

# 3 Patterns of diversity and distribution of aquatic invertebrates and their parasites

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## 3.1 Introduction

The majority of animals on this planet are invertebrates, and a great number of them are found in aquatic habitats including freshwater, brackish or marine environments. It is likely that they also harbour a significant fraction of all parasite biodiversity.

While there have been some sporadic research efforts directed at investigating the parasite fauna of aquatic invertebrates over many decades, what we know about their diversity, ecology and distribution is still relatively limited and based largely on host–parasite systems which are limited both in terms of their taxonomic diversity, habitat and geographic regions (see Kinne, 1980–1985 and Rohde, 2005 for overviews). One reason why less research effort has been directed towards investigating parasites of invertebrates compared with those of mammals, birds or fish is that with the exception of some mollusc and crustacean species, the majority of aquatic invertebrates are of little commercial value and there have been few incentives for researchers to investigate their parasites or other potential disease agents.

Another reason why we have only limited knowledge of invertebrate host–parasite systems is our incomplete knowledge of the hosts themselves, many of which remain undescribed. In general our knowledge of vertebrate diversity is far greater than that of invertebrates, and consequently we know more about the parasites of those hosts than of invertebrates (Poulin & Morand, 2004). Rohde (2002) discussed some of the problems associated with estimating species richness, most of which also apply to parasites of aquatic invertebrates. In terms of parasitological surveys of hosts in aquatic environments, most have been from fish and few are from invertebrates (discussed by Rohde, 1993; 2005). In addition to our lack of knowledge of their diversity, we know even less about their biogeographical distribution. Most studies looking at the macroecological patterns of parasite assemblages from aquatic environments have been focused on fish parasites (Rohde, 2010), but there have been comparatively fewer studies which examined such patterns in invertebrate hosts.

In this chapter we discuss what is known about the diversity of aquatic invertebrates themselves, the gaps in our knowledge of the diversity of parasites in aquatic invertebrates

and some biogeographical studies which have addressed the macroecological and biogeographical patterns of parasite communities found in aquatic invertebrates.

### 3.2 Quality and completeness of taxonomic data on aquatic invertebrates

Remarkably, there are very few examples of well-designed projects that specifically quantify the entire diversity of species in any major group. As such, our current knowledge on the number of species is based on secondary sources of data or indirect methods (Mora *et al.*, 2011). This, in turn, has generated considerable caveats and remarkable patchiness in our current knowledge of overall diversity (May, 1986; 2010; Stork, 1993; Mora *et al.*, 2011). For parasites, this picture is further obscured given that they tend to be cryptic (some of them become visible only when the host is collected and dissected) and they are often small (smaller than the host). To exemplify some of these caveats and how they apply to major invertebrate groups, we report statistics on the available taxonomic data for ten prominent invertebrate groups, as they stand at 28 October 2012. We used the data available in the most authoritative databases recording species' scientific names (i.e. the *Catalog of Life* ([www.species2000.org](http://www.species2000.org)) and the *World Registry of Marine Species* ([www.marinespecies.org](http://www.marinespecies.org))) and geographical taxonomic records (i.e. the *Global Biodiversity Information Facility* ([www.gbif.org](http://www.gbif.org))).

The simplicity of the question of how many species there are is contrasted by the difficulty in answering it. Indirect estimations suggest that the number can range between 3 and 100 million (Stork, 1993; May, 2010), whereas direct estimations indicate that we are certain to have described 1 315 754 species (which is the total number of valid species currently contained in the *Catalog of Life* at 28 October 2012) and that many more are likely to be discovered as some 6000 (Mora *et al.*, 2011) to 15 000 (Dirzo & Raven, 2003) to 16 600 (Bouchet, 2006) new species are described each year. For the invertebrate groups analysed here, the yearly average during the last ten years of the number of new species ranges from 574 species in Crustacea to just one species in Ctenophora (Table 3.1). These numbers, however, should be considered with caution for at least two reasons. First, we lack a mandatory regulation to deposit newly described species in a central database and thus updates to authoritative repositories can be delayed. Second is the issue of synonyms, which varies considerably among groups. For instance, among several classes of insects, the fraction of invalid names due to synonyms ranges from 7% to 58% (Gaston & Mound, 1993); for plants ~58.4% of existing species names are synonyms (Paton *et al.*, 2008) and 18% for all species overall (Mora *et al.*, 2011); among newly described marine species some 10–20% are likely to become synonyms (Bouchet, 2006). Among the invertebrate groups analysed here, rates of synonyms ranged from 120% for Echinodermata and 109% for Porifera to 48% for Cnidaria and 27% for Ctenophora (Table 3.1). The disparity in the rates of synonyms is commonly attributed to taxonomic reviews (Boss, 1970; Paton *et al.*, 2008), suggesting that the rate of synonyms is likely higher for poorly studied groups (Solow *et al.*, 1995) and that our estimations in the number of known species is likely to change considerably as new taxonomic reviews become available.

