

R. Poulin 

Department of Zoology, University of Otago, PO Box 56, Dunedin 9054, New Zealand

Review Article

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Corresponding author:

R. Poulin;
 Email: robert.poulin@otago.ac.nz

Abstract

The growth of knowledge and research practices in any discipline is characterised by a trade-off between depth and breadth: we can either invest efforts to learn a little about many things, or learn a lot about few things. In parasitology, breadth of knowledge corresponds to research on biodiversity and taxonomy: the discovery and description of an increasing number of new species. In contrast, depth of knowledge comes from focused research on a few model species, about which we accumulate much detailed information. Breadth and depth of knowledge are equally important for progress in parasitology. In this essay, focusing on trematodes, I demonstrate that current research is rapidly broadening our knowledge (high rate of new trematode species being discovered) but not deepening that knowledge at a comparable rate. The use of model species, with caveats, appears to offer a promising avenue for deeper knowledge. I present a case study illustrating how it is possible to develop new model trematode species at low cost to increase the depth of our understanding in areas including host-parasite ecological dynamics, co-evolution, and responses to environmental and climatic changes. The take-home message serves as a call to action to parasitologists, emphasising the need to focus as much effort on depth of knowledge as we currently invest in breadth of knowledge.

Introduction

Parasitologists specialising on any large taxon, such as Trematoda, generally know quite a lot about this taxon, and their work aims to extend our knowledge of that taxon. But what exactly does it mean to ‘know’ about a large taxon like Trematoda? And how can we increase our knowledge of that taxon? There are two ways of answering these questions. On the one hand, it could be argued that knowledge of Trematoda requires knowing all its constituent species and how they fit within the Linnaean classification scheme. Here, knowledge refers specifically to completeness of our inventory of species; that is, increasing our knowledge of Trematoda entails more thoroughly documenting its constituent species. This approach to knowledge of trematodes is that adopted by taxonomy and systematics, and it represents *breadth* of knowledge. On the other hand, it could also be argued that really knowing about trematodes involves detailed investigations of their biology, how they function, and how they interact with their hosts. This is the realm of genomics, physiology, immunology, and ecology, among other disciplines, and it represents *depth* of knowledge. Neither breadth nor depth is more important than the other, as both are necessary for true holistic growth of knowledge.

For an individual researcher, however, it is almost impossible to contribute to both breadth and depth of knowledge. Faced with limited time and resources, a trematodologist can only direct their efforts toward one of these extremes. We may thus expect a trade-off between breadth and depth of knowledge across individual researchers, between those that work on many species but know little about each one, and those that study very few species but know a lot about them (Figure 1). The trade-off may well apply to individuals; however, we would expect that, collectively, the community of researchers studying trematodes or any other large taxon should be able to cover both ends of the breadth-versus-depth spectrum, ensuring full knowledge growth.

Here, I examine growth of knowledge about trematodes from both the breadth and depth perspectives. I begin by using bibliometric data to demonstrate that our expanding breadth of trematode knowledge, seen as a growing number of named and described species, is not accompanied by any deeper research on the biology of those species. I then argue that focused studies on a select few model species, if interpreted cautiously, can yield in-depth knowledge that cannot possibly be obtained for all species within the taxon. As I explain, this is an approach from which our understanding of trematode biology and ecology could benefit even more than it has to date. Using one trematode species as a case study, I demonstrate how much can be learned from extended studies on new model species. Finally, I list the ideal characteristics of trematode species that could be established as new, low-cost model species. As a community of researchers, we do breadth of knowledge quite well; however, we can do better at depth of knowledge, and thus I end with a plea for the development of further model trematode species as the most urgent next step for knowledge growth in our field.

