1967); Jones (1975); Millar (1963).
Remarks. Howell (1966, 1967), Jones (1975), and Millar (1963) list *O. chilensis* as *Ostrea lutaria*, which is a superseded combination.

Host B

Perna canaliculus (Gmelin 1791). Mytilidae, green-lipped mussel.
Localities. Tasman Bay, Wellington Harbour.
Infection site. Gonads.
Stage. Sporocyst.
References. Haswell (1903); Jones (1975).

Other remarks

Howell (1966, 1967) and Jones (1975) refer to *A. longicornutus* as *Bucephalus longicornutus*. An adult was described and documented in New Zealand from a giant stargazer, *Kathetostoma giganteum* (Manter, 1954). The type specimen is held at the U.S. National Museum helminth collection under number 49116.

3.12 | Family Faustulidae Poche 1926 (Platyhelminthes, Trematoda, Plagiorchiida)

3.12.1 | Faustulidae gen. sp. 1

Host A

Austrovenus stutchburyi (W. Wood 1828). Veneridae, cockle.
Localities. Otago Harbour.
Infection site. Gonads.
Stage. Sporocysts.
References. Chilton (1905); Leung, Donald, et al. (2009); Mouritsen (2002); Poulin et al. (1998, 2000).

Other remarks

The cercarial stage was named *Cercaria pectinata* Huet, 1891 in the above references. This cercaria has been assigned to *Bacciger bacciger* (Rudolphi 1819) Nicoll 1914 by various sources (Bray & Gibson, 1980; Palombi, 1934) but not for New Zealand specimens. We have therefore taken a cautious approach in assigning the records from New Zealand to family level.

3.13 | Family Fellodistomidae Nicoll 1909 (Platyhelminthes, Trematoda, Plagiorchiida)

3.13.1 | *Tergestia agnostomi* Manter 1954

Host A

Mytilus galloprovincialis Lamarck 1819. Mytilidae, Mediterranean mussel.
Localities. Not specified.
Infection site. Not specified.
Stage. Sporocysts.
References. Jones (1975).
Remarks. Jones (1975) referred to *M. galloprovincialis* as *Mytilus edulis aoteanus*.

Host B

Perna canaliculus. Mytilidae, green-lipped mussel.
Localities. Not specified.
Infection site. Not specified.
Stage. Sporocysts.
References. Haswell (1903); Hickman (1978); Jones (1975); Linzey (1971).

Other remarks

Jones (1975) notes that the cercarial stage of *T. agnostomi*, originally described by Haswell (1903) as "*Echinostomum*," was named *Cercaria haswelli* Dollfus 1927. Linzey (1971) and Hickman (1978) also referred to this species as *Cercaria haswelli*. The adult stage is found in yellow-eyed mullet, *Aldrichetta forsteri* (Jones, 1975). The type specimens are held at the U.S. National Museum helminth collection under accession 49140.

3.14 | Family Gymnophallidae Odhner 1905 (Platyhelminthes, Trematoda, Plagiorchiida)

3.14.1 | *Gymnophallus* sp. 1

Host A

Austrovenus stutchburyi. Veneridae, cockle.

Localities. Company Bay, Otago Harbour, and Blueskin Bay, Otago.
Infection site. Epithelium.
Stage. Metacercariae, not encysted.
References. Leung, Donald, et al. (2009); Leung and Poulin (2007); Leung et al. (2007); Leung, Donald, et al. (2009); Poulin et al. (2000).

Host B

Macomona liliana (Iredale 1915). Tellinidae, wedge clam.
Localities. Otago Harbour.
Infection site. Epithelium.
Stage. Metacercariae, not encysted.
Reference. Leung, Donald, et al. (2009).

Host C. *Mytilus edulis* Linnaeus 1758. Mytilidae, blue mussel.
Localities. Otago Harbour.
Infection site. Epithelium.
Stage. Metacercariae.
References. This study, new record.

Other remarks

Poulin et al. (2000) listed this species as *Meiogymnophallus* sp.; Leung and Poulin (2007) referred to it as "gymnophallid metacercaria," and Leung et al. (2007), Leung, Donald, et al. (2009), and Leung, Poulin, and Keeney (2009) called it *Gymnophallus* sp.

3.15 | Family Hemiuridae Looss 1899 (Platyhelminthes, Trematoda, Plagiorchiida)

3.15.1 | *Lecithochirium* sp. 1

Host A

Macroctopus maorum. Octopodidae, New Zealand octopus.
Localities. Kaikoura Peninsula.
Infection site. Embedded in wall of stomach.
Stage. Immature adult.
References. Overstreet and Hochberg (1975)
Remarks. Overstreet and Hochberg (1975) referred to *M. maorum* as *Octopus maorum*.

Other remarks

The specimens of Overstreet and Hochberg (1975) are reported as immature adults, suggesting that the octopus is acting as paratenic host, with a probable fish as definitive host.

3.15.2 | *Lecithochirium* sp. 2

Host A. *Pterygosquilla armata* (H. Milne-Edwards 1837). Squillidae, mantis shrimp.
Localities. Otago.
Infection site. Body cavity.
Stage. Metacercariae.
References. New record.

3.16 | Family Heterophyidae Leiper 1909 (Platyhelminthes, Trematoda, Plagiorchiida)

3.16.1 | *Galactosomum otepotiense* Presswell & Bennett 2020

Host A

Zeacumantus subcarinatus (G. B. Sowerby II 1855). Batillariidae, mud whelk.
Localities. Dowling Bay, Latham Bay, Oyster Bay in Otago; Lower Portobello, Otago Harbour.
Infection site. Gonad and digestive gland.
Stage. Redia.
References. Leung, Donald, et al. (2009); Lloyd and Poulin (2011); Martorelli et al. (2008); Presswell and Bennett (2020).
Remarks. Before its description in 2019 (Presswell & Bennett, 2020), *Galactosomum otepotiense* was called *Galactosomum* sp. by the above authors.

Other remarks

The adult of this species was described from four different piscivorous birds: Caspian tern, *Hydroprogne caspia*; red-billed gull, *Chroicocephalus scopulinus*; kelp gull, *Larus dominicanus*; and little penguin, *Eudyptula novaehollandiae* (Presswell & Bennett, 2020). Type specimens are deposited at the Te Papa Museum, Wellington (accession numbers W.003498–W.003502) and the Otago Museum, Dunedin (accession numbers IV107611–IV107616).

3.17 | Family Himasthlidae Odhner 1910 (Platyhelminthes, Trematoda, Plagiorchiida)

3.17.1 | *Acanthoparyphium* sp. A of Leung, Keeney, and Poulin (2009)

Host A

Austrovenus stutchburyi. Veneridae, cockle.
Localities. Otago Harbour; Blueskin Bay, Otago.
Infection site. Foot.
Stage. Encysted metacercaria.
References. Babirat et al. (2004); Leung, Donald, et al. (2009); Leung, Keeney, and Poulin (2009)); Leung and Poulin (2007, 2011); Mouritsen and Poulin (2005); Poulin and Mouritsen (2004).

Host B

Chiton glaucus Gray 1828. Chitonidae, green chiton.
Localities. Otago Harbour.
Infection site. Mantle cavity.
Stage. Encysted metacercaria.
References. New record.

Host C

Sypharochiton pelliserpentis (Quoy & Gaimard 1835). Chitonidae, snake-skin chiton.
Localities. Otago Harbour.
Infection site. Mantle cavity.
Stage. Encysted metacercaria.
References. New record.

Other remarks

We provide a video file of metacercarial movement from this chiton host in Video S1.