**Table 3.1** Status of the taxonomy of major invertebrate groups

Phylum or class	Valid species currently catalogued	Synonyms – total names (% of valid names)	Average new species per year, 2003–2012	Species predicted here – total (% to discover)	(Chapman 2009)	
					Estimate of valid species catalogued	Total species estimated
Chaetognatha	207	160 (77)	6	258 (20)	121	Unknown
Cnidaria	11 433	5504 (48)	77	40 318 (72)	9795	Unknown
Ctenophora	196	53 (27)	1**	249 (21)	166	200
Echinodermata	7286	8771 (120)	33	19 040 (62)	7003	14 000
Mollusca	48 648	42 753 (88)	424	169 840 (71)	85 000	200 000
Nemertea	1362	1336 (98)	5	7080 (81)	1200	7 500
Porifera	8305	9063 (109)	63	8196 (–1)	6000	18 000
Crustacea	66 250	24 691 (37)	574	130 855 (49)	47 000	150 000
Polychaeta	12 163	7455 (61)	75	22 017 (45)	8432	25 000– 30 000*
Urochordata	3158	2855 (90)	22	1041 (–203)	2760	Unknown

\* Estimate for all Annelida.

\*\* The last species entered in the analysed databases was 2001; for the decade prior to that year about one species was discovered every year.

To estimate the number of species in the different groups considered here, we used a recently validated method that relies on higher taxonomic data. The method relates the numerical rank of the taxonomic level (e.g. phylum = 1, class = 2, order = 3, family = 4, genus = 5) against the number of taxa at each rank for any given group, and then fits a variety of power, exponential and hyper-exponential models to estimate the number of taxa at the level of species (i.e. species = 6; the prediction of each model is weighted by its fit to estimate a weighted average of the three different models; for details see Mora *et al.*, 2011). The method has yielded remarkably accurate predictions for well-studied taxonomic groups and relies on higher taxonomic data, which are much more complete than the data at the species level and less prone to errors of synonyms (Mora *et al.*, 2011). The reason for a correlation between higher taxonomic rank and the number of taxa is still unknown, but perhaps is related to the fact that the classification of species is now mostly based on the phylogenetic methods and thus the possibility that the higher taxonomy somehow reflects patterns of diversification that allow us to predict the number of species. Regardless of the mechanism, the approach appears to yield reliable estimations. Applying this method to our focus taxa, we found that there is a very high number of species still to be discovered for most groups (Table 3.1), although the opposite was also true in a few cases. It is worth noting that the number of predicted species here is very similar to the number of species expected by taxonomic experts on those groups (in Table 3.1 we provide the number of species predicted for the different groups of invertebrates based on the opinion of key experts). For half of the ten groups analysed, over 50% of the species remain to be discovered (Table 3.1). Interestingly, for two groups (Porifera and Urochordata) our method predicted fewer species than are actually described.

This could indicate a limitation with the method used, errors in the higher taxonomy of those groups or a more critical issue dealing with the overestimation in the number of current species due to synonyms; interestingly, those two groups are among the groups with the most synonyms (Table 3.1).