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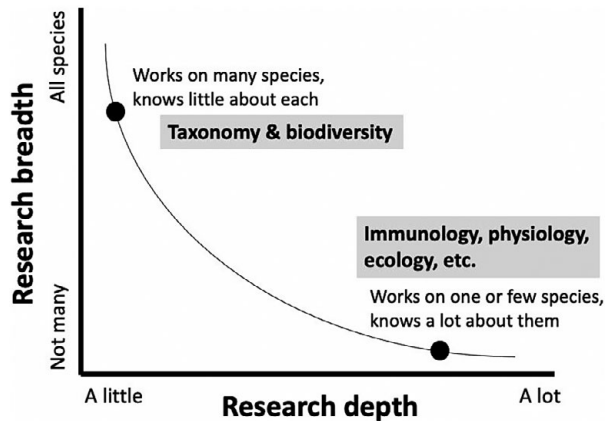


Figure 1. The expected trade-off between breadth of knowledge, representing how many trematode species any researcher can study, and depth of knowledge, representing the extent of detailed studies that are conducted on each species. Some of the subdisciplines associated with each end of the spectrum are also shown.

Breadth of knowledge on trematodes

The number of new trematode species discovered and described each year has been growing steadily in the past few decades (Poulin, 2014; Poulin and Presswell 2016). The total number of known and named trematode species at present probably amounts to about 8,000–10,000 (G. Pérez-Ponce de León and T. Cribb, personal communication), although some estimates put that number closer to 20,000 (Bray 2008; Esch *et al.* 2002). Doubtless many more trematode species await to be found. With our expanding knowledge of their diversity, one must ask the following: After first being discovered, described, and given a Latin name, how often are trematode species seen again, studied again, or even mentioned again in the scientific literature?

A recent analysis of research effort on helminth parasites provides some answers (Poulin *et al.* 2023). Out of 576 trematode species described between 2000 and 2018 in the eight English-language parasitology journals where most taxonomic studies are

published, nearly 60% had not been mentioned again in the scientific literature by early 2023 (Figure 2). Those that were mentioned again were generally only referred to in two or three articles in the many years following their description. There was one exception: one species was mentioned in over 50 articles following its description in 2004. I will return to this outlier a little later.

Of the many potential predictors of research effort post-description that were considered, only the number of years since a species description was published showed a weak but positive effect on the number of times it was later mentioned in the literature (Poulin *et al.* 2023). No host characteristic (higher taxon, body mass, conservation status, and human use status) or variable associated with the country of discovery (GDP, population size) had any effect on the number of times a species was mentioned in the literature following its description.

When a previously described trematode species is mentioned in a new article, it is usually not because new specimens have been collected or used in genetic or experimental studies. Typically, the species is mentioned as part of a list of known species within a genus or family, in the context of a phylogenetic study or for comparison with yet another new species being described (Poulin *et al.* 2023). Thus, no new knowledge is generated about the original species itself in most articles where its name comes up.

The take-home message is therefore very clear: for the majority of the hundreds of trematode species described since the year 2000, and probably for most trematodes described before that, we know that they occur in one host species in one locality, we know what they look like, and we may have their base pair sequences for one or two genes. That is all the information we have. We do not know all hosts in their life cycle, their full geographical range, the impacts they have on their hosts, how their abundance might respond to climate change, etc. Most known trematode species have never been studied again after their initial discovery. This shocking fact is not unique to trematodes: it applies to other major taxa of helminth parasites (Poulin *et al.* 2023) and more generally to small invertebrates (Titley *et al.* 2017). Taxonomic studies are doing an excellent job of expanding the breadth of our knowledge of trematode biodiversity. However, this knowledge is rather shallow when