Host D

Macomona liliana. Tellinidae, wedge clam.
Localities. Otago Harbour.
Infection site. Foot.
Stage. Encysted metacercaria.
References. Leung, Donald, et al. (2009); Leung and Poulin (2008).

Host E

Zeacumantus subcarinatus. Batillariidae, mud whelk.
Localities. Widespread, South Island and North Island.
Infection site. Gonad and digestive gland.
Stage. Redia.
References. Babirat et al. (2004); Hay et al. (2005); Keeney et al. (2015); Koprivnikar and Poulin (2009a); Leung, Donald, et al. (2009); Leung, Keeney, and Poulin (2009)); Lloyd and Poulin (2011); MacLeod and Poulin (2015, 2016a, 2016b); Martorelli et al. (2006).

Host F

Notoacmea scapha (Suter 1907). Lottiidae, estuarine limpet.
Localities. Otago Harbour.
Infection site. Not specified.
Stage. Encysted metacercariae.
References. Koppel et al. (2011).
Remarks. This host is likely to be a dead-end host (Koppel et al., 2011).

Other remarks

The name used here, *Acanthoparyphium* sp. A, follows Leung, Keeney, and Poulin (2009)) and is used mostly in the literature thereafter. Prior to that paper, Babirat et al. (2004) reported on a "23-spine echinostome"; Poulin and Mouritsen (2004) reported a "second echinostome"; Mouritsen and Poulin (2005) referred to a "second related but undescribed trematode"; Hay et al. (2005), Leung and Poulin (2007), Lloyd and Poulin (2011), and MacLeod and Poulin (2015, 2016a, 2016b) reported "*Acanthoparyphium* sp." Martorelli et al. (2006) deposited voucher specimens of cercariae and metacercariae in the Museo de La Plata, Argentina, Helminthological Collection (MPHC) under the accession numbers 5537 and 5538, named "*Acanthoparyphium* sp."

3.17.2 | *Acanthoparyphium* sp. B of Leung, Keeney, and Poulin (2009))

Host A

Zeacumantus subcarinatus. Batillariidae, mud whelk.
Localities. Otago Peninsula.
Infection site. Not specified.
Stage. Redia.
References. Keeney et al. (2015); Leung, Donald, et al. (2009); Leung, Keeney, and Poulin (2009)).

Host B

Perinereis sp. Nereididae, polychaete worm.
Localities. Otago Harbour.
Infection site. Found in the mouth parts.
Stage. Encysted metacercariae.
References. Leung, Donald, et al. (2009); Peoples et al. (2012).
Remarks. The polychaete is assumed to be an accidental host of this *Acanthoparyphium* species (Peoples et al., 2012).

3.17.3 | *Acanthoparyphium* sp. C of Leung, Keeney, and Poulin (2009)

Host A

Zeacumantus subcarinatus. Batillariidae, mud whelk.
Localities. Otago and Canterbury.
Infection site. Not specified.
Stage. Redia.
References. Keeney et al. (2015); Leung, Donald, et al. (2009); Leung, Keeney, and Poulin (2009).

3.17.4 | *Acanthoparyphium* sp. D of Leung, Keeney, and Poulin (2009)

Host A

Zeacumantus subcarinatus. Batillariidae, mud whelk
Localities. Otago and Canterbury coast, Porirua Wellington.
Infection site. Not specified.
Stage. Redia.
References. Keeney et al. (2015); Leung, Donald, et al. (2009); Leung, Keeney, and Poulin (2009).

3.17.5 | *Acanthoparyphium* sp. E of Keeney et al. (2015)

Host A

Zeacumantus lutulentus (Kiener 1841). Batillariidae, mud whelk.
Localities. Northern South Island and North East North Island.
Infection site. Not specified.

Stage. Redia.
References. Keeney et al. (2015).

3.17.6 | *Acanthoparyphium* sp.

Host A
Notoacmea scapha. Lottiidae, estuarine limpet.
Localities. Otago Harbour.
Infection site.
Stage. Metacercariae.
References. New record.

Other remarks
Based on DNA sequencing of a partial *28S* sequence, this is not *Acanthoparyphium* sp. A previously known to infect *N. scapha* (Koppel et al., 2011). It is likely to be one of the above *Acanthoparyphium* spp. B–E, but without further DNA analysis, we are unable to assign it to one of them, and have therefore left it undesignated.

3.17.7 | Himasthlidae gen. sp.

Host A
Zeacumantus lutulentus. Batillariidae, mud whelk.
Localities. North and South Islands.
Infection site. Not specified.
Stage. Redia.
References. Keeney et al. (2015).

Host B
Zeacumantus subcarinatus. Batillariidae, mud whelk.
Localities. Throughout South Island.
Infection site. Not specified.
Stage. Redia.
References. Keeney et al. (2015).

Other remarks
Keeney et al. (2015) listed this in the subfamily Himasthlinae but this is not currently accepted according to WoRMS (marinespecies.org).

3.17.8 | *Himasthla* sp. 1

Host A
Macomona liliana. Tellinidae, wedge clam.
Localities. Otago Harbour.
Infection site. Metacercaria.
Stage. Foot.
References. This study, new record.

Host B
Mytilus edulis. Mytilidae, blue mussel.
Localities. Otago Harbour.
Infection site. Metacercaria.
Stage. Foot.
References. This study, new record.

Host C
Sigapatella novaezelandiae (Lesson 1831). Calyptraeidae, limpet.
Localities. Otago Harbour.
Infection site. Metacercaria.
Stage. Foot.
References. This study, new record.

3.17.9 | *Curtuteria australis* Allison, 1979

Host A
Austrovenus stutchburyi. Veneridae, cockle.
Localities. Heathcote-Avon estuary, Christchurch; Otago Harbour.
Infection site. Foot.
Stage. Encysted metacercaria.
References. Allison (1979); Babirat et al. (2004); Leung et al. (2008); Leung, Donald, et al. (2009); Leung et al., (2010); Leung and Poulin (2007, 2010a, 2010b, 2011); McFarland et al. (2003); Mouritsen (2002); Mouritsen et al. (2003); Mouritsen and Poulin (2003a, 2003b, 2005); O'Connell-Milne et al. (2016); Poulin and Mouritsen (2004); Thomas and Poulin (1998).
Remarks. Allison (1979) referred to this host as *Chione stutchburyi*.

Host B
Cominella glandiformis. Cominellidae, mudflat whelk.
Localities. Heathcote-Avon estuary; Otago Harbour; Northland; Auckland; Tasman; Bay of Plenty.
Infection site. Gonad–digestive gland complex.
Stage. Redia.
References. Allison (1979); Babirat et al. (2004); Donald and Spencer (2016); Leung, Donald, et al. (2009); Leung, Keeney, and Poulin (2009); Lloyd and Poulin (2011); McFarland et al. (2003); Mouritsen et al. (2003); Poulin and Mouritsen (2004, 2006); Thieltges et al. (2009).

Host C
Macomona liliana. Tellinidae, wedge clam.
Localities. Lower Portobello, Otago Harbour.
Infection site. Foot.
Stage. Encysted metacercaria.
References. Leung, Donald, et al. (2009); Leung, Keeney, and Poulin (2009); Leung and Poulin (2008, 2010a).

Host D
Notoacmea scapha. Lottiidae, estuarine limpet.
Localities. Otago Harbour.
Infection site. Host tissue.
Stage. Encysted metacercaria.
References. Koppel et al. (2011).

Host E

Ampharetidae gen. sp., polychaete worm.

Localities. Otago Harbour.

Infection site. Within host tissue and coelom.

Stage. Encysted metacercaria.

References. Peoples et al. (2012).

Other remarks

Adults of *C. australis* are known from the South Island pied oystercatcher, *Haematopus finschi* (Allison, 1979). Type specimens are held at Te Papa Museum, New Zealand.