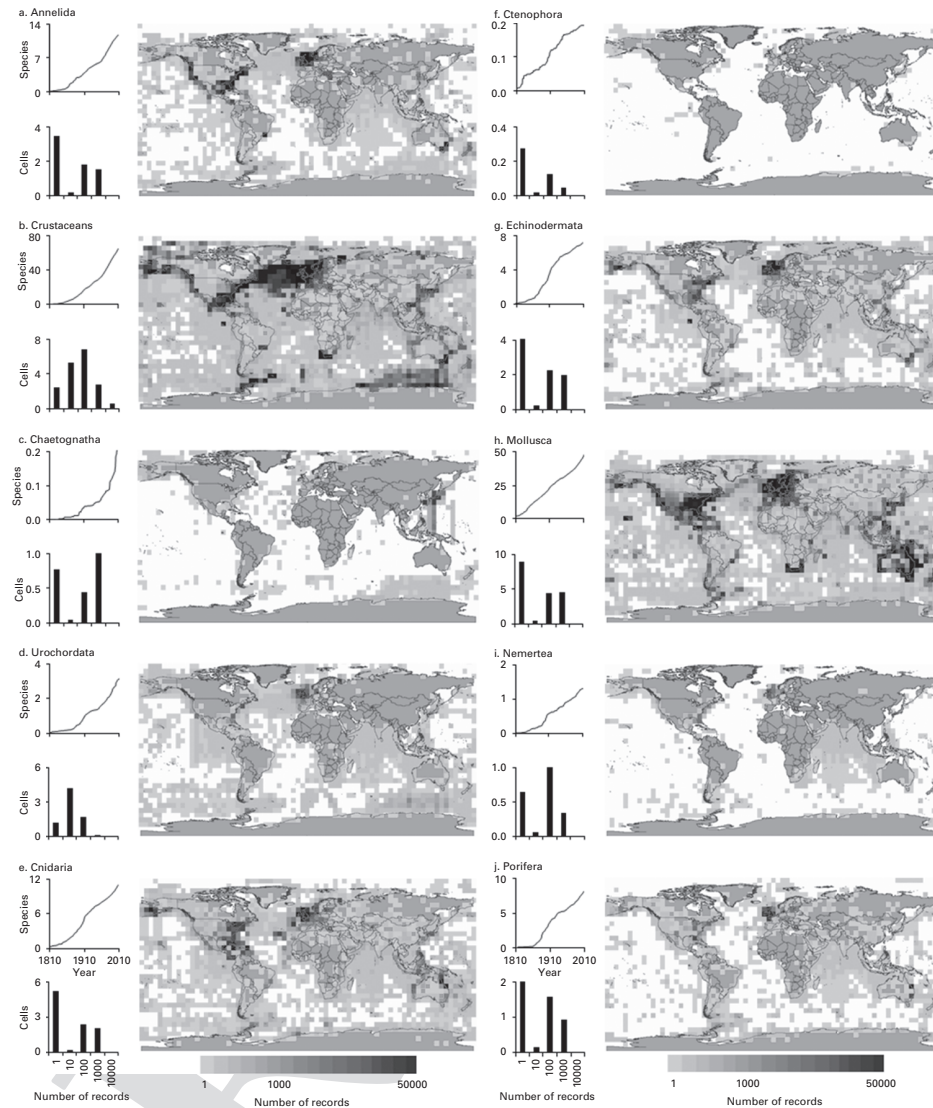
Given the yearly rate of species discoveries, the predicted number of species suggests that for some taxonomic groups a complete understanding of their diversity would take a considerable amount of time (e.g. 1140 years for Nemertea, 375 years for Cnidaria, 356 years for Echinodermata, 285 years for Mollusca). For some other groups there are fewer species to describe but they are also less diverse, implying that those groups are truly rare and thus describing their remaining species will require considerable sampling and time. These results confirm the case for our profound ignorance of biodiversity on Earth (including not only the species that remain to be discovered but also those that are already classified). Although this uncertainty should provide enough motivation to hasten efforts for the exploration, description and classification of species on Earth, the reality is that progress has failed to keep pace. We have the ongoing shortage of full-time taxonomists available to inventory and characterise the world's biodiversity (the so-called the taxonomic impediment; Wheeler *et al.*, 2004), due the limited funding support for taxonomy (Costello *et al.*, 2010). For aquatic invertebrates (marine and freshwater) and their parasites, the challenge is likely higher given the small fraction of dedicated specialised taxonomists on those invertebrate groups. We are certain that human pressures on biodiversity are mounting and many species are likely going extinct because of that (Pimm & Raven, 2000) and with them their parasites and symbionts too (Dunn *et al.*, 2009). Unfortunately, the comparatively slow pace at which species are being described raises the sad possibility that many species are likely being driven to extinction without us knowing that they have ever existed.

### 3.2.1 Biodiversity pattern

Describing spatial pattern in biodiversity is among the most fundamental tasks in ecology and biogeography and one with relevance for conservation; such patterns help to pinpoint priority areas for protection. The raw data for constructing such patterns are the geo-referenced locations where individuals of species are found. Unfortunately, analyses into the quality of such data highlight another major gap in our knowledge of biodiversity on Earth: for the great majority of the world's oceans most taxonomic groups only have a handful of species records (see bar-plots in Figure 3.1). The obvious interpretation of these results is that if we do not know where the species are found, how can we accurately describe their patterns of biodiversity and, more problematically, define the areas where conservation effort should be prioritised?

### 3.3 Parasites of aquatic invertebrates: general trends, meiofauna, deep sea and open ocean faunas

Although quantifying the overall diversity of taxonomic groups remains problematic, studies into the number of parasites within aquatic invertebrates appear to



**Figure 3.1** Available taxonomic data for major invertebrate groups. For each invertebrate group, we show the temporal description of species (line-plot), the frequency distribution of existing taxonomic records (bar-plot) and their spatial coverage (map). The frequency distribution is basically the number of grid-cells in the world according to the number of contained taxonomic records. Data on species names were obtained from [www.species2000.org](http://www.species2000.org) and [www.marinespecies.org](http://www.marinespecies.org). The geographical position of species records was obtained from [www.gbif.org](http://www.gbif.org).

reveal a general trend: the most heterogeneous host groups of invertebrates (Crustacea, Mollusca, Echinodermata, Cnidaria) have the greatest variety of parasites, whereas the least heterogeneous (such as Priapulida) have the lowest (see Table 3.2).

**Table 3.2** The following list contains information about aquatic invertebrates as hosts to parasites. Sources are Kinne (1980–1990), various authors in Rohde (2005) supplemented by literature searches (Web of Science). Host groups are listed in order of parasite diversity within them. Groups found very rarely (possibly accidentally) in a host group are in brackets. A parasite is defined here in a wide sense, i.e. including those few species that live in close commensal (possibly parasitic) relationships with their host.

