New Zealand Journal of Marine and Freshwater Research, 2009, Vol. 43: 857–865
0028–8330/09/4304–0857

Trematode parasites of Otago Harbour (New Zealand) soft-sediment intertidal ecosystems: life cycles, ecological roles and DNA barcodes

TOMMY L.F. LEUNG[1]
KIRSTEN M. DONALD[1]
DEVON B. KEENEY[2]
ANSON V. KOEHLER[1]
ROBERT C. PEOPLES[1]
ROBERT POULIN[1]

[1]Department of Zoology
University of Otago
P.O. Box 56
Dunedin, New Zealand
email: robert.poulin@stonebow.otago.ac.nz

[2]Department of Biological Sciences
Le Moyne College
Syracuse, NY, United States

Abstract Parasites, in particular trematodes (Platyhelminthes: Digenea), play major roles in the population dynamics and community structure of invertebrates on soft-sediment mudflats. Here, we provide a list of the 20 trematode species currently known to infect molluscs, crustaceans and polychaetes from Otago Harbour (New Zealand) soft-sediment intertidal areas, as well as information on their transmission modes, life cycles, and known ecological impacts. Several of the host-parasite species combinations recorded here are reported for the first time. We also provide DNA barcodes, based on sequences of the cytochrome oxidase subunit 1 (CO1) gene, for 19 of the 20 trematode species, to facilitate future identification of these parasites in marine ecological studies.

Keywords crustaceans; molluscs; parasitism; cytochrome oxidase subunit 1 gene; intertidal mudflats

M09011; Online publication date 15 July 2009
Received 23 February 2009; accepted 15 April 2009

INTRODUCTION

Parasites, though often unnoticed by most researchers, are an integral part of intertidal ecosystems (Sousa 1991; Mouritsen & Poulin 2002). Trematodes (Digenea), in particular, are common parasites of most animal taxa occurring in intertidal communities (Sousa 1991). Typically, intertidal trematodes use molluscs (sometimes bivalves, but most often snails) as first intermediate hosts (see Fig. 1) (Kearn 1998). Within the molluscan host, trematodes replace host tissue such as gonads and eventually occupy a significant portion of the volume within the shell; the outcome of infection for the mollusc is almost invariably castration (Mouritsen & Poulin 2002). After developing as sporocysts or rediae and multiplying asexually within the mollusc host, trematodes leave the mollusc as free-swimming and short-lived cercariae that seek a second intermediate host, in which they encyst as metacercariae (Kearn 1998; Poulin 2006). Depending on the trematode species, a range of animals can serve as second intermediate hosts, including crustaceans, molluscs, polychaetes, and fish (Kearn 1998). Predation on infected second intermediate hosts by definitive hosts (birds or fish, depending on the trematode species) completes the life cycle (Kearn 1998). Adult worms in the definitive hosts then release their eggs, usually in host faeces. Depending on the species, eggs are either ingested by suitable molluscs, or they hatch into free-swimming miracidia that seek and penetrate the mollusc first intermediate host to start the cycle anew (Fig. 1). Because trematodes occur at relatively high abundance in intertidal zones, and because of their well-documented impacts on the growth, survival, reproduction and behaviour of their hosts (e.g., Curtis 1987; Huxham et al. 1993; Lafferty 1993; Probst & Kube 1999; Ferreira et al. 2005; Thieltges 2006), they can be important drivers of host population dynamics, community structure, and foodweb stability (Sousa 1991; Mouritsen & Poulin 2002; Thompson et al. 2005; Lafferty et al. 2006; Wood et al. 2007).

An important hurdle for most marine ecologists encountering trematodes is the lack of basic

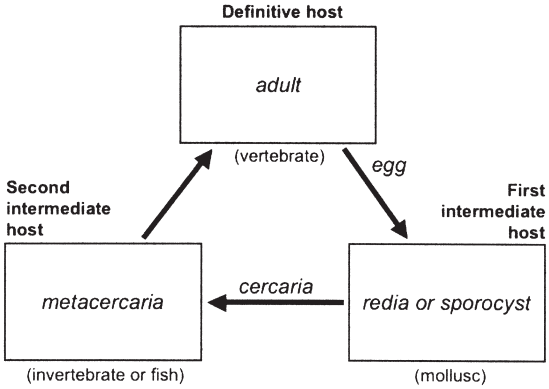

Fig. 1 Typical three-host life cycle of a trematode. The different trematode life stages are indicated in italics, and hosts are shown as boxes. The likely taxonomic identity of each host is indicated below each box.

biological information about these parasites, and the lack of rigorous methods of identification not requiring taxonomic expertise. The latter problem is exacerbated as taxonomic descriptions are often restricted to adult stages, whereas the most commonly found larval stages of trematodes (sporocysts or rediae, cercariae, and metacercariae) have generally not been described. The lack of information is a problem in parts of the world, such as New Zealand, without a long tradition in marine parasitology. Although records of adult trematodes and other parasites in New Zealand bird and fish hosts have been compiled (Hewitt & Hine 1972; Weekes 1982; McKenna 1998; Hine et al. 2000), there is no similar synopsis of the occurrence of the same parasite species in their larval stages within invertebrates.

