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Integrating parasitology and marine ecology: Seven challenges towards greater synergy

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ABSTRACT

Despite their very different historical origins as scientific disciplines, parasitology and marine ecology have already combined successfully to make important contributions to our understanding of the functioning of natural ecosystems. For example, robust assessments of the contribution of parasites to ecosystem biomass and energetics, and of their impact on community-wide biodiversity and food web structure, have all been made for the first time in marine systems. Nevertheless, for the marriage between parasitology and marine ecology to remain fruitful, several challenges must first be overcome. We discuss seven such challenges on the road to a greater synergy between these disciplines: (1) Raising awareness of parasitism as an ecological force by increasing the proportion of articles about parasites and diseases in marine ecology journals; (2) Making greater use of theory and conceptual frameworks from marine ecology to guide parasitological research; (3) Speeding up or at least maintaining the current rate at which marine parasites are found and described; (4) Elucidating a greater proportion of life cycles in all major groups of marine parasites; (5) Increasing the number of host–parasite model systems on which our knowledge is based; (6) Extending parasitological research offshore and into ocean depths; and (7) Developing, as needed, new epidemiological theory and transmission models for the marine environment. None of these challenges is insurmountable, and addressing just a few of them should guarantee that parasitology and marine ecology will continue to join forces and make further substantial contributions.

Contents

1. Introduction

The history of marine ecology as a scientific discipline has always been closely linked with the exploration of the oceans. From the *Challenger* expedition in the 1870s to modern research cruises, from the first undersea walk by a diver wearing a heavy copper helmet to the use of scuba and submersibles, research in marine ecology and oceanography has always been associated with adventure and big equipment. Marine ecology has matured as a discipline by developing its own theoretical framework, overlapping in part with general ecological theory but also accounting for the unique features of the marine

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environment. In contrast, parasitology emerged mostly as a discipline of the health sciences, with strong ties to medicine and veterinary science, and with the goal of controlling diseases of humans and domestic animals. When focused on wildlife, parasitology was long dominated by a basic natural history approach, consisting in the discovery and taxonomic description of parasite species and the elucidation of their life cycles. It is only in the last few decades that the rise of epidemiological theory and the influence of general ecological theory have impacted the ecological branch of parasitology and allowed it to develop into a more rigorous, hypothesis-driven science.

Based on their very different historical origins as scientific disciplines, it is difficult to imagine two more distinct research traditions than those of parasitology and marine ecology. Yet, the two have already combined successfully to make important contributions to our understanding of the functioning of natural ecosystems, as the following three examples illustrate. Firstly, the quantitative demonstration that parasites account for a significant proportion of the biomass and productivity of natural ecosystems was first achieved in marine habitats (Kuris et al., 2008). Secondly, the first experimental confirmations that single parasite species can have community-wide impacts, by modifying the activity of ecosystem engineers or key grazers and indirectly affecting the density and diversity of other free-living species of algae or invertebrates, were also achieved in marine systems (Thomas et al., 1998; Mouritsen and Poulin, 2005; Wood et al., 2007). Thirdly, the first and still the most thorough assessments of the impacts of parasitism on the structure and complexity of entire food webs were also performed in marine communities (Huxham et al., 1995; Thompson et al., 2005; Lafferty et al., 2006; Dunne et al., 2013). These are all important advances for ecology in general, and all came from the study of parasites in the marine realm. In addition, the work of parasitologists has also contributed to ‘applied’ marine ecology, such as through the use of parasites as biological tags for discrimination of commercial fish stocks (MacKenzie, 2002; Poulin and Kamiya, 2014) or the development of control measures against disease in aquaculture (e.g., Pike and Wadsworth, 1999).

Despite these achievements, the continued synergy between parasitology and marine ecology is faced with some serious current or near-future obstacles. Here, we identify seven such challenges on the road toward greater integration of the two disciplines. For each of these, we highlight the problem and propose a solution. None of these impediments is insurmountable, but measures must be taken now to ensure that parasitology and marine ecology can continue to team up to further our understanding of the functioning of oceanic ecosystems.

