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Hidden hosts: Limpets as key players in trematode transmission

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Research Paper

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Abstract

Limpets are abundant and ecologically important gastropods in intertidal and some riverine ecosystems, yet their role in trematode transmission remains comparatively understudied. We investigated trematode infection in intertidal limpets from Otago Harbour, New Zealand, using a molecular approach. Two species were identified: the avian schistosome *Gigantobilharzia* cf. *patagonensis* in *Siphonaria australis* and *Acanthoparyphium* sp. A metacercariae in *Notoacmea* sp. *Gigantobilharzia* cf. *patagonensis* was detected at all five sampling sites, with prevalence ranging from 2.6% to 100%. Haplotype network analysis using *cox1* revealed high haplotype diversity and a star-like topology, suggesting a recent population expansion. This study expanded the known diversity of marine schistosomes in the region and raises potential public health concerns with cercarial dermatitis. We also conducted a literature synthesis further demonstrating that limpets contribute to trematode transmission across 12 superfamilies and 23 families, with distinct parasitism profiles between freshwater and marine environments. These findings highlight limpets as overlooked but significant hosts in trematode ecology and emphasize the need for broader surveys and definitive host screening to resolve incomplete life cycles and assess epidemiological risks in coastal ecosystems.

Introduction

Limpets are ubiquitous and abundant invertebrates in aquatic environments, yet they remain comparatively understudied for parasitological research relative to other gastropod taxa. As molluscs, limpets play important roles in the transmission of digenean trematodes, serving either as first intermediate hosts harbouring sporocysts, rediae, and cercariae, or as second intermediate hosts harbouring metacercariae (Koppel *et al.* 2011). Given their wide distribution and potential role in parasite transmission, investigating the diversity of trematodes infecting limpets can help resolve partially understood life cycles and provide predictive insights into the parasite diversity of local vertebrate hosts.

In New Zealand, fewer than 0.5% of marine gastropod taxa have documented helminth parasites (Bennett *et al.* 2022b). Although knowledge of marine helminth diversity has expanded in recent years (Bennett *et al.* 2022a), many life cycles remain incomplete (Bennett *et al.* 2023). The Otago Harbour mudflats, in New Zealand's South Island, are known to support a rich diversity of trematode parasites (Leung *et al.* 2009b). While previous biodiversity surveys in Otago's coastal marine ecosystem have successfully matched various larval stages to adult parasites (Bennett *et al.* 2023), limpets (here including limpet-shaped gastropods) have been overlooked. Koppel *et al.* (2011) examined only one limpet species (*Notoacmea scapha*) and recovered metacercariae from three trematode species in Otago Harbour, highlighting limpets' potential role as viable intermediate hosts and transmitters of parasites.

Of particular interest is the role of siphonariids (false limpets), which are known to host marine schistosomes (Digenea: Schistosomatidae) in Argentina, Australia, and Kuwait (Abdul-Salam and Al-Khedery 1992; Brant *et al.* 2017; Ewers 1961; Lorenti *et al.* 2022). Schistosomes are dioecious blood flukes of birds and mammals. Unlike most trematodes, they lack a metacercarial stage, and cercariae leave the molluscan host and penetrate the definitive host (Gabrielli and Garba Djirmay, 2023). Some species cause schistosomiasis in humans, while others can induce human cercarial dermatitis (HCD, or swimmer's itch) when non-human schistosome cercariae accidentally penetrate human skin (Gabrielli and Garba Djirmay 2023; Horak *et al.* 2015). In New Zealand, outbreaks of HCD have been reported from freshwater avian schistosomes in the genus of *Trichobilharzia* (Davis *et al.* 2022), but the diversity and zoonotic potential of marine schistosomes remain poorly understood. Recently, a schistosome (Schistosomatidae gen. sp. 1) was reported from the limpet *Patelloida corticate* in New Zealand (Bennett *et al.* 2022a). However, this host may have been misidentified and is likely *Siphonaria australis*. This represents only the second marine schistosome species recorded in New Zealand, the first being *Ornithobilharzia canaliculata* from the gull *Larus dominicanus* (Bennett *et al.* 2023; Rind 1984). Therefore, examining these gastropods in

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greater depth could reveal the diversity, distribution, and public health potential of marine schistosomes in New Zealand.

