Chapter 9
Ecology of Parasites in Mudflat Ecosystems

David W. Thieltges, Kim N. Mouritsen, and Robert Poulin

Contents

Abstract Mudflats are not only home to large numbers of bivalves, polychaetes, crustaceans, fish and birds, but also to diverse communities of parasites. In this chapter, we illustrate and explore how the resulting parasite-host interactions can affect host populations, communities and food webs in mudflat ecosystems, equalling in importance the effects resulting from other species interactions, such as

---

D. W. Thieltges (✉)
Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, and
Utrecht University, Den Burg, The Netherlands
e-mail: David.Thieltges@nioz.nl

K. N. Mouritsen
Department of Bioscience, Marine Ecology, University of Aarhus, Aarhus, Denmark

R. Poulin
Department of Zoology, University of Otago, Dunedin, New Zealand

P. G. Beninger (ed.), *Mudflat Ecology*, Aquatic Ecology Series 7,
https://doi.org/10.1007/978-3-319-99194-8_9

predation and competition. We first give an overview of the distribution and ecology of typical parasites occurring in mudflat ecosystems. Then we illustrate the main abiotic and biotic drivers of parasite infection levels in mudflat hosts. Following this, we conceptualise and illustrate the many direct and indirect effects of parasite-host interactions on host populations, communities and food webs in mudflat ecosystems. Finally, we highlight the potential impact of ongoing global changes such as increasing temperature and species introductions on parasite-host interactions in mudflat ecosystems. With this condensed overview of the presence and ecological role of parasites in mudflat ecosystems, we hope to increase the appreciation of the manifold ecological effects of parasite-host interactions on host populations, communities and food webs of mudflat ecosystems, and to spark further research in this field.

1 Parasites as Protagonists on Mudflat Ecosystems

1.1 Parasites and Biological Interactions

Species interactions such as competition and predation are well known drivers of the population dynamics and community structure of organisms inhabiting mudflats. While competition is mainly limited to high-density situations (Wilson 1991; Jensen 1993; Raffaelli and Hawkins 1999), predation by typical mudflat predators such as crabs, fish and birds seems to be a universal biotic structuring factor on mudflats (Reise 1985; Wilson 1991; Kaiser et al. 2011, see Chaps. 5, 6, 12). Although the power of species interactions in shaping mudflat community structure and dynamics is generally acknowledged, other species interactions have received much less attention in this respect. Among these are parasitic interactions, i.e. interactions between parasites and their hosts. In this type of interaction, one partner (the parasite) gains a benefit while the other (the host) suffers from negative effects. The benefit is usually a trophic one as parasites feed on their hosts' tissue or pre-digested gut content. The negative effects for hosts can be manifold and range from various sub-lethal effects to mortality.

With their positive-negative dichotomy, parasite-host interactions resemble predator-prey interactions in which the predator gains a benefit and the prey suffers from a negative effect in the interaction (Raffel et al. 2008; Lafferty and Kuris 2002). However, predators differ from parasites in respect to size (predators are usually larger than their prey while parasites are usually smaller) and the number of victims attacked (predators typically attack more than one victim over their life cycle, while parasites usually attack only a single victim per life-cycle stage; Lafferty and Kuris 2002). Under this definition, blood-sucking animals such as mosquitos, leeches or lampreys are considered to be micropredators as they feed on more than a single victim during a life cycle stage (Lafferty and Kuris 2002). However, broader definitions of parasitism would subsume them under parasites (Combes 2001). Further definitional distinctions into sub-categories of the term 'parasite' exist. Based on the impact on their hosts, some authors have suggested that typical parasites such as helminths feed on a single host without necessarily killing it while for parasitoids the killing of the host is an inevitable part of the life cycle (Lafferty and Kuris 2002). Finally, parasites are often divided into two groups, microparasites and macroparasites, which, apart from size, are distinguished by their reproductive dynamics: the descendants of microparasites (e.g. protozoans such as *Toxoplasma* and *Plasmodium* spp.) may continue to infect the host, as well as being transmitted to other hosts, whereas the descendants of macroparasites (usually successive larval stages, e.g. trematodes) leave the host to infect other hosts (Schmid-Hempel 2011). Although many microparasites may undoubtedly have strong effects on infected hosts in mudflat ecosystems, we will focus on macroparasites in this chapter, as their ecology and impacts on mudflat ecosystems are much better understood. We will also mainly focus on describing the distribution and various ecological effects of parasites on 'wild' hosts in mudflat ecosystems and thus exclude more applied issues of diseases in aquaculture settings such as mussel, oyster or shrimp culture in mudflat ecosystems. In general, we do not intend to provide an exhaustive review of the topic but instead we aim to sketch the broader picture and highlight some active current and future research fields.