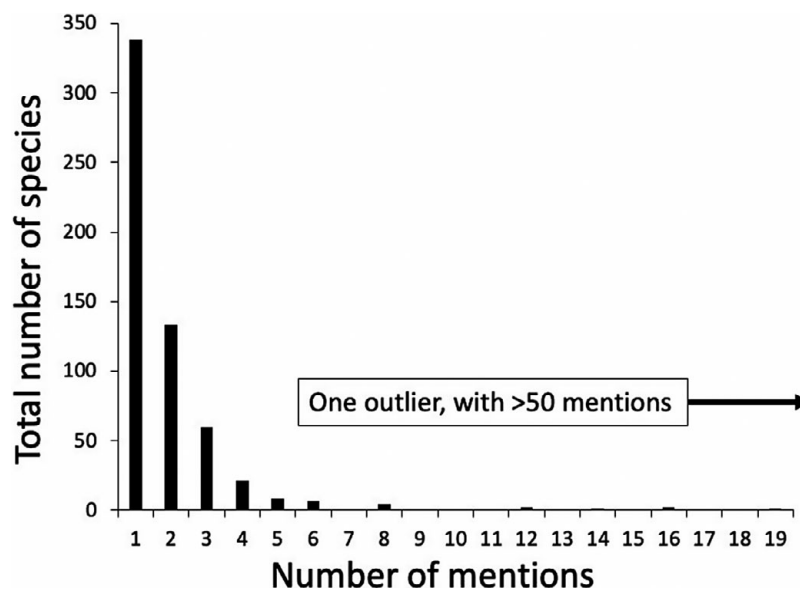


Figure 2. Frequency distribution of number of mentions of a species' name in the scientific literature, including the mention in its original description, for 576 trematodes described between the years 2000 and 2018. One outlier species, with over 50 mentions since it was described, is excluded to avoid distorting the figure. Data from Poulin *et al.* (2023).

considering how little we have learned about the biology of individual species. What can be done to improve the depth of our knowledge about trematodes?

Depth of knowledge through model species

Much progress in the biological sciences is owed to research on model animal species (Alfred and Baldwin 2015; Müller and Grossniklaus 2010). Just consider how much has been learned from the nematode *Caenorhabditis elegans*, the fruit fly *Drosophila melanogaster*, the zebrafish *Danio rerio*, the clawed frog *Xenopus laevis*, and the house mouse *Mus musculus*. These species have been selected for a range of reasons, not always because they were the best available choices or the most representative of their higher taxon. Despite their limitations (Bolker 2017; Katz 2016), they remain some of our most important research assets. Parasitological research has also greatly benefited from model helminth species, notably the cestode *Hymenolepis diminuta* (Sulima-Celińska *et al.* 2022) and the nematode *Heligmosomoides polygyrus* (Behnke *et al.* 2009; Monroy and Enriquez 1992). Multiple laboratory colonies of these helminth species exist around the world; they have yielded hundreds of articles that account for much of our modern understanding of helminth-mammal interactions in the areas of immunology, physiology, pathology, and anthelmintic action and/or resistance, among others (Poulin 2023). They epitomise depth of knowledge: an integrated and extended research programme focused on the detailed biology of single species.

Research on model parasite species such as *H. diminuta* and *H. polygyrus* must be considered in light of some clear limitations, however. Because of the way in which laboratory colonies of these helminths are established and subsequently maintained in artificial conditions over numerous generations, experimental results on some aspects of their biology may not be representative of natural populations of their own species, let alone cestodes and nematodes in general (Poulin 2023). First, most colonies are established with relatively few individuals, which makes them susceptible to founder effects. In other words, they suffer a loss of genetic variation relative to the larger source population because the small number of founder individuals do not carry the full range of gene variants (alleles) present in the source population. Second, each new generation is started with eggs from only a small subset of adult worms from the parent generation, and laboratory colonies are almost never 'refreshed' genetically by the addition of worms from outside the colony. In effect, whatever the size of the adult population, the effective population size (i.e., the number of individuals that effectively participate in producing the next generation) is much smaller and likely to consist of genetically related individuals, increasing the risk of genetic bottlenecks, allelic drift (i.e., loss of genetic diversity due to stochastic events), and/or inbreeding depression (i.e., homozygosity for deleterious recessive alleles). Third, artificial selection acting on laboratory helminth cultures due to the unnatural conditions in which they are transmitted (i.e., forced gavage instead of consumption of infected prey or accidental egg ingestion) and interact with their hosts can have unplanned, unanticipated, and very rapid evolutionary consequences (Kawecki *et al.* 2012). The upshot is that laboratory populations of model helminths may diverge from each other and from natural populations at both genetic and phenotypic levels (Abu-Madi *et al.* 2000; Cable *et al.* 2006; Kino and Kennedy 1987; Režábková *et al.* 2019). Therefore, although they remain one

of our best approaches for deeper knowledge, research findings based on multi-generational helminth colonies must be generalised with caution (Poulin 2023).