In this study, we adopt a morphological definition of 'limpet', encompassing gastropods with a patelliform (limpet-shaped) shell regardless of taxonomic lineage. Our aims are to investigate the limpet species of Otago Harbour and molecularly identify the trematode parasites they harbour. We also conducted a comprehensive review of available information on trematode parasites infecting limpets in both marine and freshwater ecosystems worldwide, to provide an up-to-date synthesis of the trematode taxa using these molluscs as hosts.

Methods

Field collection and dissection

Limpets were collected by hand at low tide from five sites along Otago Harbour, South Island, New Zealand, between December 2024 and March 2025. These sampling sites include Lower Portobello Bay (latitude, longitude: −45.832203, 170.672795), Wellers Rock (−45.797962, 170.715378), Macandrew Bay (−45.868997, 170.596806), Broad Bay (−45.848534, 170.619328), and Company Bay (−45.856851, 170.598893). Sample sizes vary across sampling sites (Table 1). Prior to dissection, limpets were maintained in aerated containers with fresh seawater. Each limpet was removed from its shell using forceps, and internal organs were examined under a dissection microscope. Muscle tissue was firmly pressed between two glass plates and examined under the dissection microscope for parasites. All parasites recovered were preserved in 70% ethanol for subsequent DNA sequencing. Limpets were identified to species or genus using published keys (Carson and Morris 2017; Jones *et al.* 2005), and through personal communication with expert molluscan taxonomist Prof. Hamish Spencer (Zoology Department, University of Otago, Dunedin, New Zealand).

Table 1. Parasite prevalence from the limpets collected at five Otago Peninsula sites facing the Otago Harbour

Location	Host (sample size)	Parasite (prevalence)
Wellers Rock	*Siphonaria australis* (n = 39)	*Gigantobilharzia* cf. *patagonensis* (2.6%)
	Cellana ornata (n = 3)	–
	Cellana strigilis (n = 5)	–
	Notoacmea sp. (n = 2)	–
Lower Portobello	*Siphonaria australis* (n = 2)	*Gigantobilharzia* cf. *patagonensis* (100%)
	Notoacmea sp. (n = 35)	*Acanthoparyphium* sp. A (11.4%)
	Cellana ornata (n = 2)	–
Broad Bay	*Siphonaria australis* (n = 69)	*Gigantobilharzia* cf. *patagonensis* (39.1%)
	Notoacmea sp. (n = 2)	–
Company Bay	*Siphonaria australis* (n = 113)	*Gigantobilharzia* cf. *patagonensis* (2.7%)
	Cellana ornata (n = 1)	–
Macandrew Bay	*Siphonaria australis* (n = 7)	*Gigantobilharzia* cf. *patagonensis* (28.6%)
	Notoacmea sp. (n = 5)	–

Parasite identification and haplotype network

Genomic DNA was extracted from individual cercariae or metacercariae using the DNeasy® Blood &Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol. Two genetic markers were targeted for amplification: a partial region of the *28S* rRNA gene and the cytochrome c oxidase subunit I (*cox1*) gene. For the *28S* rRNA gene, primers T16 and T30 (Harper and Saunders 2001) were used under the following thermal cycling conditions: initial denaturation at 94°C for 5 min; 38 cycles of denaturation at 94°C for 30 s, annealing at 45°C for 30 s, and extension at 72°C for 2 min; followed by a final extension at 72°C for 7 min. For the *cox1* gene, primers JB3 (Bowles 1993) and Trem.cox1.rrnl (Kralova-Hromadova 2008) were used with the following protocol: initial denaturation at 95°C for 2 min; 40 cycles of denaturation at 95°C for 30 s, annealing at 48°C for 40 s, and extension at 72°C for 1 min; followed by a final extension at 72°C for 10 min. PCR products were cleaned using ExoSAP-IT™ Express PCR Product Cleanup Reagent (USB Corporation, Cleveland, OH, USA) following the manufacturer's instructions. Sanger sequencing by capillary electrophoresis was performed by the Genetic Analysis Service, Department of Anatomy, University of Otago, New Zealand.