1.2 Parasites Occurring in Mudflat Ecosystems

Mudflat ecosystems harbour a large variety of parasites (Fig. 9.1). Recent studies that include parasites in food web analyses give an idea about the typical composition of parasite communities in mudflat ecosystems (Table 9.1). These parasite-inclusive food webs do not cover all types of mudflats, but showcase a sub-set of mudflat ecosystems such as mudflats in estuarine salt marshes (Carpinteria, Bahia Falsa, Estero de Punta Banda) and shallow water ecosystems (Flensburg Fjord), mudflats behind back-barrier islands (Sylt tidal basin) and in large tidal inlets (Otago Harbour). The dominant parasite group in these mudflat ecosystems are trematodes, followed by other helminths such as nematodes, cestodes and acanthocephalans, and a variety of other parasitic groups (Table 9.1). The various parasite species in these food webs constitute between 16 and 76% of the richness of free-living (host) species, indicating that parasites contribute significantly to the biodiversity of mudflat ecosystems.

Although the parasite inventories from these six mudflat food webs give an idea about the general composition of parasite communities in mudflat ecosystems, they are far from being complete, since some host groups such as birds are notoriously

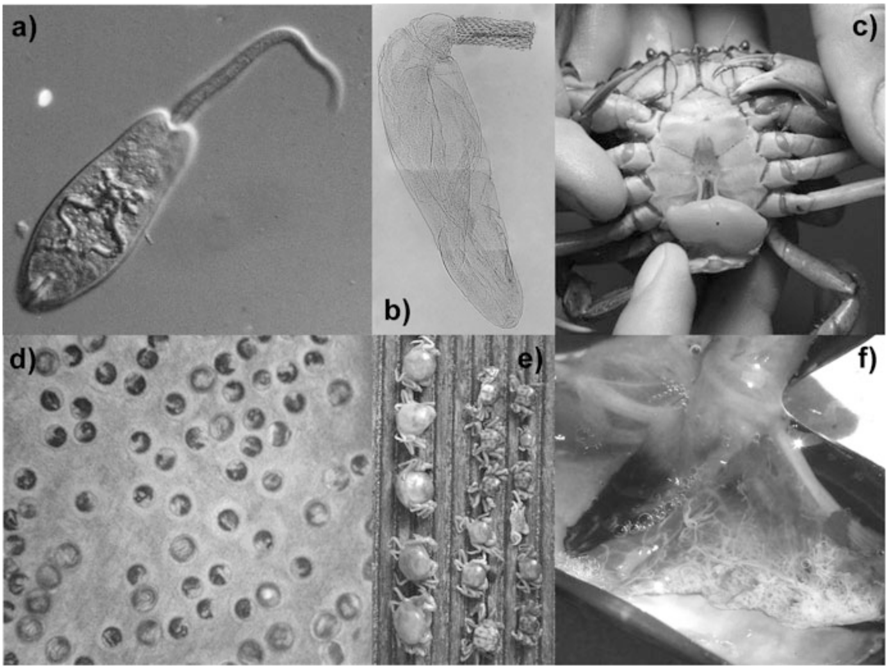


Fig. 9.1 Examples of metazoan parasites occurring in invertebrate hosts living on mudflats. (**a**) Free-living cercarial stage of the trematode *Maritrema subdolum* (length including tail ca. 340 μm); (**b**) cystacanth stage (with everted proboscis) of the acanthocephalan *Plagiorhynchus allisonae* (trunk length ca. 2.5 mm) from the amphipod *Transorchestia chiliensis*; (**c**) sac-like externa of the rhizocephalan barnacle *Sacculina carcini* underneath the pleon of an infected shorecrab *Carcinus maenas* (ca. 6 cm carapax width); (**d**) metacercarial stages of the trematode *Acanthoparyphium* sp. (380–470 μm diameter), encysted in the foot tissue of the New Zealand cockle *Austrovenus stutchburyi*; (**e**) pea crabs *Pinnotheres novaezelandiae* (ca. 8–16 mm carapax width) collected from inside green-lipped mussels *Perna canaliculus*; (**f**) white mesh-like structure of the sporocyst stages of the trematode *Prosorhynchus squamatus* infecting the gonads and hepatopancreas of a blue mussel *Mytilus edulis* (ca. 4 cm shell length) (Published with kind permission of (**a**), (**c**), (**e**): © Kim N. Mouritsen 2018; (**b**) © Bronwen Presswell 2018; (**d**) © Tommy Leung 2018; (**f**) © Tabea Stier 2018. All Rights Reserved).

understudied. Further complications arise from the fact that some host groups (e.g. fish and birds) are often transient components of the local food web that carry parasites acquired elsewhere, and therefore do not necessarily cycle within the local web. In addition, parasite-inclusive food web studies have so far mainly considered macroparasites; however, there is most likely also a large diversity of microparasites in mudflat ecosystems that awaits exploration (Thieltges et al. 2013a). Hence, the presently known diversity of parasites in mudflat ecosystems is likely to increase with future research efforts.