Over the past several years, numerous studies have documented the presence of trematode parasites in New Zealand soft-sediment intertidal ecosystems, especially in the Otago region, South Island (e.g., Martorelli et al. 2004, 2006; Leung et al. 2009). Most of these species were unknown previously, and are likely widespread throughout New Zealand. These studies have also addressed the ecological impact of these trematodes on natural communities (e.g., Mouritsen & Poulin 2005a,b; Thompson et al. 2005). Our first goal here was to synthesise both published and unpublished information, to provide a summary of the known biology and life cycles of trematode species from Otago Harbour, and of their ecological importance. Our second objective was to provide DNA barcodes for all species identified to date, to facilitate the precise identification of these species in future studies. DNA barcoding provides a simple and reliable method of distinguishing between species (see Valentini et al. 2009).

METHODS

Trematode samples have been collected from invertebrate hosts on soft-sediment shores within Otago Harbour (45°50′S, 170°40′E) from 2004 to 2008. These samples were obtained as part of studies on parasites of benthic invertebrates (see Donald et al. 2004; Fredensborg et al. 2005; Mouritsen & Poulin 2005b; Martotelli et al. 2008; Leung et al. 2009). Trematodes were identified to family or genus level based on morphology (Schell 1970). When possible, DNA sequences were obtained for each species from both the asexual parthenital stages (sporocysts or rediae) in the molluscan host, and the metacercarial stages. However, for some species, only the parthenitae or metacercariae were available, whereas for one species, no specimens were available for DNA sampling. Individual parthenitae or metacercariae were isolated from host tissue and transferred into a Petri dish containing 0.22 μm-filtered sea water. They were then transferred into another Petri dish also containing filtered sea water, to rinse off residual host material. The parasites were then placed individually into a 1.5 ml Eppendorf tube for DNA extraction. DNA was extracted in 500 μl of 5% chelex containing 0.1 mg/ml proteinase K, incubated at 60°C for 4 h and boiled at 100°C for 8 min.

The cytochrome oxidase subunit 1 gene, or CO1 gene, of each individual was amplified using the JB3 (5'-TTTTTTGGGCATCCTGAGGTTTAT-3') of Bowles et al. (1993) as the forward primer. The reverse primer used was trem.cox1.rrnl (5'AATCATGATGCAAAAGGTA-3') of Králová-Hromadová et al. (2001).

All PCRs (polymerase chain reactions) were run in 30 μl reaction mixtures. The optimal cycling parameters included an initial denaturation step of 95°C (2 min), followed by 40 cycles of 95°C (30 s), 48°C (40 s) and 72°C (1 min), followed by a final extension phase at 72°C (10 min). PCR products were cut out of 1% agarose gels, gel-extracted and purified using Purelink™ Gel Extraction kits (Invitrogen, United States), sequenced using the BigDye Terminator Cycle Sequencing Kit (Applied Biosystems, United States), and resolved with an ABI PRISM 3730 Genetic Analyser (Applied Biosystems).

PCR of the CO1 gene yielded products with 607–917 base pairs of readable sequence. Alignment of sequences for comparison between specimens was performed using the MEGA v.3.1 genetic analysis programme (Kumar et al. 2004); however, sequences from the same species showed no within-species variation. The sequences were deposited at GenBank (see Table 1 for accession numbers).

RESULTS

A total of 20 trematode species were identified from soft-sediment intertidal areas of Otago Harbour (Table 1). We obtained sequences for 19 of the 20 trematode species. No DNA could be obtained from the remaining trematode species.

DISCUSSION

Several of the host-parasite species combinations recorded are reported here for the first time.

Echinostomatidae and Gymnophallidae

The echinostome trematode *Curtuteria australis* has been described by Allison (1979), whereas the sympatric echinostome *Acanthoparyphium* sp. has recently been described (Martorelli et al. 2006). Molecular evidence has revealed that both *C. australis* and *Acanthoparyphium* sp. are cryptic species complexes, with *Curtuteria* consisting of two species and *Acanthoparyphium* consisting of four (Leung et al. 2009).