What about model trematode species? Obviously, *Schistosoma mansoni* comes to mind, its health impact on human populations having driven its development as a well-studied model species in laboratory mice (Abdul-Ghani and Hassan 2010). Maintenance of this species in laboratory colonies by passage through snails and mice across multiple generations leaves it open to the same genetic issues mentioned above. For example, a recent study revealed that two laboratory strains of *S. mansoni*, both started with specimens collected from the same locality but 34 years apart, show differences in key traits such as virulence and egg production, indicating that the time (and thus the number of generations) spent in artificial laboratory culture has shaped their evolution (Dias *et al.* 2023). The differences could also be due to founder effects; either way, these observations confirm that laboratory-based trematode populations are subject to evolutionary genetic forces causing them to diverge from natural populations. Other trematodes, either of medical importance like *Clonorchis sinensis*, of veterinary concern like *Fasciola* spp., or of eco-evolutionary interest such as *Echinostoma* spp. or *Diplostomum* spp., also qualify as model species (e.g., Capasso and Gutiérrez 2023; Fried and Graczyk 2000). They have been the subject of extensive studies on their biology and host-parasite interactions; however, except maybe for *Echinostoma* spp., they are generally not maintained in multi-generational laboratory colonies. This simple fact exempts them from the potential genetic concerns discussed above for laboratory-housed helminth colonies because individual worms are obtained *ad hoc* from natural or semi-natural populations as required for each separate study.

Are these model taxa sufficient to achieve genuine and representative depth of knowledge about trematodes? I believe not, and I argue we need more. A handful of species, chosen in part for their impact on humans and domestic animals, is very unlikely to be representative of the thousands of trematode species currently known. Life cycles, hosts used, organs targeted, pathology, etc., all vary greatly among trematode taxa. The trematodes that matter to health scientists and veterinarians are also not the same that matter to ecologists. For instance, the main trematode species shown to account for substantial biomass (Kuris *et al.* 2008; Lagrue and Poulin 2016; Preston *et al.* 2013) and to play key structural roles (Friesen *et al.* 2020; Mouritsen and Poulin 2010; Wood *et al.* 2007) in aquatic ecosystems belong to families other than those of the existing trematode model species. The placement of the above model species on the latest trematode phylogeny (Pérez-Ponce de León and Hernández-Mena 2019) clearly shows that none of them occur on many important branches in the trematode tree; therefore, how could knowledge of their biology be said to capture the full diversity of trematodes? Greater depth of knowledge actually requires greater breadth of model taxa. In some ways, this is easier said than done. Some phylogenetically and ecologically distinct trematode suborders (sensu Pérez-Ponce de León and Hernández-Mena 2019), such as Bivesiculata and Heronimata, include few species with restricted geographical ranges and/or infecting hosts that are not easy to study in captivity. However, for many other trematode clades, establishing new model species poses fewer challenges. In the next section, I present an example of how new trematode model species can be developed from scratch at relatively low cost and how they can shed light on many important questions currently asked in ecological and evolutionary parasitology.

Case study: The trematode *Maritrema novaezealandense*

Let us now return to the outlier in Figure 2, the trematode discovered post-2000 that had received over 50 mentions in the scientific literature by the end of 2023. This exception to the general pattern is the New Zealand endemic species *Maritrema novaezealandense* (Microphallidae). Initially described and named as *M. novaezealandensis* by Martorelli *et al.* (2004), the spelling of the species epithet was later corrected by Presswell *et al.* (2014). It has the typical microphallid life cycle (Figure 3). The mudsnail *Zeacumantus subcarinatus* serves as the first intermediate host, in which asexually multiplying sporocysts produce cercariae. After emerging from the snail host, free-swimming cercariae seek, penetrate, and encyst as metacercariae inside small crustaceans; a wide range of amphipods, isopods, shrimps, and crabs can be used as second intermediate hosts, in which the metacercariae await ingestion by a suitable definitive host. Finally, shore birds, mainly seagulls *Larus* spp., act as definitive hosts, harbouring adult worms in their digestive tract where the latter live and reproduce sexually, releasing eggs in the bird's faeces.