Table 9.1 Composition of parasite communities in six functionally different mudflat ecosystems based on parasite richness of typical taxonomic groups

	Sylt Tidal Basin	Otago Harbour	Flensburg	Carpinteria Salt Marsh	Bahia Falsa	Estero de Punta Banda
Total host richness	116	117	60	92	101	123
Invertebrates	66	93	48	39	47	59
Fish	21	7	12	11	13	19
Birds	29	17	8	42	41	45
Total parasite richness	35	19	46	60	53	76
Trematodes	27	13	27	30	34	39
Nematodes	1	2	10	5	4	7
Cestodes	1		3	6	4	8
Acanthocephalans	1	2	2	2	2	4
Monogeneans				1	1	2
Crustaceans	4	2	1	4	3	4
Rhabdocoelans	1					1
Myxozoans				1		
Nemerteans				1		1
Microsporidians			1			
Protists			2	7	5	9
Viruses				1		1
Parasitic plants				2		

For comparison, total species richness of free-living (metazoan) host species and of major taxonomic groups are also given for each food web (excluding basal groups and bacteria, zooplankton and meiofauna). Data based on Hechinger et al. (2011), Mouritsen et al. (2011), Thieltges et al. (2011), and Zander et al. (2011)

1.3 Parasite Life Cycles

A common feature of many parasites occurring in mudflat ecosystems are their complex life cycles, i.e. they sequentially infect several different host species over their life cycle. For example, the dominant trematodes typically have a three-host life cycle (Figs. 9.1 and 9.2; Galaktionov and Dobrovolskij 2003). Fish, birds or marine mammals, depending on the trematode species, serve as definitive hosts of the adult stages of the parasites. Here, the parasites reproduce sexually and release eggs that leave the host via its faeces. From the eggs, ciliated larvae called miracidia hatch and infect a first intermediate host, which is usually a gastropod and sometimes a bivalve. In the first intermediate host, clonal reproduction by asexually reproducing intramolluscan stages (sporocysts and rediae) leads to the production of a second

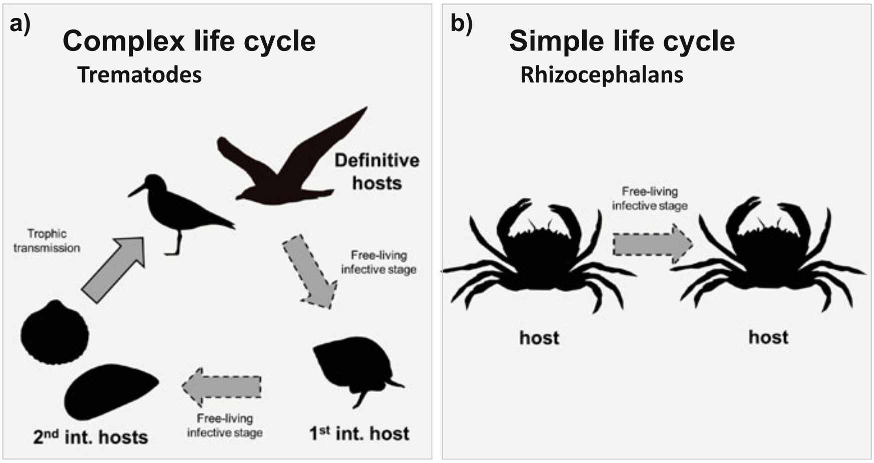


Fig. 9.2 Examples of typical life cycles of parasites occurring on mudflats. (**a**) Complex life cycle of a trematode parasite, including three sequential host species (one definitive host and two intermediate hosts). Host specificity is usually highest in 1st intermediate hosts and lower in 2nd intermediate and definitive hosts. Transmission occurs via a free-living infective stage or via trophic transmission when definitive hosts consume infected prey. (**b**) Simple life cycle of rhizocephalan parasites (e.g. *Sacculina carcini)* infecting other crabs horizontally via a free-living infective stage, released by infected crabs (Published with kind permission of © David Thieltges 2018. All Rights Reserved).