As first intermediate host, *Curtuteria* spp. use the whelk *Cominella glandiformis* whereas *Acanthoparyphium* spp. use the mudsnail *Zeacumantus subcarinatus* (Allison 1979; Martorelli et al. 2006). The cercariae of all species leave their respective snail hosts to penetrate their second intermediate host. The cercariae of *C. australis* and *Acanthoparyphium* sp.A have been found to infect cockles, *Austrovenus stutchburyi*, by entering through the inhalant siphon, and encyst as metacercariae in the cockle's foot (Allison 1979; Martorelli et al. 2006). From this point on, these species are almost equivalent from an ecological perspective (Babirat et al. 2004) until they reach their oystercatcher (*Haematopus* spp.) definitive hosts. Cockles can accumulate large numbers of metacercariae, up to several hundred per cockle in some localities (Thomas & Poulin 1998). Heavily-parasitised cockles eventually lose their ability to crawl or burrow into the sediment, and these heavily-parasitised cockles on the sediment surface are then subjected to increased predation by oystercatchers (Thomas & Poulin 1998; Mouritsen 2002). Although impairment of cockle burrowing apparently benefits the parasites by increasing their transmission success, surface-stranded cockles are also more likely than buried cockles to have their foot cropped by fish (Mouritsen & Poulin 2003). The metacercariae lodged in the tip of the foot are thus often ingested by fish, which are dead-end hosts for the parasites. The adaptiveness for these parasites of inducing cockles to lie on the sediment surface is therefore unclear (Tompkins et al. 2004). Other second intermediate hosts that play roles in the life cycles of these echinostome trematodes include wedge shells, *Macomona liliana*, and polychaetes (see Table 1). Metacercariae of two species are found in the foot of *M. liliana* (Leung et al. 2009), whereas metacercariae of *Acanthoparyphium* sp. B have been found in the mouthparts of a nereid polychaete (R. Peoples unpubl. data). The second intermediate host(s) of the other *Curtuteria* sp. and *Acanthoparyphium* sp. C and D are unknown, though their taxonomic affinity suggests that they probably also use *A. stutchburyi* and *M. liliana* as the second intermediate host.

Echinostome species found in cockles have broader effects on the intertidal community. By causing a part of the cockle population to lie on the sediment surface, they create new microhabitats and facilitate the coexistence of epibiotic organisms living attached to cockle shells (Thomas et al. 1998). Also, the presence of many cockles on the sediment surface resulting from echinostome infection alters seabed hydrodynamics and sedimentation patterns (Mouritsen & Poulin 2005b), leading to greater physical heterogeneity in the mudflat habitat. The outcome is that the zonation patterns of some key non-host invertebrates is indirectly altered by parasitism (Mouritsen & Poulin 2005a). In addition, more benthic species (i.e., polychaetes) choose to settle in patches of mudflats with high densities of surface cockles, and thus the density, biomass and diversity of the entire benthic community are also increased (Mouritsen & Poulin 2005b, 2006). Overall, these parasites act as ecosystem engineers (Thomas et al. 1998), modifying by their action the physical properties of the intertidal habitat with community-wide repercussions.

Another trematode, *Gymnophallus* sp., uses cockles (and to a lesser extent *M. liliana*) as second intermediate hosts (Leung & Poulin 2007). Its metacercariae do not form cysts, but lie freely on the outer mantle epithelium of cockles. In some localities,

Table 1 Intermediate and definitive hosts, and GenBank accession numbers for species-specific DNA barcodes, of Otago Harbour (New Zealand) intertidal trematodes.