After finding this trematode in local intertidal locations near our university in the early 2000s and formally describing it in 2004, my research group and I have adopted it as our main model species for a

wide range of studies in the two decades that followed (Figure 4). Over the years, we expanded our methodological toolkit and developed new resources to better investigate various facets of its biology (Figure 5). These include techniques for its use in laboratory experiments, such as inducing the release of cercariae from snail hosts, experimental infection of crustacean second intermediate hosts, *in vitro* culture methods, and fluorescent labelling of cercariae to track their movements pre- and post-infection. The tools developed for *M. novaezealandense* also include genetic ones, such as the characterisation of polymorphic microsatellite loci and sequencing of gene markers useful for studies of population structure or phylogenetic relationships. In this era of affordable genomic analysis, sequencing and annotating the whole genome of *M. novaezealandense* would be a straightforward next step, should we require it.

In the past two decades, we have applied this expanding toolkit to address a growing number of questions relating to the biology of *M. novaezealandense* and its interaction with its hosts (Figure 5). Here, I only present a selection of key findings. These began with investigations into its ecological and evolutionary impacts on its intermediate hosts. With respect to the snail first intermediate hosts, we established that the castration of individual snails caused by infection translates into measurable population-level impacts

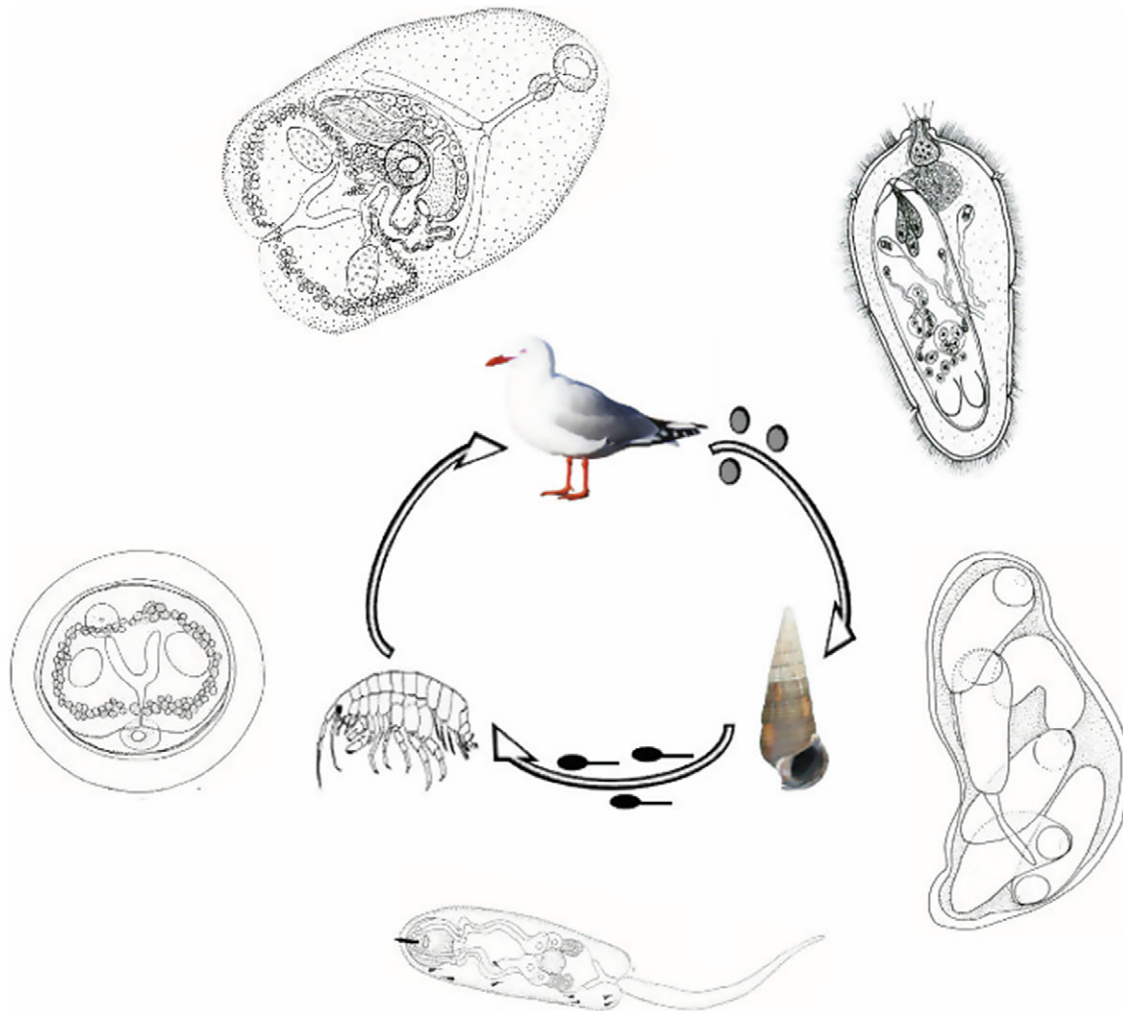


Figure 3. Life cycle of the microphallid trematode *Maritrema novaezealandense*, showing both the succession of intermediate and definitive hosts (inner diagram) and the successive life stages (outer diagram).

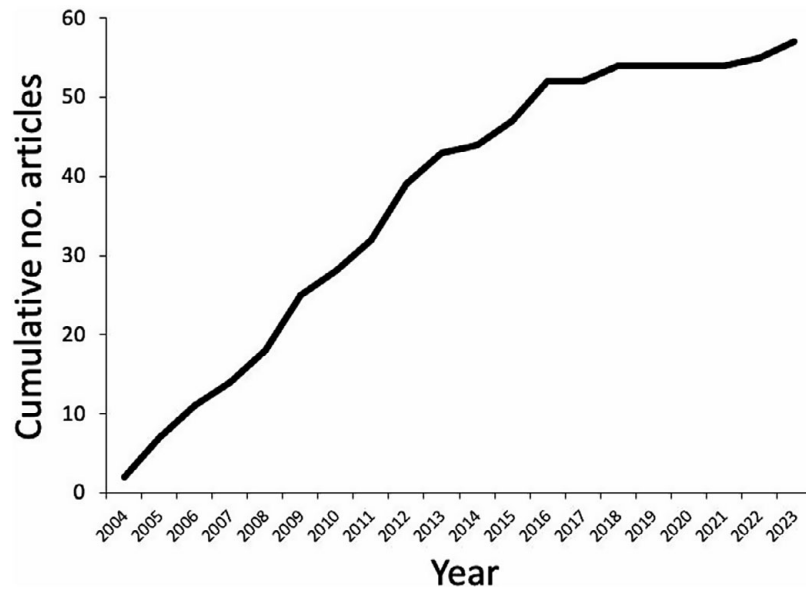


Figure 4. Cumulative number of articles published about the trematode *Maritrema novaezealandense* since its description in 2004.

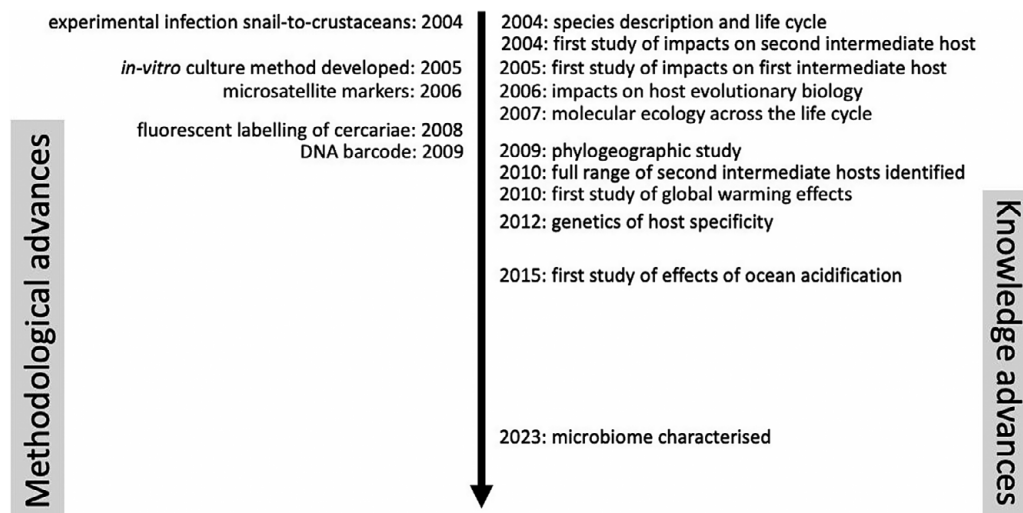


Figure 5. Timeline of the major milestones in research on the trematode *Maritrema novaezealandense* since its description in 2004, divided into methodological and knowledge advances.