Host group	Known parasite groups
Crustacea	Mastigophora, Sarcodina, Apicomplexa, Haplosporidia, Microsporidia, Ciliophora, Cnidaria, Bryozoa, Acanthocephala, Turbellaria, Digenea, Aspidogastrea, Amphilinidea, Eucestoda, Nematoda, Copepoda, Isopoda, Tantulocarida, Cirripedia/Rhizocephala, Decapoda, Hirudinea, Mollusca, Nemertea, Polychaeta, Cycliophora, Tardigrada, Cycliophora, Nematomorpha, Acari, Tardigrada, <i>Seison</i> , (Monogenea Polyopisthocotylea), (Monogenea Monopisthocotylea)
Echinodermata	Sarcodina, Mastigophora, Haplosporidia, Apicomplexa, Ciliophora, Porifera, Eucestoda, Turbellaria, Digenea, Nematoda, Myzostomida, Rotifera, Nemertea, Polychaeta, Mesozoa Orthonectida, Copepoda, Cirripedia, Ascothoracida, Amphipoda, Tanaidacea, Decapoda, Mollusca, Pycnogonida, Tanaidacea, Tardigrada, Acari, Echinodermata, Arachnida, Insecta (one trichopteran), Cnidaria (?)
Mollusca	Mastigophora, Sarcodina, Haplosporidia, Labyrinthomorpha, Microsporidia, <i>Microcytos</i> , Apicomplexa, Ciliophora, Cnidaria, Digenea, Aspidogastrea, Eucestoda, Turbellaria, Nematoda, Nemertea, Polychaeta, Oligochaeta, Mollusca, Nemertea, Mesozoa Orthonectida, Mesozoa Dicyemida, Porifera, Copepoda, Isopoda, Decapoda, Acari, Pycnogonida, Tardigrada, (Monogenea Monopisthocotylea)
Cnidaria	Mastigophora, Sarcodina, Microsporidia, Ciliophora, Porifera, Cnidaria, Ctenophora, Mollusca, Pycnogonida, Digenea, Turbellaria, Eucestoda, Nematoda, Rotifera, Nemertea, Myzostomida, Polychaeta, Amphipoda, Isopoda, Copepoda, Decapoda, Cirripedia, Mysidacea, Ascothoracida, Nemertea, Acari, Echinodermata
Tunicata (Urochordata)	Sarcodina (?), Mastigophora, Apicomplexa, Haplosporidia, Ciliophora, Dicyemida Orthonectida, Cnidaria, Ctenophora, Turbellaria, Digenea, Copepoda, Amphipoda, Decapoda, Cirripedia, Nemertea, Bryozoa, Mollusca, Polychaeta, Oligochaeta
Porifera	Mastigophora, Sarcodina, Microsporidia, Ciliophora (?), Cnidaria, Mollusca, Copepoda, Amphipoda, Decapoda (?), Cirripedia, Pycnogonida, Polychaeta, Myzostomida, Dicyemida Orthonectida, Rotifera, Acari, Echinodermata
Polychaeta	Mastigophora, Haplosporidia, Microsporidia, Apicomplexa, Ciliophora, Myxozoa, Cnidaria, Mollusca, Eucestoda, Digenea, Nematoda, Polychaeta, Dicyemida Orthonectida, Turbellaria, Eucestoda, Copepoda, Cirripedia, Polychaeta, Nemertea
Oligochaeta	Microsporidia, Apicomplexa, Myxozoa, Digenea, Eucestoda, Rotifera, Nematoda, Nemertea
Chaetognatha	Sarcodina, Mastigophora, Apicomplexa, Ciliophora, Digenea, Eucestoda, Nematoda, Copepoda, Polychaeta (?)
Bryozoa	Microsporidia, Myxozoa, Ciliophora, Pycnogonida, Dicyemida Orthonectida, Cnidaria, Copepoda
Echiura	Apicomplexa, Ciliophora, Nemertea, Eucestoda, Digenea, Echiura (intraspecific parasitism), Copepoda
Nemertea	Apicomplexa, Haplosporidia, Ciliophora, Dicyemida Orthonectida, Eucestoda, Copepoda, Acari
Ctenophora	Mastigophora, Ciliophora, Cnidaria, Eucestoda, Digenea, Nematoda, Amphipoda
Sipunculida	Apicomplexa, Myxozoa, Turbellaria, Copepoda, Digenea, Mollusca
Turbellaria	Mesozoa Orthonectida, Turbellaria, Digenea, Eucestoda, Copepoda

Table 3.2 (cont.)

Host group	Known parasite groups
Parasitic platyhelminthes	Mastigophora, Microsporidia, Haplosporidia, Digenea, unidentified micro-organisms
Brachiopoda	Copepoda, Amphipoda, Polychaeta, Digenea
Phoronida	Ciliophora, Apicomplexa, Digenea, Copepoda
Hemichordata (Enteropneusta)	Mastigophora, Apicomplexa, Copepoda
Hirudinea	Apicomplexa, Digenea
Priapulida	Myxozoa, Nematoda
Nematoda	Nematoda, Ostracoda
Xiphosura	Turbellaria
Pycnogonida	Cnidaria
Myzostomida	Turbellaria
Entoprocta	Mollusca
Mesozoa orthonectida	Microsporidia (host given as 'Mesozoa')
Apicomplexa	Microsporidia
Rotifera and <i>Seison</i>	Ciliophora
Acanthocephala	None known
Nematomorpha	None known
Mesozoa dicyemida	None known
Tardigrada	None known
Pentastomida	None known
Cycliophora	None known