3.17.10 | *Curtuteria* sp. A of Leung, Keeney, and Poulin (2009)

Host A

Austrovenus stutchburyi. Veneridae, cockle.

Localities. Otago Harbour.

Infection site. Foot.

Stage. Encysted metacercariae.

References. Leung, Donald, et al. (2009).

Host B

Cominella glandiformis. Cominellidae, mudflat whelk.

Localities. Otago Harbour; Northland; Auckland, Tasman.

Infection site. Gonad–digestive gland complex.

Stage. Redia.

References. Donald and Spencer (2016); Leung, Donald, et al. (2009); Leung, Keeney, and Poulin (2009).

Other remarks

Leung, Keeney, and Poulin (2009) originally detected this species molecularly as a cryptic sister species to *C. australis*, which we name *Curtuteria* sp. A for future comparison.

3.18 | Family Microphallidae Ward 1901 (Platyhelminthes, Trematoda, Plagiorchiida)

3.18.1 | *Levinseniella* sp. 1

Host A

Hemigrapsus sexdentatus. Varunidae, purple shore crab.

Localities. Otago Peninsula.

Infection site. Body cavity.

Stage. Metacercaria.

References. New record, this study.

3.18.2 | *Maritrema novaezealandense* Fredensborg et al., 2004

Host A

Proharpinia stephenseni (Schellenberg 1931). Phoxocephalidae, benthic amphipod.

Localities. Otago Peninsula.

Infection site. Not specified.

Stage. Metacercaria.

References. Koehler, Gonchar et al. (2011).

Remarks. Host is referred to as *Heterophoxus stephenseni* in Koehler, Gonchar et al. (2011).

Host B

Transorchestia serrulata. Talitridae, intertidal amphipod.

Localities. Otago Harbour.

Infection site. Gills, hepatopancreas, appendages, or free within the body cavity.

Stage. Metacercariae.

References. Koehler and Poulin (2010).

Host C

Paracalliope novizealandiae (Dana 1852). Paracalliopiidae, benthic amphipod.

Localities. Otago Peninsula; Otago Harbour.

Infection site. Gills, hepatopancreas, appendages, or free within the body cavity.

Stage. Encysted metacercariae.

References. Bates et al. (2010); Bryan-Walker et al. (2007); Fredensborg and Poulin (2005b); Fredensborg et al. (2004); Harland et al. (2015); Koehler, Gonchar et al. (2011); Koehler and Poulin (2010); Studer and Poulin (2013b) Leung, Donald, et al. (2009); Leung and Poulin (2006).

Host D

Cyclograpsus lavauxi H. Milne-Edwards 1853. Varunidae, smooth shore crab.

Localities. Otago Harbour.

Infection site. Gills, hepatopancreas, appendages, or free within the body cavity.

Stage. Encysted metacercaria.

References. Koehler and Poulin (2010).

Host E

Halicarcinus varius. Hymenosomatidae, pillbox crab.

Localities. Otago Harbour.

Infection site. Gills, hepatopancreas, appendages, or free within the body cavity.

Stage. Encysted metacercaria.

References. Koehler and Poulin (2010); Leung, Donald, et al. (2009).

Host F

Halicarcinus whitei (Miers 1876). Hymenosomatidae, estuarine pillbox crab.

Localities. Otago Harbour; Otago peninsula

Infection site. Body cavity.

Stage. Encysted metacercaria.

References. Leung, Donald, et al. (2009); Martorelli et al. (2004).

Host G

Hemigrapsus crenulatus. Varunidae, hairy-handed crab.

Localities. Otago Harbour; Otago Peninsula; Taieri Mouth, Otago.

Infection site. Gills, hepatopancreas, appendages, or free within the body cavity.

Stage. Encysted metacercaria.

References. Dittmer et al. (2011); Koehler and Poulin (2010); Leung, Donald, et al. (2009); Martorelli et al. (2004); Poulin et al. (2003).

Host H

Hemigrapsus sexdentatus. Varunidae, purple shore crab.

Localities. Otago Harbour.

Infection site. Gills, hepatopancreas, appendages, or free within the body cavity.

Stage. Encysted metacercaria.

References Koehler and Poulin (2010); Leung, Donald, et al. (2009).

Host I

Hemiplax hirtipes. Macrophthalmidae, stalk-eyed mud crab.

Localities. Otago Harbour; Otago Peninsula; Taieri Mouth, Otago.

Infection site. Gills, hepatopancreas, appendages or free within the body cavity.

Stage. Encysted metacercaria.

References. Dittmer et al. (2011); Fredensborg and Poulin (2005a, 2005b); Keeney et al. (2007a); Koehler and Poulin (2010, 2012); Leung, Donald, et al. (2009); Martorelli et al. (2004); Poulin et al. (2003).

Remarks. All above authors used host name *Macrophthalmus hirtipes*.

Host J

Heterosquilla tricarinata (Claus 1871). Tetrasquillidae, mantis shrimp.

Localities. Otago Harbour.

Infection site. Gills, hepatopancreas, appendages, or free within the body cavity.*Stage*. Encysted metacercaria.

References. Koehler and Poulin (2010); Leung, Donald, et al. (2009).

Remarks. Above authors used host name *Lysiosquilla spinosa*.

Host K

Zeacumantus subcarinatus. Batillariidae, mud whelk.

Localities. Otago Harbour.

Infection site. Gonads.

Stage. Sporocyst, cercaria.

References. Bates et al. (2011); Berkhout et al. (2014); Born-Torrijos et al. (2014); Fredensborg and Poulin (2005a, 2005b); Fredensborg et al. (2005); Harland et al. (2016); Hay et al. (2005); Kamiya and Poulin (2012); Kamiya et al. (2013); Keeney, Boessenkool et al. (2008); Keeney, Bryan-Walker et al. (2008); Keeney, Bryan-Walker et al. (2009); Keeney, King et al. (2009); Keeney, Lagrue et al. (2008); Keeney et al. (2006, 2007a, 2007b); Koehler, Springer et al. (2011); Koehler et al. (2012); Koprivnikar and Poulin (2009a, 2009b); Leung, Donald, et al. (2009); Lloyd and Poulin (2011, 2012, 2013); MacLeod and Poulin (2015, 2016a, 2016b); MacLeod et al. (2017); Martorelli et al. (2004); Molecular Ecology Resources Primer Development Consortium (2009); Studer, Cubillos, et al. (2012); Studer, Lamare, and Poulin (2012); Studer and Poulin (2012a, 2012b, 2013a): Studer et al. (2013, 2010).

Host L

Eurylana sp. Cirolanidae, isopod.

Localities. Otago Harbour.

Infection site. Body cavity.

Stage. Encysted metacercaria.

References. New record.

Host M

Paridotea ungulata (Pallas 1772). Idoteidae, seaweed isopod.

Localities. Otago Harbour.

Infection site. Body cavity and appendages.

Stage. Encysted metacercaria.

References. Koehler and Poulin (2010); Leung, Donald, et al. (2009); Saldanha et al. (2009).

Host N

Batedotea elongata (Miers 1876). Idoteidae, green seaweed isopod.

Localities. Otago Harbour.

Infection site. Body cavity.

Stage. Encysted metacercaria.

References. New record.

Other remarks

This species and life cycle was described by Martorelli et al. (2004) from red-billed gulls in Otago. References prior to this paper used the name *Maritrema* sp. Originally described as *M. novaezealandensis*, the name was corrected to *M. novaezealandense* by Presswell et al. (2014). Type specimens are held at Museo de La Plata, La Plata, Argentina, Helminthological Collection under numbers 5279 and 5280.