Trematode	Family	First intermediate host	Second intermediate host	Definitive host	Accession no.
Curtuteria australis	Echinostomatidae	whelk, *Cominella glandiformis*	cockle, *Austrovenus stutchburyi*; wedge shell, *Macomona liliana*	oystercatchers, *Haematopus* spp.	FJ765453–FJ765455
Curtuteria sp.A	Echinostomatidae	whelk, *Co. glandiformis*	cockle, *A. stutchburyi*	oystercatchers, *Haematopus* spp.	FJ765456
Acanthoparyphium sp.A	Echinostomatidae	mudsnail, *Zeacumantus subcarinatus*	cockle, *A. stutchburyi*; wedge shell, *M. liliana*	oystercatchers, *Haematopus* spp.	FJ765457–FJ765459
Acanthoparyphium sp.B	Echinostomatidae	mudsnail, *Z. subcarinatus*	Nereid polychaetes	oystercatchers, *Haematopus* spp.	FJ765460–FJ765462
Acanthoparyphium sp.C	Echinostomatidae	mudsnail, *Z. subcarinatus*	cockle, *A. stutchburyi* (?)	oystercatchers, *Haematopus* spp.	FJ765463–FJ765464
Acanthoparyphium sp.D	Echinostomatidae	mudsnail, *Z. subcarinatus*	cockle, *A. stutchburyi* (?)	oystercatchers, *Haematopus* spp.	FJ765465–FJ765466
Gymnophallus sp.	Gymnophallidae	unknown bivalve	cockle, *A. stutchburyi*; wedge shell, *M. liliana*	oystercatchers, *Haematopus* spp.	FJ765467–FJ765471
Maritrema novae-zealandensis	Microphallidae	mudsnail, *Z. subcarinatus*	amphipods, *Paracalliope novizealandiae*; isopods, *Paridotea ungulata*; mantis shrimps, *Lysiosquilla spinosa*; crabs, *Macrophthalmus hirtipes*, *Hemigrapsus crenulatus*, *H. sexdentatus*, *Halicarcinus whitei*, *Ha. varius*	gulls, *Larus* spp., maybe other birds	FJ765472–FJ765476
Microphallus sp.	Microphallidae	mudsnail, *Z. subcarinatus*	crabs, *Mac. hirtipes*, *H. crenulatus*, *H. sexdentatus*, *Austrohelice crassa*, *Cyclograpsus lavauxi*	shore birds	FJ765477–FJ765484
Philophthalmus sp.	Philophthalmidae	mudsnail, *Z. subcarinatus*	surfaces of mollusc shells or crustacean carapaces	gulls, *Larus* spp.	FJ765485–FJ765488
Galactosomum sp.	Heterophyidae	mudsnail, *Z. subcarinatus*	fish	piscivorous birds or marine mammals	FJ765489
Renicola sp.	Renicolidae	mudsnail, *Z. subcarinatus*	bivalves or fish	shore birds	FJ765490–FJ765493
opecoelid sp.A*	Opecoelidae	topshell, *Diloma subrostrata*	unknown crustacean (?)	fish	FJ765496–FJ765500
opecoelid sp.C*	Opecoelidae	topshell, *D.* (*Melagraphia*) *aethiops*	unknown crustacean (?)	fish	FJ765494–FJ765495
opecoelid sp.D	Opecoelidae	whelk, *Co. glandiformis*	unknown crustacean (?)	fish	FJ765501–FJ765503
opecoelid sp.E	Opecoelidae	unknown snail	Capitellid polychaetes	fish	FJ765504–FJ765508
strigeid sp.	Strigeidae	whelk, *Co. glandiformis*	fish	piscivorous birds	FJ765510
microphallid sp.	Microphallidae	whelk, *Co. glandiformis*	unknown crustacean	shore birds	FJ765509
Cercaria pectinata	undetermined	cockle, *A. stutchburyi*	unknown	unknown	Not available
unidentified	undetermined	pulmonate snail, *Amphibola crenata*	unknown	unknown	FJ765511

* Opecoelid sp.B of Donald et al. (2007) does not occur in Otago Harbour.

all cockles are parasitised by *Gymnophallus* sp., some containing over 100 metacercariae; in other localities 2–5 km distant, the parasite appears absent. Individual cockles that contain large numbers of echinostome metacercariae in their foot also harbour numerous *Gymnophallus* metacercariae (Poulin et al. 2000; Leung & Poulin 2007). The exact causes of this pattern are unclear, since the relationship is independent of the size or location of cockles on the mudflat (Leung & Poulin 2007); therefore, it is not merely owing to the passive accumulation of all types of metacercariae over time. No harmful effect of *Gymnophallus* infection on cockle growth, reproduction, or survival has been documented to date. Furthermore, this trematode's life cycle has not yet been resolved. Like other members of the family Gymnophallidae, its first intermediate host is almost certainly a bivalve, with the wedge shell *M. liliana* being the most likely since there are no other abundant bivalve species in Otago Harbour mudflats; oystercatchers and other shore birds probably serve as definitive hosts.

Microphallidae

The microphallid trematode *Maritrema novaezealandensis* is one of the most common parasites of the mudsnail *Z. subcarinatus*. Its life cycle, with full description of all developmental stages, has been elucidated by Martorelli et al. (2004). After leaving their snail host, cercariae of this parasite species penetrate and encyst within small crustaceans, including amphipods, isopods and crabs (see Table 1), to await ingestion by a suitable definitive host. To date, the red-billed gull *Larus novaehollandiae* has been confirmed as a definitive host (Fredensborg et al. 2004a), but it is likely that other shore birds also host this trematode.

In some localities within Otago Harbour, such as Lower Portobello Bay (mid-harbour), up to two-thirds of snails have been found to be infected by *Ma. novaezealandensis* (Fredensborg et al. 2005). The same individual snail can therefore be infected multiple times, resulting in many snails simultaneously harbouring multiple clones of *Ma. novaezealandensis* (Keeney et al. 2007a). The high prevalence of this parasite, combined with that of all other castrating trematodes infecting *Z. subcarinatus* (Table 1), has serious implications for snail populations. The density and biomass of *Z. subcarinatus* populations covary negatively with trematode prevalence: in localities where prevalence is high, the snails occur at low density and low overall biomass, and vice versa (Fredensborg et al. 2005). In addition, either because of local adaptation or other selective process, there are life history differences between snail populations linked with trematode parasitism: juvenile snails grow at higher rates and mature at smaller sizes in populations exposed to high trematode prevalence than in localities where trematode infections are rare (Fredensborg & Poulin 2006).