free-living stage, the cercariae, which are released into the environment in large numbers. After a short free-living dispersal period of usually less than 24 h, the cercariae infect a second intermediate host, an invertebrate or fish, depending on the trematode species. Here, most cercariae encyst as metacercariae, and await ingestion of the second intermediate host by a definitive host, before closing the life cycle via trophic transmission. While the standard trematode life cycle consists of three consecutive hosts, variations on the theme exist, with abbreviations as well as extensions of the life cycle (Poulin and Cribb 2002; Galaktionov and Dobrovolskij 2003). Complex life cycles, including the use of one or several intermediate hosts, and a definitive host, also exist in other types of marine parasites such as nematodes, cestodes and acanthocephalans (see Rhode 1993, 2005). The existence of this complexity of life cycles is puzzling and their selective benefits are still debated; increased transmission and survival are, among other benefits, thought to underlie the evolution of these complex life cycles (Poulin 2007).

Although complex life cycles prevail in mudflat ecosystems, there are also parasites that have simple life cycles in which a free-living infective stage released from infected hosts infects another host individual of the same species. For example, the rhizocephalan parasite *Sacculina carcini* infects shore crabs *Carcinus maenas*, in which it grows internally and develops a visible external sac-like structure below the abdomen of the host (the so-called externa), from which infective stages are released and infect a new crab host (Figs. 9.1 and 9.2; Høeg 1995; Høeg and Lützen 1995).

Other marine parasites with simple life cycles are shell-boring polychaetes such as *Polydora ciliata*, or monogenean flatworms infecting fish (Buschbaum et al. 2007; Rhode 2005).

1.4 Hosts Affected in Mudflat Ecosystems

Due to the complex life cycles of many parasites, a single parasite species usually affects several very different host taxa during its life, ranging from invertebrates to vertebrates. In addition, if host specificity is low, the same parasite species can infect several different host species at a given life cycle stage. Overall, this results in most free-living species inhabiting mudflats being infected by at least one parasite species. However, not all of these free-living species will serve as hosts to parasites to the same degree, due to host specificity issues or other ecological processes. For example, at the host species level, the mean number of trematode species that can be found in populations of snail first intermediate hosts in mudflat ecosystems varies widely among host species from 1 to 12.7 (Poulin and Mouritsen 2003). There may also be gastropod species that do not serve as hosts for trematodes at all (Pechenik et al. 2001). Likewise, the mean infection prevalence (the proportion of hosts infected) of the same trematodes in populations of gastropods varies widely among gastropod host species (Poulin and Mouritsen 2003), indicating varying general suitability as hosts among gastropod species.

The same pattern can also be observed within single mudflat ecosystems. For example, the number of parasite species infecting gastropods and bivalves varies widely among host species in a back-barrier islands mudflat ecosystem in German/Danish coastal waters (Fig. 9.3a). Similarly, the number of parasite species infecting crustaceans in a large tidal inlet in New Zealand varies among host species (Fig. 9.3b). In addition, the mean infection intensity (no. of parasites per infected host) of individual parasite species also differs strongly among and within host species (Fig. 9.3b), indicating that not all hosts are evenly suitable to all parasite species. In general, this suggests that some host species will be more likely to be affected by specific parasite species than others. In addition to among-host species differences in parasite richness and infection levels, there is often also considerable within-host species variation, since the spatial heterogeneity of infections is frequently high in hosts inhabiting mudflats, even within the same mudflat ecosystem (e.g. Hechinger and Lafferty 2005; Fredensborg et al. 2006; Thieltges and Reise 2007). This heterogeneity extends to even smaller scales, as not all individuals of the same host species in the same locality will be equally infected, leading to the almost universal phenomenon of parasite aggregation among hosts, generally observed in parasite-host interactions (Shaw and Dobson 1995). This suggests that not only different host species will be affected by parasitism to a different degree, but also that single host individuals may experience very different exposure to parasites, depending on the locality and other factors. We further discuss some of the underlying mechanisms below.