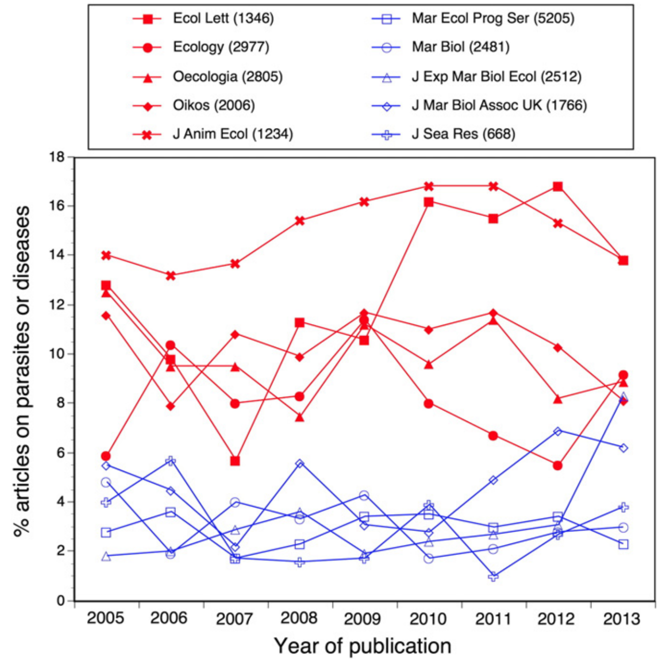

Fig. 1. Annual proportion of articles on parasites or diseases published in general ecological journals (filled symbols) and in journals of marine ecology or biology (open symbols) in the period 2005–2013. The data come from a search of the Web of Science™ using the keywords “parasit* or disease*”. Numbers in parentheses following journal names indicate the total number of articles published in each journal during that period.

2. Challenge one: research on parasites lacking from marine ecology journals

Estimates of parasite biodiversity indicate that perhaps as much as half of the species on Earth are parasites (Windsor, 1998; Poulin and Morand, 2000, 2004; de Meeûs and Renaud, 2002). Because a large proportion of them are aquatic during at least part of their life cycle, we would certainly expect that in the absence of taxonomic or other biases, parasites and the diseases they cause should receive at least equal attention in journals specializing in marine ecology as they do in more general ecological journals. This is the null expectation assuming that researchers focus on different biotic processes (predation, competition, parasitism, etc.) independently of the type of environment (terrestrial, freshwater, marine) in which they work.

Sadly, this is not the case. A survey of publication trends over the past decade indicates that articles on parasites or diseases are underrepresented in journals dedicated to marine ecology compared to journals of ecology in general (Fig. 1). On average, more than 10% of articles published annually in general ecological journals concern parasites and diseases, whereas this number is less than 5% for marine ecology journals. One strongly suspects that the same clear discrepancy would emerge from an analysis of papers presented at conferences of general ecology versus those presented at conferences of marine ecology.

Further evidence for the notion that parasites and diseases as important ecological forces has been slow to take hold in marine ecology comes from the fact that they are only mentioned in some of the most recent marine ecology textbooks. Indeed, some influential texts in marine ecology in the 1990s did not list either parasites or diseases in their subject index (e.g., Mann and Lazier, 1996; Barnes and Hughes, 1999; Mann, 2000), or only mentioned them very briefly (Nybakken, 1993; Levinton, 1995). In contrast, more recent books provide at least some content on marine parasites and the diseases they cause (e.g., Bertness et al., 2001; Castro and Huber, 2009; Speight and Henderson, 2010; Kaiser et al., 2011). Nevertheless, an informal look at the syllabus or course manual of university courses in marine biology or marine ecology that are accessible online indicates that most do not even mention the word “parasite”. Sheltering the next generation of marine ecologists from parasites represents a major impediment to the advancement of marine ecological parasitology. For the idea that “parasites matter” to get across to young marine ecologists, so that it may enter the scope of their current and future research, it first has to become established in their field. The study of parasites needs to gain a stronger foothold in marine ecology if the two disciplines are to continue to yield new and important insights. This does not necessarily demand active lobbying by parasitologists. Instead, parasitologists should simply consider marine ecology journals as potential outlets for their work, and occasionally present their findings at marine ecology conferences. Raising the parasite content of journals and conferences could be achieved in just a few years, and the greater exposure would probably be the best way to increase awareness of parasitism as an important biotic process among marine ecologists.

3. Challenge two: marine ecology concepts ignored in parasitological research

Marine ecologists might pay little attention to parasites, but they are not the only ones to blame for the limited synergy between parasitology and marine ecology. Parasitologists are just as guilty of ignoring key concepts and theory in marine ecology. Research in most disciplines at any point in time is driven by certain key ideas, sometimes merely popular bandwagons, as evidenced by a rapid rise in the number of publications on that subject. Research on marine parasites seems either completely disconnected from the main guiding themes in marine ecology or slow to react to their emergence.