The impact of *Ma. novaezealandensis* is not limited to the first intermediate host, but also extends to its second intermediate hosts. In the laboratory, infection by *Ma. novaezealandensis* cercariae causes changes in the swimming behaviour of the amphipod *Paracalliope novizealandiae* (Leung & Poulin 2006). More importantly, infection by *Ma. novaezealandensis* leads to increased mortality of amphipods, especially when several cercariae infect the host more or less simultaneously (Fredensborg et al. 2004b). Molecular evidence from field-infected amphipods confirms that in nature, infection can occur in "waves" of cercariae from the same snail penetrating the same amphipod in synchrony (Keeney et al. 2007b). This trematode may thus be an important factor in amphipod population dynamics. The finding that it is a generalist capable of infecting a wide array of crustacean second intermediate hosts (see Table 1) also suggests that this trematode is an important component of the Otago Harbour foodweb (Thompson et al. 2005).

One other common trematode species from the family Microphallidae occurs on Otago Harbour mudflats. This trematode, *Microphallus* sp., has only recently been described (Martorelli et al. 2008). It also uses the mudsnail *Z. subcarinatus* as first intermediate host, but it is relatively rare, not occurring in more than 1–2% of snails in local populations (T.L.F. Leung unpubl. data). Its metacercariae are markedly larger than those of *Ma. novaezealandensis*, and they have been found in the body cavity of several crab species including *Macrophthalmus hirtipes* and *Hemigrapsus crenulatus* (see Table 1); its definitive hosts are most probably shore birds. This parasite had earlier been misidentified as belonging to the genus *Levinseniella* (Poulin et al. 2003), but DNA sequences from metacercariae in crabs match those from *Microphallus* sp. in mudsnails. The metacercariae, inside the body cavity of crabs, act synergistically with other parasites to induce altered serotonin levels in crab brains, and thus alterations in crab behaviour (Poulin et al. 2003). These changes induced in crab hosts may serve to enhance the parasites' transmission success, by increasing the susceptibility of crabs to bird predation.

Other trematodes

Second in prevalence only to *Ma. novaezealandensis*, the other trematode species commonly found in the mudsnail *Z. subcarinatus* within Otago Harbour is *Philophthalmus* sp. First reported by Howell (1965) from the Wellington (North Island) coast, it has recently been described in detail by Martorelli et al. (2008), who suggest that, based on its morphology, it may be *P. burrili*, a species known from Australia (Howell & Bearup 1967). Whereas *Ma. novaezealandensis* is the most prevalent trematode in small-sized *Z. subcarinatus*, it is gradually replaced by *Philophthalmus* sp. in larger snails, possibly because *Philophthalmus* sp. is the dominant antagonist whenever the two parasites share the same host (Keeney et al. 2008). In addition to castrating their snail host, *Philophthalmus* sp. and *Ma. novaezealandensis* also appear to change the snail's growth patterns: snails hosting both parasite species typically have a much wider shell base than uninfected snails or snails infected by only one of the two species (Hay et al. 2005). Double infection by both parasites in the same snail results in a greater diameter of shell whorls grown post-infection. Cercariae of *Philophthalmus* sp. produced in the snail leave the host and quickly encyst on any hard substrate, such as the external surfaces of molluscs or crustaceans (or the bottom of a Petri dish in the laboratory) (Martorelli et al. 2008). There, they await eventual ingestion by gulls or other shore birds, which serve as definitive hosts.

The final two trematode species recorded from the mudsnail *Z. subcarinatus* in Otago Harbour both occur at relatively low prevalences (less than 5% of snails in all localities sampled; T.L.F. Leung unpubl. data). The first, *Galactosomum* sp., produces large cercariae, visible to the naked eye and strongly photophilic (Martorelli et al. 2008). Although the life cycle of this particular species is unknown, in other members of the genus *Galactosomum*, fish serve as second intermediate hosts; fish actively feed on swimming cercariae, and the latter encyst as metacercariae within fish tissues (Kearn 1998). The cycle is completed when an infected fish is consumed by either a fish-eating bird like a heron or shag, or, in some species, by a marine mammal, such as a seal. The other trematode in the mudsnail, *Renicola* sp., produces cercariae equipped with a penetration stylet (Martorelli et al. 2008). In other species of the genus *Renicola*, cercariae penetrate either a fish or a bivalve such as an oyster, where they encyst to await ingestion by their avian definitive host, normally a shore bird such as a gull; we, therefore, assume that the life cycle of the Otago renicolid follows this pattern.