Raw sequences were trimmed using default parameters and manually curated to correct ambiguous bases in Geneious Prime® version 2025.2.2. Depending on the parasite, we either used the *28S* gene or a combination of *28S* and *cox1* genes to identify species to the lowest taxonomic level possible through BLASTn (Basic Local Alignment Search Tool for nucleotides) searches against the NCBI GenBank database (https://blast.ncbi.nlm.nih.gov/). To examine the genetic structure of the schistosome, we constructed a haplotype network from aligned *cox1* sequence data. Approximately 33 bp downstream of the *cox1* stop codon were retained in the alignment due to their high sequence quality. Some sequences were shorter in length compared to others, but still included in the haplotype network with the assumption that they matched 100% to longer haplotype representatives. Sequences were aligned using the ClustalW algorithm implemented in the msa package (version 1.38.0) (Bodenhofer *et al.* 2015) within R Statistical Software (version 4.2.2; R Core Team, 2022). The haplotype network was constructed using the pegas package (version 1.3) (Paradis 2010) to visualize genetic relationships among haplotypes.

Literature review

To survey trematodes parasitising limpets, a topic search was conducted in Web of Science in July, 2025 using the following query: '(Tremator* OR Digenea OR Fluke OR Redia* OR Cercaria* OR Sporocyst* OR Metacercaria*) AND (Limpet* OR Patellogastropod* OR Patellid* OR Fissurellid* OR Lepetelloid* OR Siphonariid* OR Phenacolepadid* OR Tylodinid* OR Latiid* OR Latia OR Trimuscul* OR Ancylid*)'. For completeness, besides the 'true limpets' (family Patellidae), we also included in our review all major gastropod groups commonly referred to as 'limpets' in the literature (e.g., family Fissurellidae – keyhole limpets; family Siphonariidae – false limpets; family Calyptraeidae – slipper limpets). The title and abstract of all publications retrieved by the search were checked, and all relevant publications were retained. From each publication, we extracted the host species name, the trematode family and (if given) species name, the sampling locality, and (if available) the prevalence of infection.

Results

Trematode survey and molecular identification

We collected and examined four limpet taxa (*Siphonaria australis* Quoy & Gaimard, 1833, *Cellana ornata* Dillwyn, 1817, *Cellana strigilis* Hombron & Jacquinot, 1841, *Notoacmea* sp.) from five intertidal sites in Otago Harbour and identified two trematode species (Table 1). *Siphonaria australis* was the most common and abundant species, occurring at all five sites. Schistosome infections were detected in *S. australis* at every site, with a prevalence of sporocysts ranging from 2.6% to 100%, though the 100% prevalence was based on a sample size of only two limpets from Lower Portobello Bay. *Notoacmea* sp. were found at four sites, but only individuals from Lower Protobello Bay hosted metacercaeriae of *Acanthoparyphium* sp. A. (11.4% prevalence). No parasites were detected in any of the *Cellana ornata* and *C. strigilis* examined.

Cercariae from the false limpet *S. australis* were identified as *Gigantobilharzia* cf. *patagonense* (Figure 1). The *28S* rRNA sequence obtained (~560 bp, GenBank accession PX833732) differed by a single nucleotide (99.83% identity) from *Gigantobilharzia patagonense* (syn. *Marinabilharzia patagonense*) described from the kelp gull *Larus dominicanus* in Argentina (GenBank accessions OK338634-OK338636) (Lorenti *et al.* 2022). It also shared a 99.83% identity with *Schistosomatidae* sp. recorded from *L. dominicanus* (KX302891) and *Siphonaria lessonii* (KX302889) in Argentina (Brant *et al.* 2017), and a 99.81% identity (89% query coverage) with a sequence from *Patelloida corticata* in New Zealand (ON661331) (Bennett *et al.* 2022a). Additionally, the sequence shared 98.91% identity with *Schistosomatidae* sp. from penguin *Spheniscus demersus* from South Africa (KM023789) (Aldhoun and Horne 2015). For the *cox1* gene, our consensus sequence shared 96.69% identity (44% query coverage) with *G. patagonensis* from the brown-hooded gull *Chroicocephalus maculipennis* (OK338770) and 95.83% identity (55% query coverage) with *G. patagonense* from *L. dominicanus* (OK338769) (Lorenti *et al.* 2022).