For example, consider the phenomenon of ocean acidification. Over the past two centuries, anthropogenic emissions of carbon dioxide into the atmosphere have resulted in a corresponding increase in dissolved carbon dioxide in the oceans. This is gradually increasing the acidity of seawater and altering its carbonate chemistry (Doney et al., 2009). The phenomenon, referred to as ocean acidification, is known to impact the physiology, reproduction and survival of numerous marine organisms and is now considered to be one of the most significant environmental threats facing ocean ecosystems (Doney et al., 2009; Kroeker et al., 2010, 2013). The concern and interest generated by ocean acidification among scientists in recent years can be seen by the rapid rise in the number of publications devoted to the subject. A search of the Web of Science™ database using the keyword “ocean acidification” shows that during the four-year period 2000–2003, only one article on ocean acidification appeared in the scientific literature. However, in subsequent years that number rose dramatically, such that in the two-year period 2012–2013, there were about 1000 articles published on ocean acidification. In total, there have been about 1800 articles on ocean acidification published to the end of 2013, according to the Web of Science™. However, if we instead modify the search to find articles that discussed both ocean acidification and parasites (using the keywords “ocean acidification AND parasit*”), we find only a grand total of 7 articles, the first appearing in 2011. This suggests a remarkable lack of awareness by parasitologists, including the many working on marine parasites, of the main concerns of their fellow biologists studying ocean ecosystems. There are numerous ways in which ocean acidification can modify host–parasite interactions and parasites could serve as ideal sentinel species for the effects of acidification (MacLeod and Poulin, 2012), making the neglect of this phenomenon by parasitologists even more baffling.

As another example, take the concept of facilitation, which has also caught on in marine ecology (Bulleri, 2009). Facilitative interactions are those that benefit at least one of the participants and do not cause harm to either. Typically, they involve one organism making the environment more favorable for another species, either directly or indirectly (Bruno et al., 2003). Because facilitation can influence community structure and the success of invasive species, it deservedly receives attention from marine ecologists. A search of the Web of Science™ using the keywords “facilitation AND marine” shows a steady rise in the number of publications on the subject over the last ten years, from 7 in the two-year period 2000–2001 to over 30 in each of the periods 2010–2011 and 2012–2013. However, if we look instead for articles that discussed both facilitation and parasites (using the keywords “facilitation AND marine AND parasit*”), we find only a grand total of 7 articles between 2000 and the start of 2014, and only one in the last 6 years. Here too, then, we see a disconnect between what parasitologists do and what marine biologists care about. There are excellent examples of marine parasites causing indirect changes to the habitat that facilitate local colonization and establishment by non-host species (Thomas et al., 1998; Mouritsen and Poulin, 2005; Mouritsen and Haun, 2008), suggesting that cross-talk between the disciplines would benefit everyone.

We are not advocating that parasitologists blindly adopt concepts from marine ecology as their sole guiding principles; we are instead urging them to allow these concepts to inform their research decisions. Keeping abreast of major developments in other fields and using this knowledge to bridge gaps between disciplines is the surest way to achieve important inter-disciplinary breakthroughs.

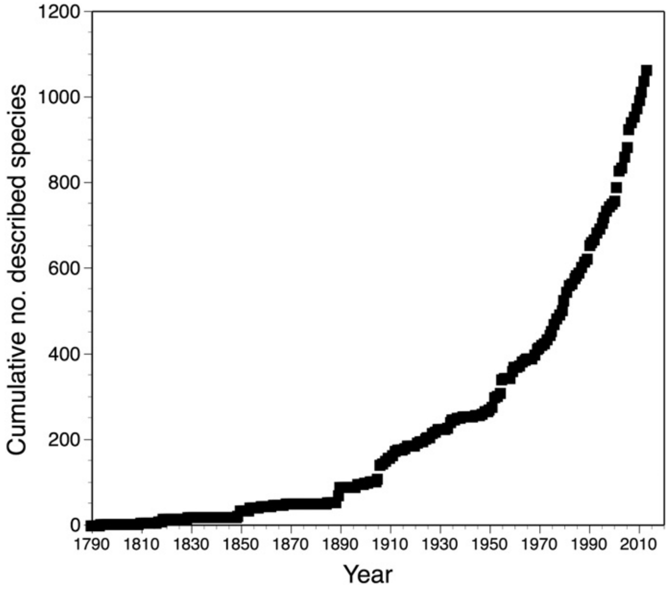

Fig. 2. Cumulative number of known and described species of cestodes (orders Cathetocephalidea, Diphyllidea, Lecanicephalidea, Litobothriidea, Onchoproteocephalidea, Phyllobothriidea, Rhinebothriidea, Tetraphyllidea, and Trypanorhyncha) parasitic in elasmobranch fish over the past two centuries. Data from an updated version of the dataset compiled by Randhawa and Poulin (2010).