(Fredensborg *et al.* 2005). We also showed that infection modifies the phenotype of snail hosts, from changing the shape of their shell (Hay *et al.* 2005) to raising their heat tolerance and shifting their preference toward high temperatures when placed in a thermal gradient (Bates *et al.* 2011). On an evolutionary scale, we provided evidence that the castration induced by *M. novaezealandense* could lead to adaptive changes in host life history traits, with snails in populations experiencing high prevalence of infection having evolved to mature at an earlier age and smaller size than those in populations where prevalence is low (Fredensborg and Poulin 2006).

Our research also quantified the impact of *M. novaezealandense* on its crustacean second intermediate hosts. For instance, we demonstrated the intensity-dependent mortality induced by the trematode and its influence on host population dynamics in both laboratory and field studies (e.g., Bates *et al.* 2010; Fredensborg *et al.*

2004). As with the snail host, *M. novaezealandense* can also act as a selective force in its crustacean host, leading to apparent local adaptation. For example, we found that variation in immunocompetence among amphipod populations is associated with the presence or absence of the trematode: in areas where it infects amphipods, the hosts show a strong encapsulation defense reaction to infection, whereas in areas where infections are absent, amphipods lack this ability (Bryan-Walker *et al.* 2007).

The genetic research we conducted on this model trematode species has also revealed intriguing aspects of the parasite's micro-evolutionary dynamics. Not surprisingly given the high mobility of its avian definitive host, *M. novaezealandense* shows little genetic structure on scales of hundreds of kilometres, with gene flow maintaining homogeneity across local populations (Keeney *et al.* 2009). Within local populations, we confirmed that the genetically identical (clonal) cercariae produced within the same snail can

sometimes end up in the same second intermediate host, which is remarkable given the highly turbulent intertidal habitat in which they are released from snails (Keeney *et al.* 2007a, 2007b). Even more remarkable, different clones of *M. novaezealandense* show markedly different performance in different crustacean species serving as second intermediate hosts, suggesting intraspecific variability in host specialisation (Koehler *et al.* 2011, 2012).

M. novaezealandense has also been a great model species for studies of the responses of host-parasite interactions to global climate and environmental changes. For instance, we showed that higher coastal water temperatures predicted by global warming scenarios are likely to positively impact the transmission of the trematode from its first to its second intermediate hosts (Studer *et al.* 2010). As a consequence, our research suggests that coastal crustacean communities may be changed drastically, as the greater susceptibility of certain crustacean species to both infection by *M. novaezealandense* and elevated temperatures will cause their populations to crash (Mouritsen *et al.* 2018). We have also investigated the likely effects of ocean acidification, another major stressor acting on marine ecosystems. We found that in seawater with even slightly lower pH, *M. novaezealandense* cercariae do not survive as well as in pH-neutral seawater (MacLeod and Poulin 2015), which may offset their generally higher infection success at lower pH (Harland *et al.* 2015).

More recently, we have characterised the microbiome of *M. novaezealandense* sporocysts, revealing that they contain multiple bacterial lineages distinct from those found in the outside environment, in the tissues of the snail host, and in other trematode species using the same snail as first intermediate host (Salloum *et al.* 2023). The above summary is far from complete. We have investigated multiple other eco-evolutionary issues using *M. novaezealandense* as a model species (e.g., within-host competition among metacercariae, predation on cercariae by sea anemones, etc.); I do not provide a full overview to avoid an excess of self-citations. The important point is that several of our results, as interesting as they may be, cannot be compared with other findings on other trematode species because there is a lack of similar research conducted elsewhere. For instance, at the time we conducted our studies and even at present, other examples of geographic variation in the immunocompetence of hosts faced with trematode infections (Bryan-Walker *et al.* 2007) or trematode-induced changes in snail thermal tolerance (Bates *et al.* 2011) can hardly be found. Any attempt to formulate generalisations about trematode biology requires a synthesis of results from comparable studies performed across a wide range of trematode species representing the full phylogenetic diversity of the group. At present, this is not achievable: we need to establish and investigate additional model trematode species.