Metacercariae found infecting *Notoacmea* sp. at Lower Portobello (Table 1) were identified as *Acanthoparyphium* sp. A. Our *28S* rRNA sequence was identical (100% match) to various representatives of *Acanthoparyphium* sp. A of (Leung *et al.* 2009a) recorded from New Zealand intertidal species, including cockle *Austrovenus stutchburyi* (OQ407748), the green chiton *Chiton glaucus* (OQ407746), and the limpet *Notoacmea scapha* (OQ407744) (Bennett *et al.* 2023). It also shared 98.72% identity with isolates of another unidentified *Acanthoparyphium* sp. from *N. scapha* (ON661320) (Bennett *et al.* 2022a).

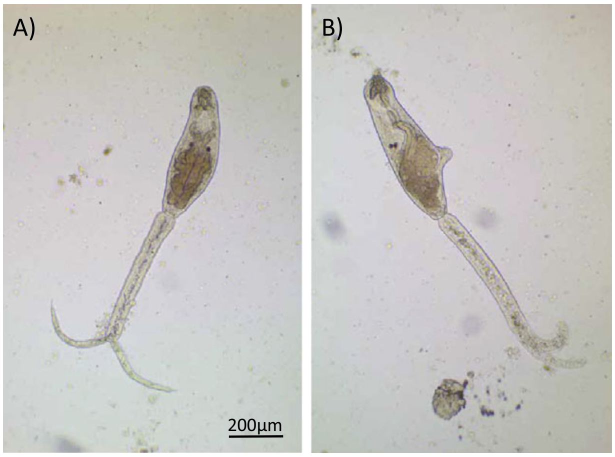

Figure 1. Photomicrographs of the cercaria of *Gigantobilharzia* cf. *patagonensis* showing (A) dorsal view and (B) lateral view.

Haplotype network analysis of Gigantobilharzia *cf.* patagonensis

We identified nine unique *G. cf. patagonensis* haplotypes based on *cox1* sequences (Figure 2A, accessions PX910024-PX910034). The network displayed a star-like topology dominated by haplotype I, which was the most common lineage and present in four of the five sampling locations (absent only from Lower Portobello) across Otago Harbour, New Zealand. Haplotypes III, V, and VI differed from haplotype I by 1bp, while haplotypes II, IV, and VII differed by 2 bp. Broad Bay exhibited the highest genetic diversity, containing all nine identified haplotypes. This included two divergent lineages found exclusively at this site: Haplotype VIII (8 mutational steps from haplotype I) and haplotype IX (a further 19 mutational steps away). Despite the variation, haplotypes were mixed among sites (Figure 2B), showing random sorting with no clear geographic structuring across the Otago Peninsula.

Literature survey of limpet-associated trematodes

The bibliographical survey recovered trematodes from 12 superfamilies and 23 families utilising marine or freshwater limpets as first or second intermediate hosts (Table 2). In the freshwater environment, trematode superfamilies included the Paramphistomoidea, Diplostomoidea, Schistosomatoidea, Echinostomatoidea, Monorchioidea, and Gorgoderoidea. In the marine environment, trematodes belonged to the superfamilies Gymnophalloidea, Hemiuroidea, Lepocreadioidea, Pronocephaloidea, Microphalloidea, and Opecoeloidea, as well as the Schistosomatoidea and Echinostomatoidea. Although the Schistosomatoidea and Echinostomatoidea superfamilies were found in both environments, no trematode families were shared between freshwater and marine systems. These trematodes utilised limpet-shaped hosts from nine families: three freshwater families (Planorbidae, Bumupiidae, Acroloxidae), and six marine families (Siphonariidae, Lottidae, Patellidae, Fissurellidae, Nacellidae, Calyptraeidae).

The prevalence of trematode infection in freshwater environments ranged from 0 to 20%, with all recorded trematodes using limpets as first intermediate hosts. In marine environments, prevalence ranged from 0.1 to 100%, and many trematode species also use limpets as second intermediate hosts. Trematodes of the genus *Proctoeces* (family Fellodistomidae) can mature into egg-producing adult worms in their molluscan host, and thus also use limpets as their definitive host. Records of limpet-associated trematodes are most numerous in the United States for freshwater systems and in Argentina and Ireland for marine systems.