### 3.3.1 Meiofauna

Surveys into the parasite of invertebrate groups have been concentrated on groups that are of particular ecological/economic importance, such as molluscs and some crustaceans which transmit infections to vertebrates at higher trophic levels, but otherwise have almost been completely ignored for small invertebrates such as those in the deep sea and meiofauna (Rohde, 2002). Even in groups that are relatively well known, little is known about geographical patterns such as latitudinal, longitudinal and depth gradients (Rohde, 2002). Parasites of marine coastal meiofauna may serve as an example of the state of our ignorance. On average, 1–10 million individuals of meiofauna are found in 1 m<sup>2</sup> of sediment, although biomass is only a few grams (Vincx, 1996). Until about ten years ago, only a single thorough study of biodiversity of total meiofauna at the species level had been carried out. A team of zoologists carried out a survey over many years around the Island of Sylt in the North Sea and found 652 species, and estimated that a further 200 or so species were omitted in their search (Armonies & Reise, 2000). Faubel (personal communication) found 259 species of meiobenthic turbellarian species on exposed sandy beaches along the Australian east coast. Only two of these species occurred both in northern Queensland and Sydney, indicating that meiofaunal species may be strongly localised and that species diversity of these organisms may be enormous. To our knowledge, studies comparable with those

at Sylt have not been conducted to this date in other geographical areas, and not a single comprehensive survey of parasites in coastal meiofaunal organisms has been made.

### 3.3.2 Deep sea

The situation is very similar for deep sea nematodes and many other invertebrates. In 1994, Lamshead *et al.* (1994) drew attention to the fact that only ten studies of deep sea nematode diversity at the species level had been made, i.e. nematode diversity was known for less than a 1 m<sup>2</sup> of seabed (for a recent estimate see Miljutin *et al.*, 2010). To our knowledge, no comprehensive survey for parasites of such nematodes has been made (Miljutin *et al.*, 2006; Zekely *et al.*, 2006). Among these nematodes, a small percentage is from the family Benthimermithidae (Miljutin & Miljutina, 2009). The non-feeding adult stages of these nematodes are found among the usual assemblage of deep sea benthic nematodes. While they comprise merely a fraction of a per cent of such deep sea nematode communities, they are widespread across the globe, having been described from both the Northern and Southern hemisphere, in three oceans so far (Miljutin & Miljutina, 2009; Miljutin, 2011). The larval stage of benthimermithids are known to be internal parasites of various deep sea benthic fauna including crustaceans, polychaetes, priapulid and even other nematodes (see references in Miljutin & Miljutina, 2009).

Over half of all known metazoan parasites from fish found at bathypelagic depths or deeper are digenean flukes (Bray, 2005). Digeneans are known for having complex life-cycles that always involve an obligate asexual proliferation stage which occurs in a molluscan (and in some species a polychaete) intermediate host, and in most species there is also a second intermediate host which may be an invertebrate and is usually a common prey item for the definitive host (which in this context are fish). The life-cycles for most of these deep sea flukes are completely unknown, but would involve invertebrate fauna which occur in those depths.

Information on parasites of animals at hydrothermal vents and cold seep is also generally quite limited (de Buron & Morand, 2004; Terlizzi *et al.*, 2004), which is likely due to the lack of study as such habitats are difficult to access. However, these habitats are inhabited by a range of invertebrates, and while the species diversity of such assemblages are relatively low compared with other habitats (Tsurumi, 2003), studying their parasite communities can help us understand how parasite transmission takes place in such extreme environments. Based on the little we know, the patterns of parasitism in deep sea invertebrates share some broad similarities with their shallow water counterparts. Parasites reported from molluscs of deep sea vents and seeps are comparable to those found in molluscs of shallow water habitats, and while in some cases infection prevalence can be quite high, both the diversity and abundance of parasites varies over the host's geographical range (Powell *et al.*, 1999; Terlizzi *et al.*, 2004; Tunnicliffe *et al.*, 2008).

An understanding of deep sea fauna and its parasites is particularly important, since the deep sea is the largest biome on Earth, and its macro- and meiofauna may be among the richest on Earth (Ramirez-Llodra *et al.*, 2010); an example is the recent finding that



674 species of isopod alone are found in the deep Southern Ocean, of which 585 are new to science (Brandt *et al.*, 2007), which shows that the diversity of potential hosts in the deep sea is very high. While parasitism in such habitat appears widespread and compromises their hosts' reproductive capacity (Powell *et al.*, 1999), their ecological impact remains unknown (Tunncliffe *et al.*, 2008).