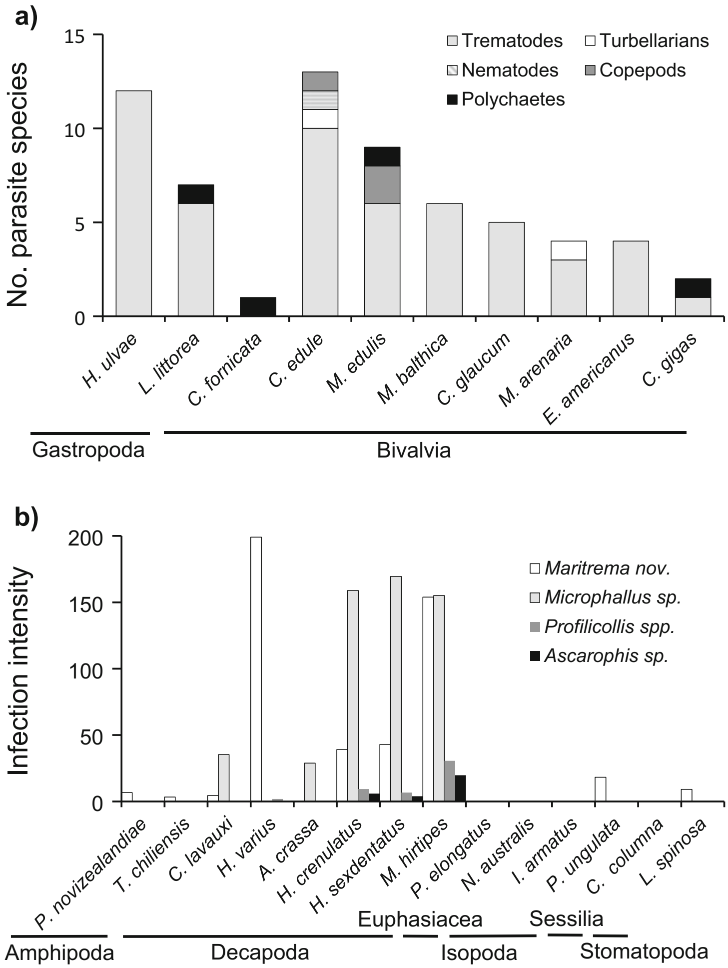


Fig. 9.3 Examples of parasite richness and infection intensities among typical host groups inhabiting mudflat ecosystems. (**a**) Parasite richness of different groups of parasites (shell boring polychaetes, intestinal copepods, nematodes and turbellarians, and trematodes in their first or second intermediate host life cycle stages) in gastropods and bivalves from a back-barrier island mudflat ecosystem in German/Danish coastal waters (Thieltges et al. 2006). (**b**) Mean infection intensity (no. of parasites per infected hosts) of four parasite taxa (two trematodes: *Maritrema novaezealandensis* and *Microphallus* sp., one acanthocephalan species group: *Profilicollis* spp. and one nematode: *Ascarophis* sp.) infecting crustaceans of different taxa in a large tidal inlet in New Zealand (Koehler and Poulin 2010). Redrawn from Thieltges et al. (2006) and Koehler and Poulin (2010).

While the general degree to which molluscs and crustaceans are affected by parasites in mudflat ecosystems is relatively well known (Lauckner 1980, 1983; Poulin and Mouritsen 2003; Thieltges et al. 2009a, b, c), we know much less about parasite infection levels in other host groups. Polychaetes are one of the dominant taxa on mudflats, but have not been studied intensively with respect to parasites. They are known to serve as intermediate hosts, not only for trematodes, but also for nematodes and cestodes (see Peoples 2013 for a recent review); however, little is known about infection levels of polychaetes in mudflat ecosystems (but see Peoples et al. 2012). Fish inhabiting mudflats serve as intermediate and definitive hosts for parasites with complex life cycles such as trematodes and other helminths, which are acquired via trophic transmission from intermediate hosts (Thieltges and Poulin 2016). Although the parasitology of marine fishes is relatively well known, the specific parasite communities and infection intensities of fishes inhabiting mudflats are less well studied, apart from scattered reports on specific fish host or parasite species (e.g. Groenewold et al. 1996), and from a very limited number of broader studies on entire mudflat ecosystems such as Californian estuarine salt marshes (Kuris et al. 2008). This results from the fact that fish parasitological studies usually focus on offshore or deeper coastal waters, and rather on commercially than ecologically relevant species. In addition, it can be difficult to link parasites found in fish with specific habitats, because many coastal fish species often only occur temporarily on mudflats (Horn et al. 1999). Hence, besides being infected with parasites locally acquired via trophic transmission, fish hosts caught on mudflats will also harbour other parasites such as parasitic copepods (e.g. Koch et al. 2014) that they acquired elsewhere, which complicates linking parasites to specific mudflat habitats. Finally, the least-studied host group with respect to parasites (mainly due to ethical constraints in conducting invasive parasitological surveys) are birds, which use mudflats mainly as feeding grounds (Chap. 12). They serve as definitive hosts to the majority of trematode parasites occurring in mudflat ecosystems, and they acquire them via trophic transmission (Thieltges and Poulin 2016). However, little is known about the actual infection levels in birds in specific mudflat ecosystems, apart from local studies on single host and/or parasite species (e.g. Latham and Poulin 2002; Kuris et al. 2008). In addition, like fish, most birds also use mudflats only temporarily, e.g. at stop-overs during their annual migrations, so that their parasite faunas are likely to be composed of parasite species acquired in different habitats (Gutiérrez et al. 2017).