Discussion

The role of limpets (in the broad sense) in trematode life cycles remains poorly documented. Here, we identified two trematode species in intertidal limpets from Otago Harbour. The first is the avian schistosome, *Gigantobilharzia* cf. *patagonensis*, which uses *Siphonaria australis* as its first intermediate host. The second is *Acanthoparyphium* sp. A metacercaria, recovered from *Notoacmea* sp., used as a second intermediate host. *Gigantobilharzia*

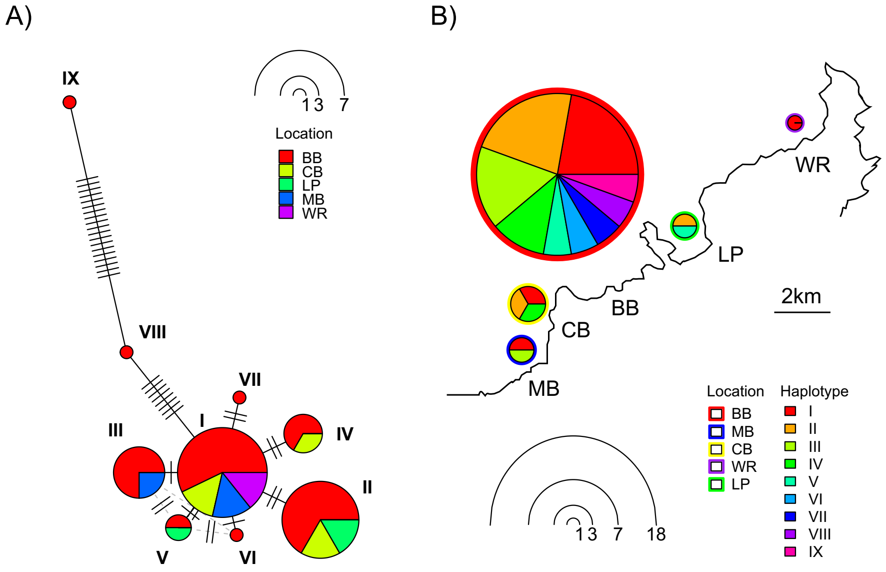

Figure 2. Haplotype network of *Gigantobilharzia* cf. *patagonensis* recovered from *Siphonaria australis*, based on *cox1* sequences from five Otago Harbour sites (A) and the distribution of haplotypes by location (B). BB, Broad Bay; CB, Company Bay; LP, Lower Portobello; MB, Macandrew Bay; WR, Wellers Rock.

cf. *patagonensis* was recovered from all five sampling sites, with prevalence reaching up to 100%. Genetic analyses revealed considerable diversity of *cox1* sequences within the Otago Harbour population. In addition, our literature review highlights the broad diversity of trematodes infecting limpets in both marine and freshwater systems around the world.

We report *Siphonaria australis* as a new first intermediate host record for *Gigantobilharzia* cf. *patagonensis.* Previous studies in Otago recovered matching sequences (Bennett *et al.* 2022a), but the host was identified as the true limpet *Patelloida corticata.* Given that schistosomes within the *Gigantobilharzia* clade are known to infect pulmonate gastropods (Siphonariidae) (Brant *et al.* 2017; Ewers 1961; Lorenti *et al.* 2022), the earlier record likely reflects host misidentification, with *S. australis* representing the intermediate host in this region.

The Otago Harbour isolate is closely related to *Gigantobilharzia patagonensis*, which infects *S. lessoni* in Argentina (Brant *et al.* 2017; Lorenti *et al.* 2022). Definitive hosts of *G. patagonensis* include the kelp gull *Larus dominicanus* in Argentina and the African penguin *Spheniscus demersus* in South Africa (Aldhoun and Horne 2015). In New Zealand, the life cycle involves the black-backed gull *L. dominicanus* (Bennett *et al.* 2023). As these gulls are non-migratory, introduction via bird migration is unlikely.

Analysis of the mitochondrial *cox1* gene of *G.* cf. *patagonensis* revealed high haplotype diversity within the Otago Harbour population. The haplotype network displayed a star-like topology dominated by a single common lineage (haplotype I), suggesting a potential recent population expansion. Broad Bay exhibited the highest diversity, containing unique, divergent lineages. This genetic diversity suggests a large, stable parasite population within the harbour, likely maintained by the constant movement of avian definitive hosts dropping schistosome eggs across different coastal sites. Prevalence in *S. australis* (2.6–100%) was notably higher than that reported for *G. patagonensis* in *S. lessoni* from Argentina (0.9–6.1%) (Alda and Martorelli 2009; Brant *et al.* 2017). However, extreme values in our dataset may result from small sample sizes (e.g., 100% prevalence at Lower Portobello Bay was based on only two limpets, and our highest number of haplotypes came from Broad Bay, which has the highest number of limpets examined).