### 3.3.3 Open ocean

Another vast and largely unexplored habitat in terms of aquatic invertebrate parasites communities is the open ocean. As well as being taxonomically diverse, marine zooplankton harbours a rich and diverse community of parasites (Théodoridès, 1989), and much like parasitism in the deep sea, the ecological impact of parasites on marine zooplankton is largely unknown. There have been a few studies which compared the parasite community of certain zooplankton species across different seasons (e.g. Øresland, 1986; Daponte *et al.*, 2008), but not across biogeographical scales. Many zooplankton species also serve as intermediate and paratenic hosts to parasites which infect oceanic fishes (Marcogliese, 1995; 2002) and the presence of parasites in marine zooplankton can serve to indicate the presence of their pelagic fish hosts (Noble, 1973). As the parasite communities of some of those fish species have been the subject of biogeographical studies (e.g. Oliva, 1999; George-Nascimento, 2000; Timi & Poulin, 2003), examining the parasite communities of zooplankton from across biogeographical regions will allow us to not only fill gaps in our knowledge regarding the life-cycles of many of these parasites, but also supplement current findings on parasitic communities of fishes and the processes which shape them.

## 3.4 Biogeographical patterns

Because invertebrates are abundant and many have wide geographical ranges, they are ideal for examining biogeographical patterns in parasite communities. In addition, many aquatic invertebrates function as intermediate hosts of parasite larvae, which then reach maturity in vertebrate definitive hosts. Since several studies of latitudinal gradients and biogeography have been conducted on parasite communities of vertebrate hosts, analysing the parasite communities of these aquatic invertebrates would bridge the knowledge gap in understanding the ecological process which helps form the parasite communities found in vertebrate hosts.

While much has been done regarding the macroecological and biogeographical pattern of parasite communities in teleost fish hosts (Rohde & Heap, 1998; Poulin, 2003; Oliva & González, 2005; Thieltges *et al.*, 2010; Timi *et al.*, 2010), less is known about such patterns in parasite communities of aquatic invertebrate hosts. Despite their abundance and ubiquity, until recently there have been relatively few comparative studies conducted on the parasite communities of invertebrate hosts. Such studies are also limited to a small subset of hosts – mostly molluscs, comprising a selected handful of gastropods and bivalves – which have had their parasite fauna extensively studied.

A number of recent papers have aimed to assess the large-scale patterns of parasite richness from invertebrate hosts. Here we present an overview of work done on various study systems so far.

### 3.4.1 Aquatic snails

The parasite fauna of aquatic snails from both marine and freshwater habits around the world has been studied for decades (see studies cited in Sorenson & Minchella, 2001; Curtis, 2002). Digenean trematodes, which use snails as their first intermediate host, are by far the most dominant and abundant type of parasites found in such hosts. In some ecosystems they are so abundant that they form a substantial percentage of the local biomass (Kuris *et al.*, 2008). Digeneans undergo asexual proliferation in the gonadal tissue and hepatopancreas of their host, resulting in a mass of asexual stages which take up 25–50% of their host's body mass (Hechinger *et al.*, 2009). Because of the digenean's ability to monopolise host resources, unlike fish or bivalves in which a single individual can be infected with multiple species of parasites, digenean-infected snails are usually only infected with one or two parasite species, though on some occasions up to four species infecting the same snail have been recorded (Curtis, 1997).

By not having a rich suite of parasites within each individual host, snails may seem less useful for comparative studies on the spatial distribution of parasites than fish (or bivalves; see below), which carry entire communities of different parasites. But while each individual snail is usually infected with a single species, a localised population can collectively harbour a few to a dozen different species (see studies cited in Sorenson & Minchella, 2001; Curtis, 2002), and some host species have been recorded to serve as host to a dozen or more different species (e.g. Cannon, 1978; Rohde, 1981; Hechinger, 2012). Therefore, at the population level, these parasites are useful for spatial comparisons of parasite communities.

Trematodes have multi-host life-cycles, and results from multiple studies indicate that their biogeographical distribution in snails depends on the mobility and biology of their vertebrate definitive host. Thieltges *et al.* (2009a) found strong decay of similarity over distances in the community of parasites found at different sites. This was attributed to the vagility of the vertebrate definitive hosts, but also highly dependent upon the presence of appropriate environmental conditions for the parasites. While fish disperse parasites over small to medium scales, birds are able to distribute the parasites at a larger scale, but at very large scale the parasite community composition is largely determined by the availability of appropriate intermediate hosts and compatible environmental conditions (Thieltges *et al.*, 2009a).

The trematode communities in snails have also been investigated in the context of invasive species – biological invasion/introduction of snails (and their parasites) provide unintended field experiments which present opportunities to compare the role of different factors (local environment, biotic community, host mobility, host life history) in structuring parasite communities. Both *Littorina saxatilis* and *Ilyanassa obsoleta* have been introduced from their native range on the east coast

of North America to various parts of the west coast, and their different invasion histories are reflected in their trematode faunas – this is particularly clear in the greater reduction of trematode diversity exhibited by the introduced *L. saxatilis* compared with *I. obsoleta*, as the former was introduced more recently to the US west coast (Blakeslee *et al.*, 2012).