Three species of the family Opecoelidae, genetically distinct though not distinguishable from each other based on morphology, use topshells of the genus *Diloma* as first intermediate hosts (Donald et al. 2004, 2007), with two of these species being found in the topshells of Otago Harbour. First reported and described by Clark (1958) in *Diloma* (*Melagraphia*) *aethiops*, molecular data now reveal that one of the distinct species, opecoelid sp.A, infects only *D. subrostrata*, whereas the second, opecoelid sp.C, is also found in other topshell species, mainly *D. aethiops*, but has not been found in *D. subrostrata* (Donald et al. 2004, 2007). Like most other gastropods infected by trematodes, topshells hosting larval stages of these opecoelid trematodes are castrated. In addition, their mobility and dispersal on the mudflat are reduced compared with uninfected conspecifics (Miller & Poulin 2001). The cercariae released by infected topshells must encyst in second intermediate hosts, probably crustaceans, to await predation by fish definitive hosts; however, the identity of these additional host species is yet to be determined.

Metacercariae of a species of opecoelid (species E in Table 1) have also been found encysted in the body cavity of capitellid polychaetes, however these were found to be genetically distinct from the species found in the topshells (R. Peoples unpubl. data); the identity of their first intermediate host is thus unknown, as is the remainder of their life cycle.

A further five species of trematodes are known from Otago Harbour mudflats. Three of these species use the mud whelk *Co. glandiformis* as first intermediate host. The first species is an undescribed member of the family Strigeidae occurring at low prevalence in *Co. glandiformis*. Presumably, it uses fish as second intermediate hosts and fish-eating birds as definitive hosts, like other members of its family. In addition, an undescribed species of opecoelid (species D in Table 1) and an undescribed species of microphallid are also found in *Co. glandiformis*. The remaining two trematode species currently known from Otago Harbour include an unidentified species that uses cockles, *A. stutchburyi*, as first intermediate host. Originally described and named *Cercaria pectinata* by Chilton (1905), its taxonomic affiliations or life cycle are unknown. It has been reported from Otago Harbour since its original description (e.g., Poulin et al. 2000), but always at very low (<1%) prevalence. The final species, also undescribed and of unknown taxonomic position, occurs at low prevalence in the

pulmonate snail *Amphibola crenata*. It was reported by W. Farnie almost a century ago (unpublished presentation, 1917 Meeting of the Otago Institute), but nothing has been documented about its ecology or transmission cycle.

CONCLUSIONS

The current list of 20 trematode species presented here is unlikely a complete inventory of the species that occur on the mudflats of Otago Harbour. In addition, the same host organisms are likely to host slightly different trematode faunas in other areas. We hope that the information summarised here, and the DNA barcodes that facilitate trematode species and life cycle identification, will prompt marine ecologists to pay greater attention to these common parasites.

ACKNOWLEDGMENTS

We thank the members of the Otago Ecological Parasitology Group who, over the years, have contributed various bits of information leading to this compilation. This work was indirectly supported by grants from the Marsden Fund and the University of Otago.

REFERENCES

Allison FR 1979. Life cycle of *Curtuteria australis* n. sp. (Digenea: Echinostomatidae: Himasthlinae), intestinal parasite of the South Island pied oystercatcher. New Zealand Journal of Zoology 6: 13–20.

Babirat C, Mouritsen KN, Poulin R 2004. Equal partnership: two trematode species, not one, manipulate the burrowing behaviour of the New Zealand cockle, *Austrovenus stutchburyi*. Journal of Helminthology 78: 195–199.

Bowles J, Hope M, Tiu WU, Xushian L, McManus DP 1993. Nuclear and mitochondrial genetic markers highly conserved between Chinese and Philippine *Schistosoma japonicum*. Acta Tropica 55: 217–229.

Chilton C 1905. On the occurrence of a species of cercaria in the cockle *Chione stutchburyi*. Transactions and Proceedings of the New Zealand Institute 37: 322–325.

Clark WC 1958. A new cotylocercous cercaria from *Melagraphia aethiops* (Gm.) (Gastropoda). Transactions of the Royal Society of New Zealand 85: 681–683.

Curtis LA 1987. Vertical distribution of an estuarine snail altered by a parasite. Science 235: 1509–1511.

Donald KM, Kennedy M, Poulin R, Spencer HG 2004. Host specificity and molecular phylogeny of larval Digenea isolated from New Zealand and Australian topshells (Gastropoda: Trochidae). International Journal for Parasitology 34: 557–568.

Donald KM, Sijnja A, Spencer HG 2007. Species assignation amongst morphologically cryptic larval Digenea isolated from New Zealand topshells. Parasitology Research 101: 433–441.