Avian schistosomes can cause HCD when their cercariae penetrate human skin. While freshwater outbreaks associated with *Trichobilharzia* are well documented (Davis *et al.* 2022; Horak *et al.* 2015), marine species also pose risks to humans (Ewers 1961). Compared with freshwater schistosomes, marine taxa remain less studied worldwide (Brant and Loker 2013; Khosravi *et al.* 2022); however, genera such as *Ornithobilharzia* have previously been reported in New Zealand (Bennett *et al.* 2023; Rind 1984). The molecular confirmation of *Gigantobilharzia* in five bays within Otago Harbour expands the known diversity of marine schistosomes in the region. Its presence in intertidal zones highlights a potential public health concern if this species has zoonotic potential, and underscores the need for monitoring schistosome populations in recreational coastal environments. In the context of climate change, swimmer's itch is likely to become increasingly prevalent in cool, temperate areas like New Zealand (Soleng *et al.* 2025), reinforcing the importance of clinical awareness and improved knowledge of parasite distribution and host knowledge.

Metacercariae recovered from *Notoacmea* sp. were identified as *Acanthoparyphium* sp. A of Leung *et al.* (2009a) (Echinostomatoidea: Himasthlidae). The *28S* rRNA sequences matched 100% with isolates previously recorded from the New Zealand cockle *Austrovenus stutchburyi* and the chiton *Chiton glaucusi* (Bennett *et al.* 2023). *Acanthoparyphium* sp. A was also reported in *Notoacmea scapha* from Lower Protobello Bay in 2010, where limpets were suggested to act as dead-end hosts unlikely to transmit metacercariae to suitable definitive hosts, such as oystercatchers, due to their small body size (Koppel *et al.* 2011). Finally, we found no trematode infection in either of the other two limpet species examined from Otago Harbour, *Cellana ornata* and *C. strigilis*; however, the numbers of specimens of these species that could be collected and examined were too low to conclude that they are not used as hosts by trematodes.

Our literature survey revealed that limpets play important roles in trematode life cycles across 12 superfamilies and 23 families. Ecological roles of limpets differ between freshwater and marine environments. Freshwater limpets (Planorbidae, Burnupiidae, Acroloxidae) serve exclusively as first intermediate hosts, whereas marine limpets (Siphonariidae, Lottidae, Patellidae, Fissurellidae,

Table 2. Summary of trematode taxa reported from limpet hosts from previous publications