The trematode fauna Blakeslee *et al.* (2012) found in the introduced *I. obsoleta* lends further support to the view that definitive host vagility mediates parasite distribution, as they found that trematodes using fish (which have a more limited distribution) as definitive hosts exhibited much lower prevalence at the introduced range of *I. obsoleta* than those with bird definitive hosts. But far from the definitive host being the sole mediator of parasite community composition, the presence of a full complement of hosts (including the appropriate second intermediate hosts) in sufficient numbers greatly increases establishment success for a trematode species in the local community (Blakeslee *et al.*, 2012).

Despite the mobility and wide dispersal capacity of trematodes which use bird definitive hosts, there are still limitations to their distribution. On a regional scale, local conditions are important for determining the recruitment success of trematodes; both directly via providing an environment suitable for the parasites to successfully establish in their first intermediate host, as well as indirectly via providing conditions which would encourage the definitive host birds to aggregate and shed eggs into the environment (Byers *et al.*, 2008). Furthermore, Thieltges *et al.* (2009b) found that while trematode species richness in *Hydrobia ulvae* did not vary across different ecoregions in the European sea, their community composition did, indicating there are restrictions on dispersal even for species which use wide-ranging definitive hosts such as birds, and that local ecological conditions can further influence recruitment success of different trematode species.

While marine snails are long-lived (some with lifetimes measured in decades) and retain infections which may persist for many years or even the rest of the snail's life (Curtis, 2002), the shorter lifespan of freshwater snails results in more frequent seasonal turnover, with the parasite communities essentially being reset every season, and a new community of trematodes recruited within a very short time (Soldánová & Kostadinova, 2011).

### 3.4.2 Bivalves

Of all the bivalves, the parasite fauna of soft-sediment intertidal bivalves has been most heavily studied because of their accessibility. Like snails, their parasite communities have been characterised from a number of geographical region around the world (e.g. de Montaudouin *et al.*, 2000; Poulin *et al.*, 2000; Russell-Pinto *et al.*, 2006). Bivalves are usually infected concurrently with multiple species; this array of parasites makes them good sentinels for collecting information on parasite distribution. They commonly serve both as first and second intermediate hosts of trematodes as well as various other taxa with different life-cycles; in contrast to digeneans in snails, these parasites occupy different organs within the bivalve (gonad, foot, gills, etc.) and exploit the host

differently, so there is less potential for direct interactions and competitive exclusion. However, there is some indication of mutual facilitation and interspecific exclusion between different parasites from both field (Leung & Poulin, 2007) and laboratory studies (Leung & Poulin, 2011). So the possibility that some species may predispose or preclude infection by another must be taken into consideration when looking at the parasite assemblage of bivalves.

There are only a few studies which have quantified the spatial and biogeographical variation in parasite communities of bivalves. When de Montaudouin & Lancelleur (2011) examined the parasite community of the European cockle (*Cerastoderma edule*) they found different patterns at different scales. At 100 m scale the parasite community composition and abundance was determined by the presence and abundance of the first intermediate host, while at the kilometre scale, environmental condition and the occurrence of definitive hosts were more important factors.

In another study, de Montaudouin *et al.* (2012) found significant heterogeneity in the parasite communities of cockles over kilometre scales. Most of the parasites are digeneans in their metacercariae stage, the availability of which is itself dependent upon the presence of infected first intermediate hosts; thus high infection prevalence can also serve as an indicator of the presence of infection in such hosts. However, this heterogeneity becomes homogenised over time as older bivalves eventually accumulate most of the available trematode species in the region and even outlive infections (e.g. Tompkins *et al.*, 2004). Bivalves reveal a different snapshot of parasite biogeography and distribution to that revealed through snails. Whereas the digenean asexual stages found in snails are from vagile definitive hosts, the infections in bivalves are mostly accumulated from cercariae-shedding intermediate hosts which live in sympatry with the bivalves; thus they serve to concentrate and reveal the presence of parasites which otherwise would not be detected due to their low prevalence in the first intermediate host.

### 3.4.3 Intertidal crustaceans

In addition to molluscs, intertidal ecosystems are inhabited by a wide variety of crustaceans, and many of them are parasitised (see Koehler & Poulin, 2010). Decapods can be concurrently infected with a taxonomically diverse array of parasites, including those with complex life-cycles such as endohelminths, and parasites with direct life-cycles such as rhizocephalans and other parasitic crustaceans. Despite the diversity of crustaceans present in the intertidal, the parasite communities of only a few orders – the amphipods, isopods and decapods – have been studied in detail. Of those, only a handful of studies compared biogeographical trends in their parasite communities.

For the trematode communities of intertidal crustaceans there is a trend towards greater infection prevalence, intensity and increasing diversity with decreasing latitudes, which persisted even after correcting for host phylogeny, body size and sampling effort (Thieltges *et al.*, 2009d). This trend mirrors those known for other organisms that have higher species richness at lower latitudes (Rohde, 1992; Gaston, 2000). However,

Thieltges *et al.* (2009d) pointed out that this trend is mainly based upon data obtained from parasites in amphipods – the only crustacean taxa for which data on parasitism are available from a wide latitudinal range.