Ferreira SM, Jensen KT, Martins P, Sousa SF, Marques JC, Pardal MA 2005. Impact of microphallid trematodes on the survivorship, growth, and reproduction of an isopod (*Cyathura carinata*). Journal of Experimental Marine Biology and Ecology 318: 191–199.

Fredensborg BL, Poulin R 2006. Parasitism shaping host life history evolution: adaptive responses in a marine gastropod to infection by trematodes. Journal of Animal Ecology 75: 44–53.

Fredensborg BL, Latham ADM, Poulin R 2004a. New records of gastrointestinal helminths from the red-billed gull (*Larus novaehollandiae scopulinus*). New Zealand Journal of Zoology 31: 75–80.

Fredensborg BL, Mouritsen KN, Poulin R 2004b. Intensity-dependent mortality of *Paracalliope novizealandiae* (Amphipoda: Crustacea) infected by a trematode: experimental infections and field observations. Journal of Experimental Marine Biology and Ecology 311: 253–265.

Fredensborg BL, Mouritsen KN, Poulin R 2005. Impact of trematodes on host survival and population density in the intertidal gastropod *Zeacumantus subcarinatus*. Marine Ecology Progress Series 290: 109–117.

Hay KB, Fredensborg BL, Poulin R 2005. Trematode-induced alterations in shell shape of the mud snail *Zeacumantus subcarinatus* (Prosobranchia: Batillariidae). Journal of the Marine Biological Association of the United Kingdom 85: 989–992.

Hewitt GC, Hine PM 1972. Checklist of parasites of New Zealand fishes and of their hosts. New Zealand Journal of Marine and Freshwater Research 6: 69–114.

Hine PM, Jones JB, Diggles BK 2000. A checklist of parasites of New Zealand fishes, including previously unpublished records. NIWA Technical Report no. 75. National Institute of Water and Atmospheric Research Ltd, Wellington, New Zealand.

Howell M 1965. Notes on a potential trematode parasite of man in New Zealand. Tuatara 13: 182–184.

Howell MJ, Bearup AJ 1967. The life histories of two bird trematodes of the family Philophthalmidae. Proceedings of the Linnean Society of New South Wales 92: 182–194.

Huxham M, Raffaelli D, Pike A 1993. The influence of *Cryptocotyle lingua* (Digenea: Platyhelminthes) infections on the survival and fecundity of *Littorina littorea* (Gastropoda: Prosobranchia): an ecological approach. Journal of Experimental Marine Biology and Ecology 168: 223–238.

Kearn GC 1998. Parasitism and the platyhelminths. London, Chapman & Hall. 544 p.

Keeney DB, Waters JM, Poulin R 2007a. Clonal diversity of the marine trematode *Maritrema novaezealandensis* within intermediate hosts: the molecular ecology of parasite life cycles. Molecular Ecology 16: 431–439.

Keeney DB, Waters JM, Poulin R 2007b. Diversity of trematode genetic clones within amphipods and the timing of same-clone infections. International Journal for Parasitology 37: 351–357.

Keeney DB, Boessenkool S, King TM, Leung TLF, Poulin R 2008. Effects of interspecific competition on asexual proliferation and genetic diversity in larval trematode infections of snails. Parasitology 135: 741–747

Králová-Hromadová I, Špakulová M, Horáčková E, Turčeková L, Novobilský A, Beck R, Koudela B, Marinculić A, Rajský D, Pybus M 2001. Sequence analysis of ribosomal and mitochondrial genes of the giant liver fluke *Fascioloides magna* (Trematoda: Fasciolidae): intraspecific variation and differentiation from *Fasciola hepatica*. Journal of Parasitology 94: 58–67.

Kumar S, Tamura K, Nei M 2004. MEGA3: integrated software for molecular evolutionary genetics analysis and sequence alignment. Briefings in Bioinformatics 5: 150–163.

Lafferty KD 1993. Effect of parasitic castration on growth, reproduction and population dynamics of the marine snail *Cerithidea californica*. Marine Ecology Progress Series 96: 229–237.

Lafferty KD, Dobson AP, Kuris AM 2006. Parasites dominate food web links. Proceedings of the National Academy of Sciences of the United States 103: 11211–11216.

Leung TLF, Poulin R 2006. Effects of the trematode *Maritrema novaezealandensis* on the behaviour of its amphipod host: adaptive or not? Journal of Helminthology 80: 271–275.

Leung TLF, Poulin R 2007. Interactions between parasites of the cockle *Austrovenus stutchburyi*: hitch-hikers, resident-cleaners, and habitat-facilitators. Parasitology 134: 247–255.