2 Drivers of Infection Levels

2.1 Biotic Factors

Because parasites, by the nature of their life style, depend on their hosts for a living, the presence of parasites depends on the presence of their hosts. Hence, host diversity and abundance usually drive parasite richness and infection levels. This relationship can be observed on large regional, as well as on small local spatial scales. For example, the diversity and prevalence of trematodes infecting a common gastropod species (serving as first intermediate host) which inhabits mudflats depends on the presence and abundance of bird definitive hosts (which are the upstream hosts in the parasites' life cycles) on regional scales (Fredensborg et al. 2006). Likewise, the same relationship can also be observed on small local spatial scales such as in intertidal mud channels and pans within a single estuarine salt marsh ecosystem (Hechinger and Lafferty 2005). Similar relationships have also been observed in second intermediate hosts of trematodes. For example, the infection intensity of metacercarial stages of trematodes in cockles (*Cerastoderma edule),* which serve as second intermediate hosts for the parasites, is positively correlated with the abundance of snail first intermediate hosts in the field (Thieltges and Reise 2007), and with densities of infected snails in field experimental settings (Thieltges 2007).

It is not just the upstream hosts in the complex life cycles of parasites, but also the receiving hosts themselves which can affect parasite richness and infection intensities. Host body size is a host trait that is generally positively correlated with both parasite diversity and infection intensity, as larger hosts provide more space and niches for parasites (Poulin 2007; Kamiya et al. 2014). In addition, larger hosts are also often older hosts, and may thus have accumulated parasite infections over a longer exposure period, resulting in higher infection levels in larger and older host individuals. In some cases, the effect of age or exposure time may be a stronger factor than host body size. For example, experimental exposure of cockles (*Cerastoderma edule*) of different body size, showed that exposure time was a much stronger determinant of trematode infection levels than body size (Thieltges 2008). Host body size can also be important in cases where it co-varies with the general infection suitability of the host. For example, trematodes that use gastropods as first intermediate hosts mainly infect mature snails, since they depend on the gonadal tissue of the snails (Galaktionov and Dobrovolskij 2003). This results in infection thresholds in snails, with small juvenile snails usually being uninfected, and thus produces a typical skewed size-class distribution of infections in gastropod hosts (see e.g. review by Lauckner 1980). Besides the traits of individual hosts, it can also be the density of all conspecific hosts at a specific location that can affect parasite infection levels. Usually, parasite infection intensities and host density are positively correlated, as a result of basic epidemiological mechanisms (Poulin 2007; Kamiya et al. 2014). However, in mudflat ecosystems, host density can also have a negative effect on infection intensities of individual hosts, in cases where free-living infective stages are diluted by conspecific downstream hosts. This can, for example, be observed in second intermediate hosts of trematodes where high densities of hosts lead to lower infection intensities in individual hosts in field observational and experimental settings (Mouritsen et al. 2003; Thieltges and Reise 2007).

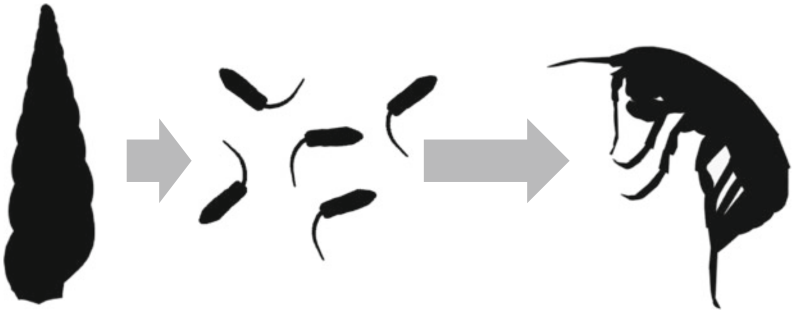
Besides the upstream hosts and the hosts themselves, organisms that do not serve as hosts can also affect parasite infection levels. At first sight, this sounds counterintuitive, but there are various ways by which non-hosts can affect parasite infection levels. A particularly well-studied mechanism in this respect is the interference of non-hosts with the transmission of infective stages of parasites (Thieltges et al. 2008a; Johnson and Thieltges 2010). For example, many organisms inhabiting mudflats are capable of interfering with the transmission of the free-living infective cercarial stages of trematodes, either by preying on cercariae (e.g. crabs, shrimps, amphipods, anemones, bivalves) or by constituting a physical obstacle such as algae

(Thieltges et al. 2008b; Hopper et al. 2008; Welsh et al. 2014). This transmission interference does not only reduce the number of infective stages in the environment, but also leads to reduced infection intensities in the downstream hosts in experimental settings (Thieltges et al. 2008b, 2009d). Such a transmission interference by non-hosts may be common in mudflat ecosystems, as recent food web studies using parasite-inclusive webs indicate that predation on free-living infective stages accounts for 10–20% of the total number of trophic links in the six food webs mentioned above (Table 9.1; Thieltges et al. 2013b).