Trematode superfamily	Trematode family*	Trematode species	Host family**	Host species	Location	Prevalence (%)	References
Paramphistomoidea	Paramphistomidae^{IH-1}		Planorbidae^{FW}	*Ferrissia rivularis (Ferrissia parallela)*	Michigan	20	Smith (1967)
Diplostomoidea	Diplostomidae^{IH-1}	*Posthodiplostomum nanum, P. minimum*	Planorbidae^{FW}	*Gundlachia ticaga, Laevapex fuscus*	Brazil, Louisiana	0–7	López-Hernández *et al.* (2018); Turner and Beasley (1982)
	Strigeidae^{IH-1}		Planorbidae^{FW}	*Ancylus fluviatilis, Ferrissia fragilis, F. rivularis*	Central Morocco, Michigan	1–6	Laamrani *et al.* (2005); Smith (1967)
	Cyathocotylidae^{IH-1}		Planorbidae^{FW}	*Laevapex fuscus*	Michigan	1	Smith (1967)
Schistosomatoidea	Clinostomidae^{IH-1}		Planorbidae^{FW}		Brazil	–	Mattos *et al.* (2013)
	Sanguinicolidae^{IH-1}		Planorbidae^{FW}, Burnupiidae^{FW}	*Ancylus fluviatilis, Burnupia mooiensis, B. transvaalensis, B. trapezoidea*	Spain, South Africa	1–3.5	Simon-Martin and Gomez-Bautista (1986); Martin and Vazquez (1984); Outa and Avenant-Oldewage (2024)
	Schistosomatidae^{IH-1}		Siphonariidae^{MR}	*Siphonaria denticulata, S. lessoni, S. rosea*	South Africa, Australia, Argentina, Kuwait	0.2–35	Appleton (2003); Ewers (1961); Brant *et al.* (2017); Alda and Martorelli (2009); Gilardoni *et al.* (2018); Abdul-Salam and Al-Khedery (1992)
	Spirorchiidae^{IH-1}	*Spirorchis scripta*	Planorbidae^{FW}	*Ferrissia fragilis*	Louisiana, Michigan	1–6	Turner and Corkum (1977); Smith (1967)
Echinostomatoidea	Echinostomatidae^{IH-1}	*Echinostoma* spp., *Eschinoparyphium recurvatum, Petasiger radiatus, Petasiger* sp.	Acroloxidae^{FW}, Burnupiidae^{FW}	*Acroloxus lacustris, Burnupia mooiensis, B. transvaalensis, B. trapezoidea, Ferrissia fragilis, F. rivularis, Laevapex fuscus*	Caspian Sea, South Africa, Michigan	0.3–19	Mekhraliev (1978); Outa and Avenant-Oldewage (2025); Smith (1967)
	Himasthlidae^{IH-2}	*Acanthoparyphium* sp. A, *Curtuteria australis*	Lottiidae^{MR}	*Notoacmea scapha*	New Zealand	53	Koppel *et al.* (2011)
	Philophthalmidae$^{IH-1, IH-2}$	*Echinostephilla patellae*	Patellidae^{MR}	*Patella vulgata*	Ireland, Scotland	3.3–67	Prinz *et al.* (2010); Firth *et al.* (2017); Geraghty (2018); Kollien (1996)
	Rhopaliidae^{IH-1}	*Rhopalias* sp.	Planorbidae^{FW}	*Gundlachia ticaga*	Brazil	0.6	López-Hernández *et al.* (2023)
Gymnophalloidea	Fellodistomidae$^{IH-2, DH}$	*Proctoeces lintoni, P. humboldti, P. maculatus*	Fissurellidae^{MR}, Patellidae^{MR}	*Fissurella crassa, F. latimarginata, F. maxima, F. limbata, F. pulchra, Fissurella spp., Patella vulgata*	Chile, Peru, Ireland	0.1–100	Oliva and Vega (1994); Loot *et al.* (2005); Oliva and Huaquin (2000); Aldana *et al.* (2014); Oliva and Zegers (1988); Oliva (1992); García-Huidobro *et al.* (2024); Oliva and Vásquez (1999); Aldana *et al.* (2020); Oliva and Diaz (1988); Wood *et al.* (2013); Oliva and Alvarez (2011); Oliva (1993); Oliva and Diaz (1992); Bretos and Chihuailaf (1993); George-Nascimento *et al.* (1998); Valdivia *et al.* (2014); Oliva *et al.* (2018); Geraghty (2018)
	Gymnophallidae^{IH-2}	*Parvatrema obscurus, Lacunovermis* sp., *Gymnophalloides nacellae, Gymnophallus* sp.	Lottiidae^{MR}, Nacellidae^{MR}, Patellidae^{MR}	*Lottia digitalis, L. scabra, Nacella deauratam, N. magellanica, N. cocinna, Patella vulgata*	California, Argentina, Soviet Antarctic, Magellan, Southwest	0.1–100	Ching and Grosholz (1988); Martorelli and Morriconi (1998); Cremonte *et al.* (2013); Feiler (1986); Flores *et al.* (2019); Gilardoni *et al.* (2020); Geraghty (2018)

(*Continued*)

Table 2. (*Continued*)