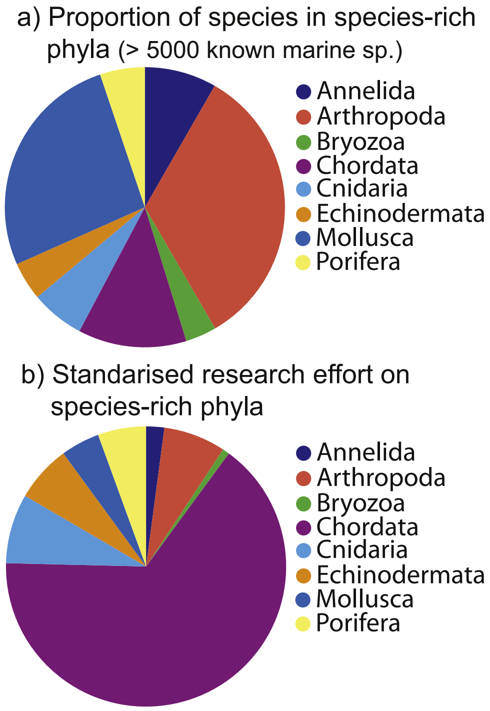

Fig. 3. Relative diversity of host phyla and relative research effort on parasitism in these host groups. a) Proportional number of species in the most species-rich phyla, i.e. those comprising more than 5000 species in the marine realm according to Appeltans et al. (2012). b) Relative standardised research effort on parasitism in the above species-rich phyla. The phyla appear in alphabetical order, clockwise from the top, in both charts. The data come from searches of the Web of Science™ using as keywords each phylum's name and “(parasit* OR pathog* OR diseas*) AND (marine OR sea OR ocean)”, from 2003 to date. Standardisation was achieved by dividing the number of records found in each search by the total number of known species in each phylum as reported in Appeltans et al. (2012).

4. Challenge three: insufficient rate of parasite species discovery

To fully appreciate the impact that parasites may have on the structure and functioning of marine ecosystems, we first need to find and identify most of the key parasite species. For a given and constant effort aimed at finding and describing new species, a slowing down in the rise of the cumulative number of known species over time would suggest that the remaining species are becoming more difficult to find, and therefore that we have already found a substantial proportion of total diversity. Even allowing for the fact that the effort and resources directed at the discovery of new parasite species are not constant over time, we appear to be a long way from completing our inventory of marine parasites. For many taxa of marine parasites, like the Cestoda, Digenea and Acanthocephala, the cumulative curve of known species is still rising steeply (Appeltans et al., 2012), suggesting that we still have some way to go before reaching an advanced stage in our inventory.

As a specific example, consider cestodes parasitic in elasmobranchs. The first species were described and named in the late 18th century, and the number has been rising ever since (Randhawa and Poulin, 2010). However, this cumulative number is now rising faster than ever: far from slowing down, the rate of species description is higher than it has ever been (Fig. 2). We appear far from a total inventory of these cestodes, and will not be able to extrapolate the asymptote of the curve in Fig. 2 until the number of new species found annually starts to slow down.

If this is the case for parasites of a highly visible and charismatic megafauna of hosts like sharks and rays, the situation must be far worse for less-studied taxa of marine invertebrates. Indeed, our knowledge of marine parasites is taxonomically biased: we know a lot more about the parasites (and their effects) for certain taxa of host than for others, and this skewed research effort is not simply proportional to the species richness of the different host groups (Fig. 3). We might expect that phyla with higher species richness would be more often reported in the literature for their parasites or disease. However, by searching the Web of Science™, we found a discrepancy between the species richness of a phylum and the study effort directed at its parasites or diseases. Whereas the phyla with highest species richness are, in order, Arthropoda, Mollusca, Chordata and Annelida (Fig. 3a), those with the most parasite-related records in the Web of Science™ (independently of their species richness) are Chordata, followed far behind by Cnidaria, Arthropoda and Echinodermata (Fig. 3b). This suggests that general research effort on parasitism is disproportionately focused on certain host groups, being particularly biased towards chordates, which typically represent the definitive hosts of many parasitic groups (e.g. cestodes, trematodes, acanthocephalans, nematodes, myxozoans, etc.) and are of greater relevance for humans. Our continued discovery of parasite biodiversity in the oceans not only needs to be maintained at its current rate, it also needs to become more balanced.