3.18.3 | *Maritrema* sp. 1

Host A (experimentally infected)

Cominella glandiformis. Cominellidae, mudflat whelk.

Localities. Otago Harbour.

Infection site. Digestive tract (passed in feces).

Stage. Metacercaria.

References. Latham et al. (2003).

Remarks. Latham et al. (2003) state that the metacercariae are ingested by scavenging freshly dead crabs (*H. hirtipes*, *H. crenulatus*, and *H. sexdentatus*) infected with *Maritrema* sp. and that the whelk is a temporary paratenic host.

Other remarks

As this is not mentioned in the description of *Maritrema novaezealandense* from Martorelli et al. (2004), we are cautiously assuming that this is a different species until such time as its identity can be confirmed.

3.18.4 | Microphallidae gen. sp. 1

Host A

Cominella glandiformis. Cominellidae, mudflat whelk.
Localities. Otago Peninsula; Otago Harbour; Marlborough, Auckland.
Infection site. Gonads.
Stage. Sporocyst, cercaria.
References. Donald and Spencer (2016); Leung, Donald, et al. (2009); Thieltges et al. (2009).

Other remarks

Although there is no genetic evidence, we assume that the references above refer to the same species of microphallid. We have named this sp. 1 for convenience. The GenBank accession number listed in Leung, Donald, et al. (2009) is incorrect; the number given, FJ765509, should read FJ765510.

3.18.5 | Microphallidae gen. sp. 2

Host A

Zeacumantus subcarinatus. Batillariidae, mud whelk.
Localities. Otago Harbour.
Infection site. Digestive gland and gonad.
Stage. Sporocyst, cercaria.
References. Martorelli et al. (2008).

Other remarks

This is either *Microphallus* sp. or *Megalophallus* sp., according to Martorelli et al. (2008). It is possible that this species is the same as *Microphallus* sp. reported from *Z. subcarinatus* by other authors (see below). We have named this sp. 2 for convenience.

3.18.6 | *Microphallus* sp. 1

Host A

Austrohelice crassa. Varunidae, tunnelling mud crab.
Localities. Otago Harbour.
Infection site. Gonads and hepatopancreas.
Stage. Encysted metacercaria.
References. Koehler and Poulin (2010); Leung, Donald, et al. (2009).

Host B

Cyclograpsus lavauxi. Varunidae, smooth shore crab.
Localities. Otago Harbour.
Infection site. Gonads and hepatopancreas.
Stage. Encysted metacercaria.
References. Koehler and Poulin (2010); Leung, Donald, et al. (2009).

Host C

Hemigrapsus crenulatus. Varunidae, hairy-handed crab.
Localities. Otago Harbour.
Infection site. Gonads and hepatopancreas.
Stage. Encysted metacercaria.
References. Dittmer et al. (2011); Koehler and Poulin (2010); Leung, Donald, et al. (2009).

Host D

Hemigrapsus sexdentatus. Varunidae, purple shore crab.
Localities. Otago Harbour.
Infection site. Gonads and hepatopancreas.
Stage. Encysted metacercaria.
References. Koehler and Poulin (2010); Leung, Donald, et al. (2009); Poulin et al. (2003).

Host E

Hemiplax hirtipes. Macrophthalmidae, stalk-eyed mud crab.
Localities. Otago Harbour.
Infection site. Gonads and hepatopancreas.
Stage. Encysted metacercaria.
References. Dittmer et al. (2011); Koehler and Poulin (2010); Leung, Donald, et al. (2009); Poulin et al. (2003).
Remarks. All above authors use host name *Macrophthalmus hirtipes*.

Host F

Zeacumantus subcarinatus. Batillariidae, mud whelk.
Localities. Otago Harbour.
Infection site. Gonads.
Stage. Sporocyst, cercaria.
References. Fredensborg et al. (2005, 2006); Keeney, Boessenkool, et al. (2008); Keeney et al. (2007a); Leung, Donald, et al. (2009); Martorelli et al. (2008); Studer and Poulin (2012b).
Remarks. It is possible that this *Microphallus* sp. is the same as the microphallid described by Martorelli et al. (2008) (see above).

Other remarks

This was listed as *Microphallus* sp. in the above references. We have given it the appellation "sp. 1" to make it comparable in future studies.

3.18.7 | *Microphallus* sp. NZ of O'Dwyer, Blasco-Costa, et al. (2014)

Host A

Austrolittorina cincta (Quoy & Giamard 1833). Littorinidae, brown periwinkle.
Localities. Otago Harbour.
Infection site. Not specified.
Stage. Sporocyst, cercaria.
References. O'Dwyer, Blasco-Costa, et al. (2014).
Other remarks

O'Dwyer, Blasco-Costa, et al. (2014) showed genetic distinction between *Microphallus* sp. NZ and *Microphallus* sp. 1 above. Voucher material is deposited at Institute of Parasitology, Academy of Sciences of the Czech Republic, under accession number HCIP D-702.

3.19 | Family Notocotylidae Lühe, 1909 (Platyhelminthes, Trematoda, Plagiorchiida)

3.19.1 | Notocotylidae gen. sp. 1 NZ of O'Dwyer, Blasco-Costa, et al. (2014)

Host A

Austrolittorina cincta. Littorinidae, brown periwinkle.
Localities. Otago Harbour.
Infection site. Not specified.
Stage. Redia, cercaria.
References. O'Dwyer, Blasco-Costa, et al. (2014).

Host B

Austrolittorina antipodum (Philippi 1847). Littorinidae, banded periwinkle.
Localities. Otago Harbour, Kaikoura, Paihia.
Infection site. Not specified.
Stage. Redia, cercaria.
References. O'Dwyer, Blasco-Costa, et al. (2014).
Other remarks
The redia and cercaria of this species were described fully by O'Dwyer, Blasco-Costa, et al. (2014). Voucher material is deposited at Institute of Parasitology, Academy of Sciences of the Czech Republic under accession number HCIP D-701.

3.19.2 | Notocotylidae gen. sp. 2 NZ of O'Dwyer, Blasco-Costa, et al. (2014)

Host A

Austrolittorina antipodum. Littorinidae, banded periwinkle.
Localities. Kaikoura.
Infection site. Not specified.
Stage. Not known.
References. O'Dwyer, Blasco-Costa, et al. (2014).
Other remarks
This species was detected by genetic signal only. No morphological data are available (O'Dwyer, Blasco-Costa, et al., 2014).

3.20 | Family Opecoelidae Ozaki 1925 (Platyhelminthes, Trematoda, Plagiorchiida)

3.20.1 | *Neolebouria maorum* (Allison, 1966) Gibson 1976

Host A

Macroctopus maorum. Octopodidae, New Zealand octopus.
Localities. Kaikoura.
Infection site. Lobes of the kidney and in the kidney coelom.
Stage. Adult.
References. Allison (1966); Jones (1975); Short and Powell (1968).
Remarks. All above authors used host name *Octopus maorum*.

Host B

Octopus australis Hoyle 1885. Octopodidae, hammer octopus.
Localities. Portobello, Otago Harbour.
Infection site. Renal sacs and beneath nearby membranes of other viscera.
Stage. Adult.
References. Jones (1975); Short and Powell (1968).
Remarks. Jones (1975) and Short and Powell (1968) used host name *Robsonella australis*.

Other remarks

Allison (1966) described this species as *Plagioporus maorum* and placed it in family Allocreadiidae. The type specimens are in the Canterbury Museum, and we have deposited paragenophore specimens to Te Papa museum under accession W.003619.