Trematode superfamily	Trematode family*	Trematode species	Host family**	Host species	Location	Prevalence (%)	References
					Atlantic Ocean, Ireland		
Hemiuroidea	Hemiuridae$^{IH–1}$		Siphonariidae^{MR}	*Siphonaria lessoni*	Argentina	0.5–10	Alda and Martorelli (2009); Gilardoni *et al.* (2011); Gilardoni *et al.* (2018)
Lepocreadioidea	Lepocreadiidae$^{IH–1}$		Calyptraeidae^{MR}	*Crepipatella dilatata*	Argentina		Gilardoni *et al.* (2018)
Monorchioidea	Lissorchiidae$^{IH–1}$	*Asymphylodora* sp., *Lissorchis mutabile*	Acroloxidae^{FW}, Planorbidae^{FW}	*Acroloxus lacustris, Ferrissia rivularis, Laevapex fuscus*	Caspian Sea, Michigan	4–12	Mekhraliev (1978); Smith (1968); Smith (1967)
Paramphistomoidea	Cladorchiidae$^{IH–1}$	*Megalodiscus temperatus*	Planorbidae^{FW}	*Ferrissia fragilis*	Michigan	14	Smith (1967)
Pronocephaloidea	Notocotylidae$^{IH–1, IH–2}$	*Paramonostomum deseado* n. sp.	Nacellidae^{MR}	*Nacella magellanica*	Argentina	0.5–1.8	Bagnato *et al.* (2022)
Gorgoderoidea	Encyclometridae$^{IH–1}$	*Polylekithum ictaluri (Allocreadium ictaluri* Pearse)	Planorbidae^{FW}	*Laevapex fuscus*	Oklahoma, Indiana	–	Cable and Peters (1986)
Microphalloidea	Microphallidae$^{IH–1, IH–2}$	*Maritrema* spp., *M. madrynense*	Calyptraeidae^{MR}, Siphonariidae^{MR}	*Crepidula dilatata, C. fornicata, Crepipatella dilatata, Siphonaria lateralis, S. lessoni, S. rosea*	Argentina, UK, Kuwait	0.2–81	Gilardoni *et al.* (2011); Quinn *et al.* (2022); Gilardoni *et al.* (2018); Alda and Martorelli (2009); Abdul-Salam and Al-Khedery (1992)
	Renicolidae$^{IH–1, IH–2}$	*Renicola* spp.	Lottiidae^{MR}, Nacellidae^{MR}, Patellidae^{MR}	*Lottia digitalis, Nacella deaurata, N. magellanica, Patella vulgata*	California, Magellan, Argentina, Ireland	0.3–1.4	Martin (1982); Flores *et al.* (2019); Gilardoni *et al.* (2018); Geraghty (2018)
Opecoeloidea	Opecoelidae$^{IH–2}$	*Opecoelid* sp.	Lottiidae^{MR}	*Notoacmea scapha*	New Zealand	23	Koppel *et al.* (2011)

*IH-1 = First intermediate host; IH-2 = second intermediate host; DH = definitive host.
**FW, Freshwater; MR, marine.

Nacellidae, Calyptraeidae) can serve as both first and second intermediate hosts. No trematode families exploit both marine and freshwater limpets, although members of superfamilies Echinostomatoidea and Schistosomatoidea occur in both environments. Prevalence tends to be higher in limpets serving as second intermediate hosts, likely resulting from accumulating metacercarial encystment, whereas first intermediate host infections, which often result in castration and increased mortality due to cercariae asexual amplification, occur at much lower prevalences.

Different limpet families exhibit distinct parasitism profiles. For example, Siphonariidae (air-breathing false limpets) are key first intermediate hosts for marine Schistosomatidae and Hemiuridae, and second intermediate hosts for Microphallidae (Gilardoni *et al.* 2011). In contrast, the Fissurellidae (keyhole limpets) are often exploited by Fellodistomidae, specifically the genus *Proctoeces.* Notably, *Proctoeces lintoni* is reported to exhibit progenesis (precocious maturity) in Fissurellidae in Chile, whereby limpets act as alternative definitive hosts alongside clingfish (George-Nascimento *et al.* 1998).

Although sample size varied among limpet species and sampling sites and may influence prevalence estimates or the likelihood of detecting rare haplotypes, this study provides important insights into the diversity and ecology of marine schistosomes in New Zealand. We documented high *G.* cf. *patagonensis* prevalence and genetic diversity in Otago Harbour, thus highlighting potential public health risks of the zoonotic disease HCD. Future work can expand geographic sampling and incorporate definitive host screening to resolve life cycles fully and assess the distribution of *G.* cf. *patagonensis* and the risk of HCD in recreational coastal environments.

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