In addition, marine ecosystems have been altered significantly by human activity over the past few decades. We are at a juncture where delaying further marine parasitological work may lead to the extinction of parasite taxa prior to their discovery. For instance, shark populations are declining globally at alarming rates due to the fishing industry (Randhawa et al., 2014), yet only a fraction of their parasite communities have been described (Randhawa and Poulin, 2010). Without a concerted effort between marine ecologists and parasitologists, their discovery and the ecological roles they play will remain forever a mystery.

Several other issues plague the discovery and proper description of new parasite species. For instance, parasite discovery rates in tropical marine systems still lag far behind those in temperate areas (Poulin, 2010a). Also, the widespread application of molecular tools to the study of parasite diversity has uncovered numerous cryptic species, i.e. sets of genetically distinct species that look similar morphologically but may have very different ecological properties (Nadler and Pérez-Ponce de León, 2011). However, perhaps the greatest challenge with respect to maintaining current rates of parasite species discovery and description is the impending global shortage of professional parasite taxonomists and systematists that has been feared for several years (Brooks and Hoberg, 2000, 2001). The majority of recent descriptions of new marine parasite species are the work of a small number of renowned taxonomists in the latter part of their prolific career. If we are to complete our inventory of marine parasite biodiversity, we need to overcome this taxonomic impediment, by promoting the continued appointment of parasite systematists and taxonomists to stable, long-term positions.

5. Challenge four: vast majority of life cycles unresolved

A large number of parasites, from protozoans to worms, have complex life cycles involving distinct life stages spent in different host species. In the case of helminth parasites like cestodes, digeneans, acanthocephalans and nematodes, all species (with rare exceptions like trypanorhynch cestodes, which may be described from the tentacular armature of juvenile stages in intermediate hosts) are described on the basis of adult specimens recovered from their definitive host, i.e. the host in which these parasites reach maturity and reproduce sexually. In practically all cases, this definitive host is a vertebrate. Because of the disproportionate focus of parasitological studies on marine fish, birds and mammals in relation to invertebrates, we almost always know parasite species on the basis of their adult stages only, and have no idea of the precise morphology of their juvenile stages or, more importantly from an ecological perspective, the identity of the hosts they use prior to reaching the final vertebrate host.

The available evidence supports the assertion that the life cycles of the vast majority of marine helminth parasites remain unresolved (Table 1). It is probably safe to say that life cycles have been fully elucidated for much less than 5% of all marine helminth parasites, and not just for the specific groups or geographical areas listed in Table 1. Efforts are underway to connect the juvenile stages of helminths in one host to their morphologically distinct adults in different host species using molecular markers (e.g., trematodes on the Great Barrier Reef: Miller et al., 2009; Downie and Cribb, 2011; cestodes in the northern Gulf of Mexico: Jensen and Bullard, 2010), but these are far from being completed. The accumulation in online databases of sequences from parasite life stages found in different host species will increasingly allow life cycles to be resolved that way.

Table 1
Total number of described species from a given marine parasite taxon and geographical area, and number of those for which the life cycle is fully known.

Parasite taxon	Geographic area	Total no. species described	No. species with known life cycle	Sources
Trematoda	Great Barrier Reef	~310	3	Pearson (1968), Rohde (1973), Downie and Cribb (2011), Miller et al. (2011)
Trypanorhyncha (Cestoda)	Worldwide	~245	4	Sakanari and Moser (1989), Mattis (1986), Ruszkowski (1934)
Tetraphyllidea (Cestoda)	Worldwide	~175	0 (?)	Caira and Reyda (2005)
Diphyllidea (Cestoda)	Worldwide	~55	0 (?)	Caira and Reyda (2005)
Lecanicephalidea (Cestoda)	Tropical/subtropical waters	~117	0 (?)	Caira and Reyda (2005)
Onchoproteocephalidea (Cestoda)	Worldwide	~250 (marine species only)	0 (?)	Caira and Reyda (2005)
Phyllobothriidea (Cestoda)	Worldwide	~105	0 (?)	Caira and Reyda (2005)
Rhinebothriidea (Cestoda)	Worldwide	~110	0 (?)	Caira and Reyda (2005)
Tetrabothriidea (Cestoda)	Primarily Polar waters	~65	0 (?)	Caira and Reyda (2005)

Our ignorance of the life cycles of marine parasites has implications for our understanding of their roles in ecosystems and their transmission pathways. For instance, helminths can manipulate the behavior of their intermediate host to facilitate trophic transmission to their final host (Lafferty, 1999; Poulin, 2010b), thereby affecting prey selection and the flow of energy through a food web. They can also exploit the strongest trophic links in the system as their main transmission routes (Thompson et al., 2013), thus coupling energy flow and infection risk for top predators. Elucidating complex life cycles is the first step toward addressing these broader issues. We need a greater emphasis on resolving parasite life cycles; the description of a new species should not stop at the morphological description (and increasingly also, genetic characterization) of its adult stage, but should involve a genuine effort to identify which series of host species it requires to complete its cycle.