3.20.2 | Opecoelidae gen. sp. A

Host A

Diloma subrostratum (Gray 1835). Trochidae, mudflat top shell.
Localities. Otago and Southland.
Infection site. Soft tissues.
Stage. Sporocyst, cercaria.
References. Donald et al. (2004, 2007).
Remarks. Donald et al. (2004, 2007) used the incorrect host name *D. subrostrata*.

Host B

Notoacmea scapha. Lottiidae, estuarine limpet.
Localities. Otago Harbour.
Infection site. Host tissues.
Stage. Encysted metacercaria.
References. Koppel et al. (2011).

Other remarks

Donald et al. (2004) used molecular phylogenies to show that a single morphotype of opecoelid species found in New Zealand could be separated into three clades. Their "Clade 2" species, infecting only *Diloma subrostratum* in Otago and Southland, was subsequently called Opecoelidae sp. A in their paper of 2007. Koppel et al. (2011) subsequently found specimens in limpets that matched genetically with Opecoelidae sp. A.

3.20.3 | Opecoelidae gen. sp. B

Host A

Diloma subrostratum. Trochidae, mudflat top shell.
Localities. Auckland, Canterbury, Otago and Southland.
Infection site. Soft tissues.
Stage. Sporocyst, cercaria.
References. Donald et al. (2004, 2007).
Remarks. Donald et al. (2004, 2007) used the incorrect host name *D. subrostrata*.

Other remarks

Donald et al. (2004) used molecular phylogenies to show that a single morphotype of opecoelid species found in New Zealand could be separated into three clades. Their "Clade 3a" species, infecting only *Diloma subrostratum* throughout New Zealand, was subsequently called Opecoelidae sp. B in their paper of 2007.

3.20.4 | Opecoelidae gen. sp. C

Host A

Diloma aethiops (Gmelin 1791). Trochidae, spotted top shell.
Localities. Canterbury and Otago.
Infection site. Soft tissues.
Stage. Sporocyst, cercaria.
References. Clark (1958); Donald et al. (2004, 2007).
Remarks. Clark (1958) and Donald et al. (2004) used the host name *Melagraphia aethiops*.

Host B

Diloma aridum (Finlay 1926). Trochidae, black top shell.
Localities. Little Akaloa, Canterbury.
Infection site. Soft tissues.
Stage. Sporocyst, cercaria.
References. Donald et al. (2004).
Remarks. Donald et al. (2004) used the host name *Diloma arida*.

Host C

Diloma nigerrimum (Gmelin 1791). Trochidae, bluish top shell.
Localities. Little Akaloa, Canterbury; Moeraki, Otago.
Infection site. Soft tissues.
Stage. Sporocyst, cercaria.
References. Donald et al. (2004).

Other remarks

Donald et al. (2004) used the host name *Diloma nigerrima*. Donald et al. (2004) used molecular phylogenies to show that a single morphotype of opecoelid species found in New Zealand could be separated into three clades. Their "Clade 3b" species, infecting three *Diloma* species throughout New Zealand (but not *Diloma subrostratum*), was subsequently called Opecoelidae sp. C in their paper of 2007. Clark (1958) described the opecoelid found in *Diloma aethiops* as *Cercaria melagraphia*, and Donald et al. (2004) recognized the cercarial species as their species C.

3.20.5 | Opecoelidae gen. sp. D

Host A

Cominella glandiformis, Cominellidae, mudflat whelk.
Localities. Otago, Tasman, Marlborough, Northland, Auckland, Tauranga.
Infection site. Not specified.
Stage. Sporocyst, cercaria.
References. Donald and Spencer (2016); Thieltges et al. (2009).

Host B

Cominella virgata H. Adams & A. Adams 1853. Cominellidae.
Localities. Murrays Bay, Auckland.
Infection site. Not specified.
Stage. Sporocyst, cercaria.
References. Donald and Spencer (2016).

Host C

Cominella adspersa (Brugière 1789). Cominellidae, speckled whelk.
Localities. Mangonui, Northland and Bucklands Beach, Auckland.
Infection site. Not specified.
Stage. Sporocyst, cercaria.
References. Donald and Spencer (2016).

Other remarks

Donald and Spencer (2016) isolated a further species from whelks, which they called Opecoelidae sp. D. Thieltges et al. (2009) did not name their opecoelid, but, based on host identity, we assume their specimens were also Opecoelidae sp. D.

3.20.6 | Opecoelidae gen. sp. E

Host A

Abarenicola affinis (Ashworth 1903). Arenicolidae, polychaete lugworm.
Localities. Lower Portobello, Otago Harbour.
Infection site. Muscular tissue and coelom, throughout host.
Stage. Encysted metacercaria.
References. Peoples and Poulin (2011); Peoples et al. (2012).

Host B

Capitella sp. Capitellidae, polychaete worm.
Localities. Lower Portobello, Otago Harbour.
Infection site. Muscular tissue and coelom.
Stage. Encysted metacercaria.
References. Peoples et al. (2012).

Host C

Heteromastus filiformis (Claparède 1864). Capitellidae, polychaete worm.
Localities. Lower Portobello, Otago Harbour.
Infection site. Muscular tissue and coelom, anterior portion of host.
Stage. Encysted metacercaria.
References: Leung, Donald, et al. (2009); Peoples and Poulin (2011); Peoples et al. (2012).

Other remarks

Leung, Donald, et al. (2009) gave the name Opecoelidae sp. E to opecoelids collected from polychaetes by R. Peoples in order to keep consistency in the naming of these larval stages. Peoples and

Poulin (2011) and Peoples et al. (2012) later wrote about them in two studies, retaining the name, Opecoelidae sp. E.

3.20.7 | Opecoelidae gen. sp. F

Host A

Trizocheles spinosus (Henderson 1888). Pylochelidae, hermit crab.
Localities. Otago Harbour.
Infection site. Body cavity.
Stage. Encysted metacercariae.
References. This study, new record.

Other remarks

This species, defined by genetic identity, has been named Opecoelidae sp. F for the sake of consistency with the foregoing published species.

3.20.8 | *Opecoelus* sp. 1

Host A

Nyctiphanes australis G.O. Sars 1883. Euphausiidae, krill shrimp.
Localities. Otago Harbour.
Infection site. Body cavity.
Stage. Encysted metacercariae.
References. This study, new record.

3.21 | Family Philophthalmidae Looss 1899 (Platyhelminthes, Trematoda, Plagiorchiida)

3.21.1 | *Philophthalmus attenuatus* Bennett & Presswell, 2019

Host A

Zeacumantus subcarinatus. Batillariidae, mud whelk.
Localities. Otago Harbour Christchurch, Blueskin Bay, Otago Peninsula, Bluff Harbour.
Infection site. Gonads.
Stage. Redia, sporocyst, cercaria.
References. Bates et al. (2011); Bennett and Presswell (2019); Born-Torrijos et al. (2014); Fredensborg et al. (2005, 2006); Guilloteau et al. (2016); Hay et al. (2005); Kamiya and Poulin (2012); Kamiya et al. (2013); Keeney, Boessenkool, et al. (2008); Keeney, King, et al. (2009); Koprivnikar and Poulin (2009b); Lei and Poulin (2011); Leung, Donald, et al. (2009); Leung and Poulin (2011); Lloyd and Poulin (2011, 2013, 2014a, 2014b); MacLeod and Poulin (2015, 2016a, 2016b), MacLeod et al. (2017); Martorelli et al. (2008); Vielma et al. (2019).

Other remarks

Hay et al. (2005) listed this as an "undescribed philophthalmid species," Fredensborg et al. (2005) listed it as "Philophthalmidae," and it was named "*Philophthalmus* sp." in subsequent publications, until its description in Bennett and Presswell (2019). Type specimens are deposited in Te Papa Museum, Wellington (accession number 21899) and the Otago Museum, Dunedin (accession numbers IV101950–IV101952).