Leung TLF, Keeney DB, Poulin R 2009. Cryptic species complexes in manipulative echinostomatid trematodes: when two become six. Parasitology 136: 241–252

Martorelli SR, Fredensborg BL, Mouritsen KN, Poulin R 2004. Description and proposed life cycle of *Maritrema novaezealandensis* n. sp. (Microphallidae) parasitic in red-billed gulls *Larus novaehollandiae scopulinus* from Otago Harbor, South Island, New Zealand. Journal of Parasitology 90: 272–277.

Martorelli SR, Poulin R, Mouritsen KN 2006. A new cercaria and metacercaria of *Acanthoparyphium* (Echinostomatidae) found in an intertidal snail, *Zeacumantus subcarinatus* (Batillaridae) from New Zealand. Parasitology International 55: 163–167.

Martorelli SR, Fredensborg BL, Leung TLF, Poulin R 2008. Four trematode cercariae form the New Zealand intertidal snail *Zeacumantus subcarinatus* (Batillariidae). New Zealand Journal of Zoology 35: 73–84

McKenna PB 1998. Checklist of helminth and protozoan parasites of birds in New Zealand. Surveillance 25: 3–12.

Miller AA, Poulin R 2001. Parasitism, movement and distribution of the snail *Diloma subrostrata* (Trochidae) in a soft-sediment intertidal zone. Canadian Journal of Zoology 79: 2029–2035.

Mouritsen KN 2002. The parasite-induced surfacing behaviour in the cockle *Austrovenus stutchburyi*: a test of an alternative hypothesis and identification of potential mechanisms. Parasitology 124: 521–528.

Mouritsen KN, Poulin R 2002. Parasitism, community structure and biodiversity in intertidal ecosystems. Parasitology 124: S101–S117.

Mouritsen KN, Poulin R 2003. Parasite-induced trophic facilitation exploited by a non-host predator: a manipulator's nightmare. International Journal for Parasitology 33: 1043–1050.

Mouritsen KN, Poulin R 2005a. Parasitism can influence the intertidal zonation of non-host organisms. Marine Biology 148: 1–11.

Mouritsen KN, Poulin R 2005b. Parasites boosts biodiversity and changes animal community structure by trait-mediated indirect effects. Oikos 108: 344–350.

Mouritsen KN, Poulin R 2006. A parasite indirectly impacts both abundance of primary producers and biomass of secondary producers in an intertidal benthic community. Journal of the Marine Biological Association of the United Kingdom 86: 221–226.

Poulin R 2006. Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. Parasitology 132: 143–151.

Poulin R, Steeper MJ, Miller AA 2000. Non-random patterns of host use by the different parasite species exploiting a cockle population. Parasitology 121: 289–295.

Poulin R, Nichol K, Latham ADM 2003. Host sharing and host manipulation by larval helminths in shore crabs: cooperation or conflict? International Journal for Parasitology 33: 425–433.

Probst S, Kube J 1999. Histopathological effects of larval trematode infections in mudsnails and their impact on host growth: what causes gigantism in *Hydrobia ventrosa* (Gastropoda: Prosobranchia). Journal of Experimental Marine Biology and Ecology 238: 49–68.

Schell SC 1970. How to know the trematodes. Dubuque, Iowa, WC Brown Company. 355 p.

Sousa WP 1991. Can models of soft-sediment community structure be complete without parasites? American Zoologist 31: 821–830.

Thieltges DW 2006. Parasite induced summer mortality in the cockle *Cerastoderma edule* by the trematode *Gymnophallus choledochus*. Hydrobiologia 559: 455–461.

Thomas F, Poulin R 1998. Manipulation of a mollusc by a trophically transmitted parasite: convergent evolution or phylogenetic inheritance? Parasitology 116: 431–436.

Thomas F, Renaud F, de Meeüs T, Poulin R 1998. Manipulation of host behaviour by parasites: ecosystem engineering in the intertidal zone? Proceedings of the Royal Society of London Series B 265: 1091–1096.

Thompson RM, Mouritsen KN, Poulin R 2005. Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. Journal of Animal Ecology 74: 77–85.

Tompkins DM, Mouritsen KN, Poulin R 2004. Parasite-induced surfacing in the cockle *Austrovenus stutchburyi*: adaptation or not? Journal of Evolutionary Biology 17: 247–256.

Valentini A, Pompanon F, Taberlet P 2009. DNA barcoding for ecologists. Trends in Ecology and Evolution 24: 110–117.

Weekes PJ 1982. Checklist of helminth parasites of birds in New Zealand. New Zealand Journal of Zoology 9: 451–460.

Wood CL, Byers JE, Cottingham KL, Altman I, Donahue MJ, Blakeslee AMH 2007. Parasites alter community structure. Proceedings of the National Academy of Sciences of the United States 104: 9335–9339.