6. Challenge five: more host–parasite model systems needed

Most biological disciplines still rely on a few core model species from which we derived much of what we know about living systems. Huge contributions to our knowledge came from studies of fruit flies in genetics, the nematode *Caenorhabditis elegans* in developmental biology, and the mouse in medical science. However, focusing on a few convenient models comes at a cost (Bolker, 2012). There is a clear trade-off between achieving depth of knowledge by focusing on a few model systems, and attaining broader general knowledge by studying less thoroughly a wider range of organisms. There is a real risk that our knowledge of the ecology of marine parasites will tend toward the former end of the spectrum, i.e. in-depth knowledge of few systems, if we follow the paths taken in other biological sciences and adopt too few model systems.

Consider the interactions between trematodes and the snails that almost all species use as the first intermediate host in their life cycle. In intertidal and coastal ecosystems, trematodes are often the most common and influential parasites (Sousa, 1991; Mouritsen and Poulin, 2002; Kuris et al., 2008). We know quite a lot about how different trematode species might interact in the same snail, how trematodes can castrate their snail host and alter its growth, and how parasitism by trematodes can impact snail populations (e.g., Kuris and Lafferty, 1994; Sorensen and Minchella, 2001; Curtis, 2002; Fredensborg et al., 2005). However, practically all we know is based on extensive studies of about ten species of snails belonging to five genera: *Cerithidea*, *Hydrobia*, *Ilyanassa*, *Littorina* and *Zeacumantus*. These few model systems were not chosen because they were a priori believed to be representative models; they were chosen because those species happened to occur near the research institutions where scientists interested in marine parasites were based. Given that the number of currently described marine snail species is close to 40,000 and that the total diversity of marine gastropods is estimated at approximately 100,000 species (Appeltans et al., 2012), it would be unwise to assume that our in-depth knowledge of trematode–host interactions involving this handful of species generally applies to all other snail species.

Interactions between snails and trematodes are probably the best-studied marine host–parasite relationships. We have even fewer good model systems involving other parasite taxa. Whatever the host or parasite taxa considered, particular host–parasite combinations possess unique and idiosyncratic features. We definitely need to add new model systems to our research agenda, to broaden the perspectives we obtain and either confirm the universality of previously observed patterns, or quantify the variability in other aspects of host–parasite interactions. If they are chosen carefully to cover a wide phylogenetic spectrum and a range of habitat types, we will not need too many new models; perhaps doubling the current number might suffice. Models should also be chosen in light of the goals of the research to avoid poor fits that generate misleading information (Bolker, 2012). Ideally, we want an acceptable compromise between overall breadth and depth of knowledge, and this will require a slight shift away from the in-depth/limited breadth end of the spectrum where we sit currently.

7. Challenge six: knowledge of marine parasites limited to coastal zone

Just as a small number of model host–parasite systems can constrain our understanding of the ecology of marine parasites, so too can a narrow range of marine habitats investigated for parasites and their effects. Because of its easy access, we tend to know much more about parasite ecology in the intertidal zone, followed by the near subtidal zone. Coral reefs have also been relatively well-studied, for the same reason and also because they are intrinsically attractive study areas. Additionally, much information is also available for the parasites of commercially important fish species, some of which are caught offshore. Nevertheless, because most existing studies have been limited to shallow coastal waters, it is impossible to infer any general patterns of parasitism and diseases applicable to other marine habitats. In particular, although there have been some studies of parasitism in the deep sea and around hydrothermal vents (e.g., Campbell et al., 1980; Gartner and Zwerner, 1989; Moreira and López-Garcia, 2003; de Buron and Morand, 2004), these are still very few and they raise as many questions as they answer.

For example, consider the geographical distribution of published studies of trematode infections in marine crustacean hosts (Thieltges et al., 2009). It shows the usual biases: more studies have been conducted in temperate than tropical areas, and in the northern hemisphere compared to the southern hemisphere (Fig. 4). The localities sampled also cluster close to the institutions where the most active marine parasitology research groups are based. In addition, what stands out from the distribution of sampled localities is that they firmly hug the coastlines (Fig. 4), illustrating very clearly that our knowledge of marine parasites and their impacts does not extend far out from the shore. Any other geo-referenced database of marine parasitological studies would show the same pattern.