3.21.2 | *Parorchis* sp. NZ of O'Dwyer, Blasco-Costa, et al. (2014)

Host A

Austrolittorina antipodum (Philippi 1847). Littorinidae, banded periwinkle.
Localities. Otago Harbour.
Infection site. Gonad and digestive gland.
Stage. Redia, cercaria.
References. O'Dwyer, Kamiya, and Poulin (2014); O'Dwyer, Lynch, and Poulin (2014); O'Dwyer, Blasco-Costa, et al. (2014); O'Dwyer and Poulin (2015).

Host B

Austrolittorina cincta. Littorinidae, brown periwinkle.
Localities. Otago Harbour.
Infection site. Gonad and digestive gland.*Stage*. Redia, cercaria.
References. Guilloteau et al. (2016); O'Dwyer, Kamiya, and Poulin (2014); O'Dwyer, Lynch, and Poulin (2014); O'Dwyer, Blasco-Costa, et al. (2014); O'Dwyer and Poulin (2015).
Other remarks
O'Dwyer, Kamiya, and Poulin (2014) and O'Dwyer, Lynch, and Poulin (2014) referred to this parasite as a "philophthalmid trematode." Voucher material is deposited at Institute of Parasitology, Academy of Sciences of the Czech Republic under accession number HCIP D-700.

3.22 | Family Renicolidae Dollfus 1939 (Platyhelminthes, Trematoda, Plagiorchiida)

3.22.1 | *Renicola* sp. NZ of O'Dwyer, Blasco-Costa, et al. (2014)

Host A

Austrolittorina antipodum. Littorinidae, banded periwinkle.
Localities. Paihia.
Infection site. Not specified.
Stage. Sporocyst, cercaria.
References. O'Dwyer, Blasco-Costa, et al. (2014).
Other remarks
Voucher material is deposited at Institute of Parasitology, Academy of Sciences of the Czech Republic under accession number HCIP D-703.

3.22.2 | *Renicola* sp. of Martorelli et al. (2008)

Host A

Zeacumantus subcarinatus. Batillariidae, mud whelk.
Localities. Otago Harbour.
Infection site. Digestive gland and gonad.
Stage. Sporocyst, cercaria.

References. Leung, Donald, et al. (2009); Martorelli et al. (2008).

Other remarks

Based on *cox1* genetic data, this is not the same as *Renicola* sp. NZ of O'Dwyer, Blasco-Costa, et al. (2014).

3.23 | Family Syncoeliidae Looss 1899 (Platyhelminthes, Trematoda, Plagiorchiida)

3.23.1 | *Copiatestes thyrsitae* Crowcroft 1948

Host A

Nyctiphanes australis. Euphausiidae, krill shrimp.
Localities. Otago Harbour.
Infection site. Body cavity, under carapace.
Stage. Metacercaria.
References. New record, this study.

Other remarks

We provide a video file of metacercaria movement from within a euphausiid host in Video S3 and an individual metacercaria ex situ in Video S4. We have deposited a hologenophore specimen to Te Papa museum under accession W.003620.

3.24 | Family Schistosomatidae Stiles & Hassall 1898 (Platyhelminthes, Trematoda, Diplostomida)

3.24.1 | Schistosomatidae gen. sp. 1

Host A

Patelloida corticata (Hutton 1880). Lottiidae, encrusting limpet.
Localities. Otago Harbour.
Infection site. Body cavity.
Stage. Sporocyst, cercaria.
References. New record, this study.

Other remarks

Based on 28S genetic data, this schistosome is probably a sister species to that found by Brant et al. (2017) in the false limpet *Siphonaria lessoni* and in the gull *Larus dominicanus* in Argentina, as well as in the penguin *Spheniscus demersus* in South Africa. We provide a video file of schistosome cercaria shedding from the limpet host in Video S2 and have deposited ethanol-preserved cercarial paragenophore specimens to Te Papa museum under accession W.003622.

3.25 | Family Strigeidae Railliet 1919 (Platyhelminthes, Trematoda, Diplostomida)

3.25.1 | Strigeidae gen. sp. 1

Host A

Cominella glandiformis. Cominellidae, mudflat whelk.
Localities. Otago Harbour, Otago Peninsula.
Infection site. Not specified.
Stage. Cercaria.
References. Leung, Donald, et al. (2009); Thieltges et al. (2009).

Other remarks

We have named this species Strigeidae gen. sp. 1 for convenience. This species is referred to as "strigid" throughout Thieltges et al. (2009).

3.25.2 | Strigeidae gen. sp. 2

Host A

Streblosoma toddae Hutchings & Smith 1997. Terebellidae, polychaete worm.
Localities. Otago Harbour.
Infection site. Host tissue and coelom.
Stage. Sporocyst, metacercaria.
References. Peoples et al. (2012).

Other remarks

We have named this species Strigeidae gen. sp. 2 for convenience.

3.26 | Trematoda *incertae sedis*

Remarks

In addition to the above records, "Trematoda sp." were reported infecting the mud snail *Amphibola crenata* by Poulin & Mouritsen, 2006 and Leung, Donald, et al. (2009); "Family A" trematodes were reported infecting *Cominella maculosa*, spotted whelk, and *Cominella virgata*, red-mouth whelk, by Donald et al. (2016); "Family B" trematodes were reported infecting *Cominella glandiformis*, mudflat whelk, by Donald and Spencer (2016); "Family C" trematodes were reported infecting *Cominella virgata*, red-mouthed whelk, by Donald and Spencer (2016).

3.27 | Family Acuariidae Railliet, Henry & Sisoff 1912 (Nematoda, Chromadorea, Rhabditida)

3.27.1 | Acuariidae gen. sp. 1

Host A

Hemigrapsus crenulatus. Varunidae, hairy-handed crab.
Localities. Lower Portobello, Otago.
Infection site. Not given.
Stage. Larva, stage not specified.
References. Dittmer et al. (2011).

Host B

Hemiplax hirtipes. Macrophthalmidae, stalk-eyed mud crab.
Localities. Papanui Inlet, Otago Peninsula; Lower Portobello, Otago Harbour.
Infection site. Body cavity.
Stage. L3 larva.
References. Dittmer et al. (2011); Moravec et al. (2003); Poulin et al. (2003).
Remarks. All references referred to the host as *Macrophthalmus hirtipes*.

Host C (experimentally infected)

Cominella glandiformis. Cominellidae, mudflat whelk.
Localities. Waipuna Bay, Otago Harbour.
Infection site. Digestive tract (detected in feces).
Stage. Larva, stage not specified.
References. Latham et al. (2003).
Remarks. Latham et al. (2003) state that the larvae are ingested by scavenging freshly dead crabs (*H. hirtipes*, *H. crenulatus*, and *H. sexdentatus*) infected with acuariid larvae and that the whelk is a temporary paratenic host.

3.28 | Family Anisakidae Railliet & Henry 1912 (Nematoda, Chromadorea, Rhabditida)

3.28.1 | *Anisakis simplex* (Rudolphi 1809) Dujardin 1845 sensu *lato*

Host A

Nyctiphanes australis. Euphausiidae, krill shrimp.
Localities. North Cape, Bay of Plenty, Cook Strait, west and east coast of New Zealand.
Infection site. Body cavity.
Stage. Larva.
References. Hurst (1984).

Host B

Moroteuthopsis ingens. Onychoteuthidae, greater hooked squid.
Localities. Chatham Rise.
Infection site. Visceral cavity.
Stage. L3 encysted larvae.
References. New record, this study.