2.2 *Abiotic Factors*

Infection levels in mudflat hosts are further mediated by a variety of abiotic factors. They affect both parasites and hosts, as well as their interactions, often resulting in complex net effects of environmental drivers on infection levels. Best studied in this respect is the effect of temperature on trematode infections in second intermediate hosts, such as bivalves and crustaceans, which are infected via free-living cercarial stages released from first intermediate gastropod hosts (Fig. 9.4). The production and release of cercarial stages is generally strongly positively correlated with temperature (Poulin 2006), a pattern also commonly observed in parasites occurring on mud flats (e.g. Mouritsen 2002a; Thieltges and Rick 2006; Studer et al. 2010; see also Chap. 15). At the same time, infectivity of cercariae (i.e. the successful infection of the down-stream second intermediate host) increases with temperature, while the longevity of cercarial stages decreases (e.g. Thieltges and Rick 2006; Studer et al. 2010). Temperature can also influence infection levels of host species, e.g. by stressing hosts and compromising immunity and thus increasing susceptibility, or by increasing parasite-induced host mortality (Lafferty et al. 2004; Harvell et al. 2009). Finally, temperature may also affect the development and survival of parasites in their second intermediate hosts, potentially compromising future infectivity with respect to the definitive hosts.

Potentially, temperature can have very different effects at different stages of parasite transmission. This is illustrated by a study from Studer et al. (2010) on temperature effects on the transmission of the trematode *Maritrema novaezealandensis* from its first intermediate host, the mud snail *Zeacumantus subcarinatus*, to its second intermediate host, the amphipod *Paracalliope novizealandiae* (Fig. 9.4). A series of laboratory experiments that decomposed the different transmission stages, showed that parasite transmission and host mortality were very slight at low temperatures (<20 °C), while at intermediate temperatures (20–25 °C), parasite transmission peaked, and amphipod hosts showed increased mortality. Finally, at the highest temperatures (≥ 30 °C), amphipod mortality was very high while parasite transmission was strongly reduced, due to both low numbers of infective stages being released, and low infectivity. Hence, temperature had very different effects on the different stages of the infection process, and the second intermediate amphipod host turned out to be the particularly vulnerable part. Similar complex temperature



T	Parasite Production	Parasite Survival	Parasite Infectivity	Host Susceptibility	Host Survival	Parasite Development
16°C	+	+++	+	+	+++	+
20°C	++	++	++	+	++	++
25°C	+++	++	+++	+	++	+++
30°C	++	+	++	+	-	-
34°C		+	+	+	-	-

Fig. 9.4 Conceptual illustration of the effect of temperature on different stages in the transmission process of a trematode species from its first intermediate gastropod host over the free-living cercarial stages to the second intermediate host and subsequent parasite development in the host. The table shows the direction and strength of temperature (T) effects on the different stages of the transmission process in laboratory experiments with the trematode *Maritrema novaezealandensis*, which uses the mud snail *Zeacumantus subcarinatus* as its first and the amphipod *Paracalliope novizealandiae* as its second intermediate hosts. Data based on Studer et al. (2010). (Published with kind permission of © David Thieltges 2018. All Rights Reserved).

effects probably exist in other parasite-host systems on mudflats (and elsewhere), but this largely remains to be studied.

Independent of temperature, the presence of water is of high importance for the dispersal of the free-living infective stages of trematodes. Hence, on mudflats transmission will generally take place only during high tide, or in the residual water of pools and puddles remaining at low tide. Such small water bodies probably serve as hotspots for infections, since they may warm up considerably during low tide in the summer, and trigger the temperature-induced mechanisms discussed above (Studer and Poulin 2012). The resulting positive effect on transmission is exemplified by experimental observations that cockles (*Cerastoderma edule*) exposed over several months in shallow tidal pools on a mudflat in the German Wadden Sea showed 43–73% higher infection intensities with trematode metacercarial stages, compared to cockles exposed outside the pools (Thieltges and Reise 2007).