As parasitologists, we have but dipped our feet into the fringes of vast and deep oceans, we are yet to actually dive in, and thus we still know little of the parasites harbored in the seas. This problem is not exclusive to parasites; knowledge of marine biodiversity in general is also more advanced for shallow coastal seas than for deeper waters (Costello et al., 2010). To remedy this, we need a concerted effort to extend parasitological investigations away from the shore and over a broader section of the continental shelf. In addition, there should be serious attempts to gather solid parasitological data from deep-sea sampling missions, instead of relying on serendipitous findings and handouts from the marine biologists and oceanographers who typically lead those expeditions. Parasitologists can achieve this by being proactive and contacting the organizers of oceanic cruises or deep-sea missions to offer to participate in designing the sampling programme and processing the samples to maximise the parasitological information generated. Unlike some of the other challenges identified in this essay, overcoming this one will require multidisciplinary collaborative ventures and financial support. However, the huge knowledge gaps that could be filled by extending parasitological research offshore and into the deep make the effort worthwhile.

8. Challenge seven: marine epidemiological theory urgently required

Epidemiological theory consists of a body of mathematical models that aim to capture and predict the transmission dynamics of parasites within natural host populations (see Anderson and May, 1979; May and Anderson, 1979). It is responsible for major advances in our understanding of the spread, maintenance and impact of pathogens within populations. Although not explicitly acknowledged, epidemiological theory has been developed within the context of terrestrial host–parasite systems, being driven by the need to understand diseases

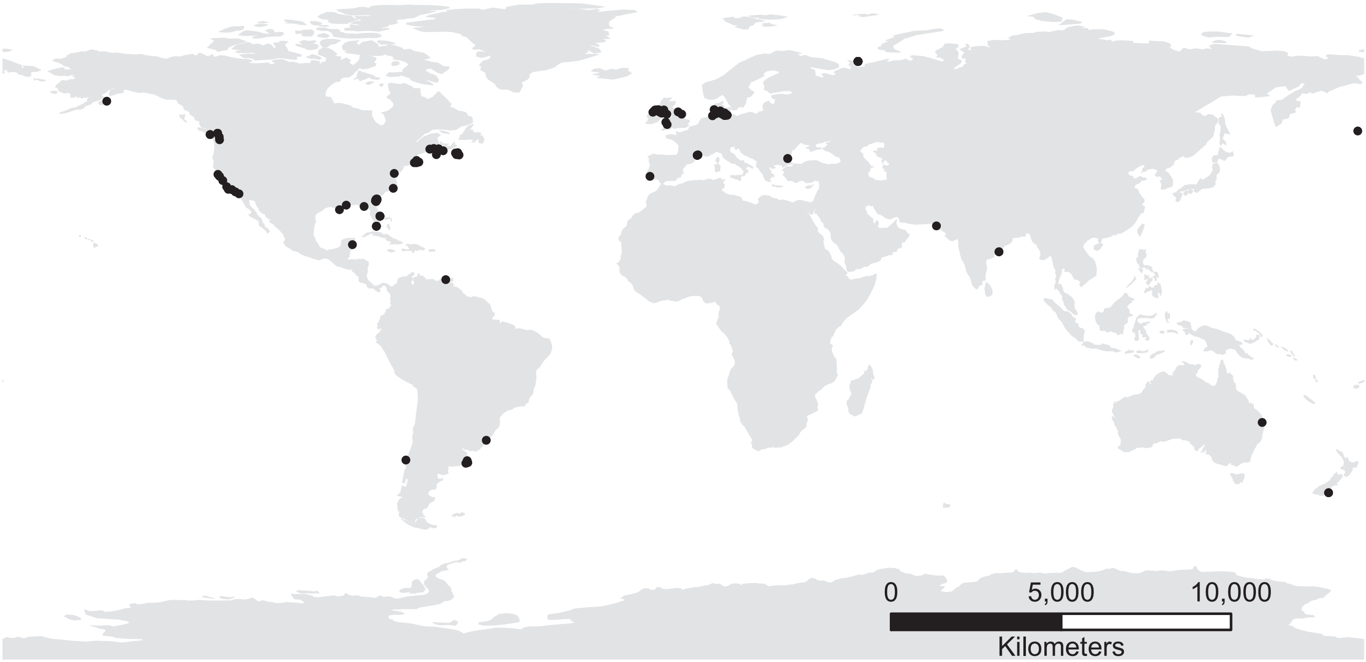

Fig. 4. Geographical distribution of sampling effort in published studies of trematode infections of marine crustaceans. Each point represents a study sample, i.e., a collection of individuals of one host species from one locality made over a short period of time for the purpose of quantifying infection levels. In some areas, distinct points are not visible as they are stacked on top of each other. Data from Thieltges et al. (2009).