The makings of new model species

We did not select *M. novaezealandense* as a model species for our research without also considering other candidate species. In the end, *M. novaezealandense* met several criteria that made it the ideal choice for us. I have no doubt the same criteria are also met by many other trematode species worldwide, providing us with a wide array of potential species from which to select novel model species. Here, I summarise the main characteristics of potentially good candidate species for the establishment of new models to address general questions relating to the ecology and evolution of host-parasite interactions. The emphasis is on low-cost options that require no

significant logistic resources. I do not consider the possibility of setting up multi-generational laboratory populations; as discussed above, these are not without limitations, and they are not always necessary to achieve greater depth of knowledge about trematode biology. Further, I assume that most experimental research on vertebrate definitive hosts, especially birds or mammals, is usually not possible for either logistical or ethical reasons; therefore, I focus on model species that can be investigated in their first and second intermediate hosts. Ideal candidates as model species should meet the following criteria:

- (i) Hosts should occur near the researchers' institution and be easy to collect without necessitating undue expenses (e.g., no need for a boat).
- (ii) Hosts should be abundant, and their sampling should not be unduly limited by legal or ethical considerations.
- (iii) Prevalence of infection, especially in the first intermediate host, should not be too low, allowing infected individuals to be obtained easily.
- (iv) Hosts should be easy to maintain in the lab. They should ideally be small so that housing them is simple, they should be tolerant of variable laboratory conditions (e.g., fluctuating temperatures, photoperiod), and the food they require should be easy to source.
- (v) Hosts that can be easily bred in captivity would be ideal. Although not essential, laboratory-bred hosts provide a standardised source of uninfected individuals of known age for experimental purposes.
- (vi) Basic methods to induce cercarial emergence from first intermediate hosts and for controlled infection of second intermediate hosts should be straightforward to develop and to standardise for repeated use.
- (vii) If the trematode species is amenable to in-vitro studies (i.e., culturing sporocyst/rediae or metacercariae in an artificial medium), then further research possibilities would open up.

No doubt many invertebrates and small fish, and their trematodes, meet most of the above conditions. Ideally, chosen trematode species would belong to different families, to expand the phylogenetic coverage of new model species, and would display a wide variety of life cycles. Individual researchers may have additional requirements or preferences. We should also aim to standardise research protocols for the different questions investigated, to achieve comparable results that can be used in meta-analyses and synthesis to seek general patterns across trematode taxa. The bottom line is that new model species are needed, and establishing them should become a priority if we are to achieve deeper understanding of trematode biology.

Concluding remarks

Along the continuum representing the trade-off between breadth and depth of knowledge, there is one thing that the global community of trematodologists does very well, and that is breadth: our inventory of known trematode species is growing steadily as new species are found and described every month. However, we do not do depth of knowledge that well. To be fair, we have accumulated much knowledge about general trematode biology (e.g., Fried and Graczyk 2000; Galaktionov and Dobrovolskij 2003), yet this is based mostly on the in-depth study of relatively few species. Therefore, I end this short essay with a simple plea for those interested in

trematodes: we need more model species beyond the conventional ones relevant mostly to health and veterinary science. A similar call to arms has been made for growth of knowledge in biology more generally (Russell *et al.* 2017). Deep understanding of trematode biology requires in-depth investigations of several species spanning the full phylogenetic and functional diversity of trematodes. There have been numerous studies of the effects of trematodes on their hosts, of their responses to changing environmental factors, etc. However, these have mostly been one-off or limited investigations (for example, representing the research for a single PhD thesis), as opposed to the integrated, comprehensive, and extended research programme that would be desirable to really understand the biology of a species. What is required to establish a trematode as a new model species and probe its biology as part of a long-term research programme is not unreasonable. My research group has done it, and I can only hope other researchers take up the challenge.

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Competing interest. The author declares no conflict of interest.

Ethical standard. Not applicable.

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