In another study, Thieltges *et al.* (2009c) found consistency in parasite load of crustaceans across geographical range, with local factors playing a relatively minor role in determining infection level and prevalence, and that such factors seem to be far more important in bivalves. Thieltges *et al.* (2009c) suggested that the smaller body size of most crustaceans and density-dependent mortality limits the number of parasites that can be found in each host, thus limiting the level of infection variations across different localities.

The above studies uncovered a few general trends, but they also reveal a clear gap in knowledge as only amphipods have been well studied for their parasites across a large geographical range, and parasites of most intertidal crustaceans have not been studied at all.

#### 3.4.4 Freshwater crustaceans

The coevolutionary dynamics and ecology of parasite communities of *Daphnia* have been well studied (e.g. Ebert *et al.*, 1998; Cáceres *et al.*, 2006; Duffy & Sivars-Becker, 2007; Wolinska *et al.*, 2007). While they have served as model systems for looking at host–parasite coevolution and epidemiology, very few studies have compared their parasite communities across their geographical distribution, despite their abundance and ubiquity (e.g. Ebert *et al.*, 2001).

From the few studies available, there are indications that different microparasites of *Daphnia* have different dispersal capabilities. In a study on the distribution of parasites in two species of *Daphnia* in rockpools of central Sweden, Bengtsson & Ebert (1998) found that while the microsporidian *Larssonia* sp. was found at all the sites they examined, the other parasites were more restricted in their distributions. The infection dynamics of different parasites can also contribute to their dispersal capacity, and certain vectors (such as insects) might not carry enough spores for them to successfully establish in a new batch of hosts, while parasites with mixed (vertical and horizontal) transmission strategy may allow them to co-disperse with their hosts (Ebert *et al.*, 2001). Wolinska *et al.* (2011) also found that while a microsporidian parasite was evenly distributed across multiple reservoirs with little change in prevalence, the presence and prevalence of other parasites were heavily influenced by local reservoir characteristics.

In addition to small zooplankton like waterfleas, there are other freshwater crustaceans that harbour a rich and varied parasite community. Freshwater crayfish are host to a wide variety of parasites and pathogens (Longshaw, 2011). Crayfish have been the subject of phylogeographic studies (Nguyen *et al.*, 2004; Apte *et al.*, 2007) and would be ideal candidates for comparative studies of the host's phylogeography and parasite communities across the host's distributional range, similar to studies by Keeney *et al.* (2009) on the parasites of New Zealand intertidal snails.

### 3.5 Concluding remarks

Aquatic invertebrates, and in particular those from marine environments, are far from well known, and their parasite fauna even less so. Therefore, any conclusions regarding biogeographical trends of their parasites must be considered to be very preliminary. Nevertheless, some patterns are beginning to emerge.

It is known that similarities of parasite communities in vertebrate hosts decay exponentially with increasing distances, and this trend is strongly influenced by local factors such as the ecology and habitat of the host (Poulin, 2003). The influence of local factors is also evident in parasite communities of invertebrates based on the studies conducted so far, with different factors operating at different levels.

Digenean trematodes are widely regarded as being highly host specific, yet little is known about how this affects the distribution and composition of parasite communities. Poulin *et al.* (2011) suggested comparing the niche breadth/host specificity of parasites in its relation to geographic distribution, as has been tested for fleas on small mammals (Shenbrot *et al.*, 2007; Krasnov *et al.*, 2010). Yet this has not been done with parasites of aquatic invertebrates – indeed, little is known about the host range of some of these parasites, despite their ubiquity (e.g. trematode metacercariae in bivalves).

There is evidence that the host genotype plays a role in recruitment/infection success of parasites in molluscs (King *et al.*, 2011; Levakin *et al.*, 2013) and crustaceans (Duneau *et al.*, 2011; Wolinska *et al.*, 2007). Surrounding biotic components also shape parasite communities by either acting as decoy hosts or predators of infective stages (Thieltges *et al.*, 2008). Local adaptation affects the infection success and influences the composition of these communities. The next step forward would be to combine phylogeography of the host and parasite communities (Keeney *et al.*, 2009).

Our current knowledge of parasite community structure in aquatic invertebrates is limited to a handful of host taxa, from a limited subset of habitats. But there are many other hosts groups which can provide additional insight into the structuring of parasite communities in aquatic invertebrates. For example, polychaete worms are abundant and infected by a variety of parasites (e.g. Peoples *et al.*, 2012), but their parasite fauna has not been investigated as extensively as those of snails, bivalves or decapods. Furthermore, most of the aquatic invertebrates which have been investigated are from either freshwater or intertidal marine habitats. But rich communities of parasites can be found in invertebrates from habitats which are usually not considered in parasitological studies.

Future studies should concentrate on parasite distributions that might reveal multi-scale biogeographical patterns (see mollusc–trematode studies) and on parasites with direct life-cycles, since most of the parasites in gastropods, bivalves and intertidal crustaceans discussed above have complex life-cycles. Such studies will contribute to our understanding of how different biotic and abiotic factors contribute to shaping parasite communities across wide spatial scales.

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