of humans, crops, domesticated animals and wildlife. McCallum et al. (2004) asked whether epidemiological theory, in its current form, could be applied to marine host–parasite systems. They identified several fundamental differences between terrestrial and marine systems. For instance, marine hosts not only belong to a broader taxonomic spectrum than their terrestrial counterparts, they include a greater proportion of modular colonial life forms, they often disperse as drifting larvae, and they tend to form open rather than closed populations, i.e. local adult densities do not determine local recruitment because of extensive exchanges among populations. In this respect, freshwater hosts share many characteristics with their terrestrial counterparts (narrower taxonomic spectrum, mostly closed populations, few modular colonial species) compared to marine hosts. However, among both freshwater and marine parasites, the relative frequencies of parasite taxa with various modes of transmission and host exploitation (see Poulin, 2011, for discussion of these strategies) are different than in terrestrial ecosystems. Thus, in the oceans there appears to be a lower proportion of vector-transmitted and vertically-transmitted parasites, a lower proportion of parasitoids and a higher proportion of parasitic castrators. Furthermore, while the genetic structure of parasite species is driven by host traits such as mobility, parasites that cycle exclusively through the marine environment may experience higher variation in genetic differentiation among populations than those of freshwater environments (Blasco-Costa and Poulin, 2013) or even be influenced by different drivers. Such knowledge is currently lacking despite its relevance for disease management decisions. In addition to these differences pointed out by McCallum et al. (2004), we could add that water is very different from air or soil as a medium for the small- and large-scale dispersal of parasite propagules or infective stages. Its density and viscosity may affect the speed of transmission, local retention and/or dispersal of infective stages, and thus the dynamics of infection.

To our knowledge, there has been little effort to address the basic question raised by McCallum et al. (2004). As they say, the basic principles of epidemiology are the same on land as in the oceans, and there is no doubt that the existing epidemiological models could provide a rough approximation of the dynamics of marine diseases. However, it is in the details that models developed for terrestrial systems might fail to fully apply to marine ones. The challenge of adjusting the models to the particular conditions encountered in marine host–parasite systems is not a daunting one, but will need to be taken seriously by theoreticians.

9. Looking ahead

The list of 'seven deadly sins' we present here reflects our personal views; no doubt other researchers would come up with a different list. For instance, some researchers might add to our list the fact that we still have little understanding of the geographical variation in the impact of parasitism. In other words, there may be yet-to-be-discovered patterns whereby the impact of parasites and diseases tends to be greater in some geographic regions or parts of the oceans than others (e.g., Leung and Bates, 2013), making the identification of these hotspots a priority.

Our intention was simply to show that the marriage between parasitology and marine ecology is a work in progress, and that none of the obstacles on the road ahead are insurmountable. The simple steps needed for a stronger partnership between the two disciplines are generally achievable: (i) greater willingness of parasitologists to communicate their findings to the marine ecological community, and greater receptiveness of the latter to parasitological research; (ii) increased awareness by members of one discipline of the key principles and new concepts guiding the other one; (iii) continued support for taxonomy and basic parasitological research on life cycles and transmission routes; (iv) addition of a few, new model systems for all major host–parasite taxonomic groups to achieve more general answers to fundamental questions; and (v) adjustments to the mathematical models underpinning epidemiological theory to fit the organisms and conditions present in the oceans. Because funding is always limited, survey-based research (in contrast to hypothesis-driven research) may struggle to receive support even if it is essential to advance some of the above goals. A way of overcoming this funding shortage may be for parasitologists to join collaborative research programs integrating multidisciplinary approaches aimed at loftier goals. The only challenge that would require a substantial investment of funds and resources is the need to extend studies of parasites to offshore and deep-water habitats. This is not unique to parasitological research, however, as these requirements also plague the study of free-living organisms in those same habitats. This exception notwithstanding, the impediments preventing a greater synergy between parasitology and marine ecology have simple solutions, and are within our reach. With human impacts on marine ecosystems intensifying, we must take the necessary steps to better position ourselves to forecast, monitor and mitigate the many changes in marine disease dynamics that may follow from environmental changes.

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