Host C

Nototodarus sloanii. Ommastrephidae, arrow squid.
Localities. Throughout New Zealand: Chatham Rise, Auckland and Stewart islands, Karamea Bight, Tasman Bay, and Egmont.
Infection site. Visceral cavity and muscles.
Stage. Larva, stage not specified.
References. Smith et al. (1981); Wharton et al. (1999).

Other remarks

Anisakis simplex is a species complex, and it is impossible to discern the identity of specimens without thorough genetic comparison, so we cannot be certain whether these examples are the same as *A. simplex s. l.* found in a multitude of definitive hosts. We also recovered *A. simplex s.l.* from *N. sloanii* and assume it is the same species as Smith et al. (1981). We have deposited a hologenophore specimen recovered from *M. ingens* to Te Papa museum under accession W.003621.

3.28.2 | *Contracaecum* sp. 1

Host A

Nototodarus sloanii. Ommastrephidae, arrow squid.
Localities. Kaikoura, Cape Campbell, and Kapiti Island (Cook Strait).
Infection site. Lumen of stomach and mantle cavity.
Stage. Type 2 larva.
References. Brunsdon (1956), unpublished PhD thesis.

3.28.3 | *Hysterothylacium aduncum* (Rudolphi 1802) Deardorff & Overstreet 1981

Host A

Unidentified cnidarian sp. Cnidaria, jellyfish.
Localities. Cook Strait.
Infection site. Inside.
Stage. Larva.
References. Hurst (1984).

Host B

Unidentified decapod sp. Decapoda.
Localities. Cook Strait.
Infection site. Inside carapace.
Stage. Larva.
References. Hurst (1984).

Host C

Serratosagitta tasmanica (Thompson 1947). Sagittidae, arrow worm.
Localities. North Cape, Bay of Plenty, Cook Strait, and west coast of New Zealand.
Infection site. Haemocoel.
Stage. Larva.
References. Hurst (1984).
Remarks. Hurst (1984) reported this host as *Sagitta tasmanica* which is a synonym of *Serratosagitta tasmanica*.

Other remarks

Hurst (1984) recovered larval *H. aduncum* from the above hosts under the synonym *Thynnascaris adunca*.

3.28.4 | Anisakidae gen. sp. 1

Host A

Balanus sp. Balanidae, barnacle.

Localities. Otago Harbour.
Infection site. Mantle cavity.
Stage. Larva.
References. New record, this study.

3.29 | Family Cystidicolidae Skrjabin 1946 (Nematoda, Chromadorea, Rhabditida)

3.29.1 | *Ascarophis* sp. 1

Host A

Austrohelice crassa. Varunidae, tunnelling mud crab.
Localities. Lower Portobello, Otago.
Infection site. Not specified.
Stage. Larva, stage not specified.
References. Koehler and Poulin (2010).

Host B

Cyclograpsus lavauxi. Varunidae, smooth shore crab.
Localities. Lower Portobello, Otago.
Infection site. Not specified.
Stage. Larva, stage not specified.
References. Koehler and Poulin (2010).

Host C

Hemigrapsus crenulatus. Varunidae, hairy-handed crab.
Localities. Lower Portobello, Otago.
Infection site. Not specified.
Stage. Larva, stage not specified.
References. Dittmer et al. (2011); Koehler and Poulin (2010).

Host D

Hemigrapsus sexdentatus. Varunidae, purple shore crab.
Localities. Lower Portobello, Otago.
Infection site. Not specified.
Stage. Larva, stage not specified.
References. Dittmer et al. (2011); Koehler and Poulin (2010).

Host E

Hemiplax hirtipes. Macrophthalmidae, stalk-eyed mud crab.
Localities. Lower Portobello, Otago.
Infection site. Body cavity.
Stage. Third-stage larva.
References. Dittmer et al. (2011); Koehler and Poulin (2010); Moravec et al. (2003).
Remarks. All above references use the host name *Macrophthalmus hirtipes*.

3.29.2 | Ascaridoidea gen. sp. 1

Host A

Ovalipes catharus. Ovalipidae, paddle crab.
Localities. Nelson.
Infection site. Cardiac stomach.
Stage. Larva, stage not specified.
References. Miller et al. (2006).

Other remarks

Miller et al. (2006) state that this and sp. 2 below are different species.

3.29.3 | Ascaridoidea gen. sp. 2

Host A

Charybdis japonica (A. Milne-Edwards 1861). Portunidae, Asian paddle crab.
Localities. Waitemata Harbour.
Infection site. Midgut to hindgut region.
Stage. Larva, stage not specified.
References. Miller et al. (2006).

3.30 | Family Mermithidae Braun 1883 (Nematoda, Enoplea, Mermithida)

3.30.1 | *Thaumamermis zealandica* Poinar et al., 2002

Host A

Bellorchestia quoyana (H. Milne-Edwards 1840). Talitridae, intertidal amphipod.
Localities. Long beach, Otago; Aramoana, Smails, Tomahawk, Taieri Mouth, and Tautuku, Otago; Porpoise Bay and Oreti, Southland.
Infection site. Body cavity.
Stage. Parasitic or post-parasitic juvenile.
References. Currey and Poulin (2006); Poinar et al. (2002); Poulin and Latham (2002a, 2002b); Poulin and Rate (2001); Tobias et al. (2017); Williams et al. (2004).
Remarks. All authors prior to Tobias et al. (2017) used the host name *Talorchestia quoyana*.

Other remarks

The endemic mermithid *T. zealandica* was described by Poinar et al. (2002), and type material is accessioned at Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand: ZW1509-10.

4 | DISCUSSION

This study provides both the first comprehensive checklist of parasitic helminths infecting New Zealand's marine invertebrates and insights into their ecological interactions. We present data on 73 parasite taxa and their 62 invertebrate hosts. All taxa are recorded as larval stages, with the exception of *Neolebouria maorum*, a trematode that completes its life cycle within two octopus species, *Macroctopus maorum* and *Octopus australis*. This study documents 20 new parasite taxa infecting marine invertebrates and adds 13 invertebrates as hosts that previously had no records of parasitic helminths. We present only the second record of chitons as trematode hosts and the third record of limpets as hosts to schistosome parasites, anywhere in the world. Below, we give a brief history of invertebrate parasitology in New Zealand and highlight some of the unusual or interesting findings that have increased our knowledge of the New Zealand fauna.

Historically, the first mention of a helminth infection in a New Zealand marine invertebrate was by Haswell (1903), who recovered two types of trematode cercaria from the green-lipped mussel *Perna canaliculus*, since identified as *Alcicornis longicornutus* and *Tergestia agnostomi*. Since then, few records have appeared in the literature until the establishment of the Ecological and Evolutionary Research Group at the University of Otago, which has conducted much research on coastal marine parasites, primarily as models to test processes and patterns of ecology and evolution. From 2000 to 2021, the cumulative records of parasite–invertebrate associations increased by over 1200%, from a total of 30 to 381 host–parasite associations. Of those, 33 associations come from the survey conducted in this study.

The mud snail *Zeacumantus subcarinatus* harbors the largest complement of helminth parasites and has been widely used as a model organism to test ecological and evolutionary hypotheses (e.g., host–parasite co-evolution, Keeney, King, et al., 2009; behavioral manipulation, Thomas & Poulin, 1998; host specificity, Keeney et al., 2015). The large number of parasites known from *Z. subcarinatus* may simply be the product of the extensive sampling conducted on this snail. Alternatively, the high parasite count may be indicative of the central role that this species plays in the mudflat ecosystem. Other host species are typically found to be infected with a single parasite species (Figure 1A). Further sampling of these hosts on a broader geographic scale will be necessary to determine whether a single parasite species per host is the norm. Indeed, parasite species richness per host generally correlates with sampling effort (Walther et al., 1995).

Similarly, the trematode *Maritrema novaezealandense*, with the broadest host spectrum, is another species that has been well studied. Is it truly a generalist, or is its large number of recorded hosts a result of sheer study effort? This question could only be answered by exhaustive, ecosystem-wide surveys of all free-living taxa.

We present only the second documented record worldwide of chitons (Polyplacophora) hosting trematodes. The single previous record was by Prévot (1965), who reported finding *Proctoeces maculatus* (Looss 1901) Odhner 1911 (Fellodistomidae) in *Acanthochitona* ("*Acanthochites*") *discrepens* in the Mediterranean. We collected trematode parasites belonging to *Acanthoparyphium* sp. A (Himasthlidae) from two species of chiton, *Sypharochiton pelliserpentis* and *Chiton glaucus*. These metacercariae were recovered from the mantle cavity and were molecularly identified as *Acanthoparyphium* sp. A (of Leung, Keeney, & Poulin, 2009) using a partial *28S* gene sequence that matched 100% in a BLASTn search to *Acanthoparyphium* sp. A haplotype 24 (accession KJ956275). That the encysted metacercariae were clearly alive and well within the chitons was evident by their movement (See Video S1). *Acanthoparyphium* sp. A has been recovered from six invertebrate intermediate hosts indicating low host specificity at this life stage. The definitive hosts are thought to be oystercatchers, and according to Marchant and Higgins (1993), New Zealand oystercatchers often consume chitons. It is therefore likely that chitons contribute to the transmission of this parasite and completion of its life cycle. Chitons are common, distinctive, and cosmopolitan, so it is surprising that there are no more reports of their parasites in the literature. It is not clear whether the lack of reports is simply due to insufficient study or whether they are rarely infected. With 56 polyplacophoran species in New Zealand waters (Wassilieff, 2006), members of the class clearly require further investigation.

Parasites can provide insights into the evolutionary history and historical distribution of parasite taxa and, sometimes, their hosts. Avian schistosomes (Trematoda) evolved from a basal clade of marine forms which branched into a large number of freshwater forms. Brant et al. (2017) discovered avian schistosomes comprising a distinct marine clade within the larger freshwater clade, suggesting a secondary return of the lineage to a marine environment. Their specimens were from the false limpet *Siphonaria lessoni*, the gull *Larus dominicanus* from Argentina, and the penguin *Spheniscus demersus* from South Africa. Here, we have recovered specimens from the limpet *Patelloida corticata* which match 98.9%–99.7% with Brant et al.'s (2017) sequences (*28S* rDNA) and which we consider to be conspecific. This is the first time a schistosome from this clade has been identified in New Zealand waters, supporting Brant et al.'s (2017) contention that members of this clade exhibit a Southern Hemisphere distribution, while showing that dispersal within the region is greater than expected (Brant et al., 2017).

New Zealand and the Southern Pacific Ocean are one of the main regions particularly lacking in cephalopod parasite research (Tedesco et al., 2020). It is therefore not surprising that only three of the 100 + cephalopod species in New Zealand waters (Gordon et al., 2010) currently have records of parasitic helminths. Next to nothing is known about which cephalopods are important intermediate hosts and trophic connectors for parasite life cycles. In this study, we recovered six new parasites infecting the arrow squid *Nototodarus sloanii*, all of which are larval cestodes never reported in this host species before. Surveys of other cephalopod species may yet yield equally diverse infections. Further studies on cephalopod parasite assemblages would shed greater light on parasite life cycles, especially because cephalopods hold varying positions within marine food webs as both predators and prey (Navarro et al., 2013).

The commercial fishing industry is worth over $4 billion to the New Zealand economy, over $1.2 billion of which comes from invertebrates (shellfish and arrow squid) (Williams et al., 2017). It is therefore essential to identify and monitor the parasites that can have an influence on fisheries. The green-lipped mussel *Perna canaliculus*, for example, is New Zealand's most valuable aquaculture species (Castinel et al., 2019). Green-lipped mussels are known to host two trematode cercariae, *Tergestia agnostomi* and *Alcicornis longicornutus*, with prevalence in New Zealand populations ranging 1%–16% in some areas (Linzey, 1971). Unfortunately, their impact on the production of the mussel populations remains unclear (Castinel et al., 2019), although trematodes at this stage of their life cycle often castrate their molluscan host and affect its growth. Similarly, arrow squid constitute 11% of the deep water fisheries catch (Williams et al., 2017) and have played a huge role in the fisheries industry since the 1970s. Early in the history of the squid fishery, Smith et al. (1981) was able to differentiate two populations into different species, in part, using the prevalence of infections of *Anisakis* sp. and *Nybelinia* sp. This led to the suggestion that fisheries set individual quotas for each species to prevent overfishing of one species and effectively manage resources.

There are over 80 adult cestode species known to infect marine animals in New Zealand (Bennett, Presswell, et al., 2021), most, if not all, of which must use invertebrates in at least one stage of their life cycles. Prior to this study, however, there were only two records of larval cestodes in marine invertebrates, and the first and second records did not appear until 1981 and 2016, respectively (Lagrue et al., 2016; Smith et al., 1981). This is not surprising, as data on cestode life cycles are generally lacking, primarily due to the fact that larval and adult stages cannot easily be matched using morphological characteristics alone. DNA sequencing, however, is improving this situation. For example, Bennett et al. (2019) matched larval and adult forms of the cestode species *Acanthobothrium* sp. 1 infecting the red swimming crab *Nectocarcinus antarcticus* and the rough skate *Zearaja nasuta* using *28S* sequence data. The application of molecular tools to resolve parasite life cycles can also greatly enhance food web reconstruction in marine environments (Blasco-Costa & Poulin, 2017).

Parasitic helminths comprise a number of phylogenetically distinct taxa, and inevitably, a variety of molecular markers have been employed in their study over the last 20 years, both in New Zealand and worldwide. For example, larval nematodes are more often characterized using *18S* or *cox1* sequence data, whereas acanthocephalans have been typically characterized with *28S* sequences. In addition, molecular markers used can vary between studies depending on their goal. For example, opecoelid trematodes have been the subject of population level discrimination and therefore the highly variable *16S* and *ITS1* markers have been employed (Donald & Spencer, 2016). On the other hand, himasthlid trematodes are typically the focus of surveys aiming to place them into a higher phylogenetic context (e.g., Tkach et al., 2016). Additionally, choice of molecular markers is often a product of the authors' personal preference. Consequently, much of the genetic data available is not comparable, and taxa from different sources cannot easily be matched. If these data were comparable, future researchers could readily explore the genetic diversity of parasites that infect invertebrates and identify biogeographic, evolutionary, and ecological patterns. Notwithstanding pleas to the contrary (e.g., Zimmermann et al., 2014), consistency of molecular marker use remains a distant goal.

Parasites of marine invertebrates have long been overlooked though their ecological role in influencing host health, trophic interactions, and energy flow within natural systems is undeniable (Kuris et al., 2008; Mouritsen & Poulin, 2005). Here, in the first of its kind for any country, we have provided a checklist of all known records of helminth parasites in New Zealand marine invertebrates and highlighted a few instances in which knowledge of parasites impacts directly on our knowledge of invertebrate ecology, economics, and taxonomy. Many marine invertebrate host groups play key roles in ecological communities, with high socioeconomic value for humans (e.g., arrow squid and green-lipped mussel), so data about their parasites are essential. Our study, by collecting new data and organizing known parasite–host associations and their genetic data, establishes a baseline for future advances in this discipline.

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CONFLICT OF INTEREST

Authors declare that they have no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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