In addition to the presence of water, the chemical properties of water can affect parasite transmission. Waterbody salinity is known to vary considerably on mudflats due to riverine freshwater input, surface runoff, or rainfall. Experimental studies in

New Zealand with the trematode *Philophthalmus* sp., which uses the snail *Zeacumantus subcarinatus* as first intermediate host, showed that cercarial production, encystment success (the parasite has a resting stage in the environment), and the survival of cysts were reduced under long-term (6–12 weeks) exposure to lower salinities of 25 or 30 psu, compared to the normal salinity of 35 psu (Lei and Poulin 2011). Such effects of salinity on trematode transmission may further be mediated by temperature. For example, Mouritsen (2002a) reported that salinity effects in the trematode *Maritrema subdolum*, which infects the mud snail *Hydrobia ulvae*, only occurred at certain temperatures in short-term (12 h) exposure experiments.

Another chemical property of water that can affect parasite transmission in mudflat ecosystems is the pH of the water, a property that has gained increasing interest in the contest of the expected future ocean acidification (MacLeod and Poulin 2012, see also below), but that can also vary considerably in the coastal waters of today (Melzner et al. 2013). Experimental studies with the trematode *Martitrema novaezealandense* have shown that cercarial survival decreases with decreasing pH of the seawater medium (MacLeod and Poulin 2015). However, the infection success in second intermediate amphipod hosts (*Paracalliope novizealandiae*) is actually highest under low pH conditions, which may result from negative effects of low pH on the hosts, leading to increased susceptibility (Harland et al. 2015). These examples show that we are far from understanding the full range of effects of biotic and abiotic drivers on parasite infections levels in hosts inhabiting mudflats. However, they illustrate that these effects may often differ between different stages of the transmission process, and also between parasites and hosts, and that the different biotic and abiotic drivers may often interact.

2.3 Large-Scale Drivers and Biogeography

Some of the biotic and abiotic factors discussed above also act on larger spatial scales and shape biographical patterns of parasites inhabiting mudflats. Like on smaller spatial scales, the presence and abundance of hosts is pivotal for the existence of parasites on large biogeographical scales, as illustrated by a study that investigated metacercarial trematode infections in the New Zealand cockle *Austrovenus stutchburyi* along the entire coastline of New Zealand (Studer et al. 2013b). The prevalence of parasites in the first intermediate host at the respective sampling sites proved to be the strongest determinant of infection intensities, besides the size of the cockle's foot (the parasites encyst mainly in the foot tissue).

Temperature is also expected to drive large-scale distributional patterns of parasites, resulting in latitudinal gradients in parasite species richness and infection intensity (Kamiya et al. 2014). Given the strong effects of temperature on trematode transmission, one would expect higher infection levels at higher average temperatures occurring at lower latitudes. However, this pattern may actually not be very strong in hosts inhabiting mudflat ecosystems. For example, Studer et al. (2013b) did not find a significant latitudinal gradient in trematode infection intensity in the New Zealand cockle *Austrovenus stutchburyi* along the coast of New Zealand, although there was a strong seawater temperature gradient from the North to the South. Large-scale patterns in parasite richness also do not universally follow the expectation. For example, when aggregating local host population data into larger geographical regions, Galaktionov (2017) found a decrease in trematode richness with increasing latitude in gastropod hosts (*Littorina* spp. and *Hydrobia* spp.). However, on the scale of local host populations, Thieltges et al. (2009a) did not find a latitudinal gradient in trematode infections of mud snails *Hydrobia ulvae* along the European Atlantic coast, nor did they find any robust latitudinal gradient in the infection prevalence of periwinkles *Littorina littorea.* Other studies have even reported latitudinal patterns opposite to the expectation. For example, Torchin et al. (2015) found that trematode species richness and prevalence actually increased with latitude in the Pacific horn snail *Cerithideopsis californica* and the Atlantic horn snail *Cerithideopsis pliculosala* along the coasts of North and Central America. These examples suggest that infection levels in individual hosts are more strongly affected by local factors, such as those emphasised above, than by large-scale temperature gradients.

This rule of thumb may also be true for latitudinal gradients involving across-species comparisons, i.e. studies based on data of parasite richness and infection intensity from different host species. In this case, latitude is not only a correlate for temperature but also serves as a general proxy for evolutionary rates which are considered to be higher at lower latitude due to increased solar influx (Willig et al. 2003; Turner et al. 1987; Cardillo 1999). Based on this, one would expect not only higher infection intensities, but also higher parasite species richness at lower latitudes. Indeed, in some cases, this pattern has been observed. For example, trematode species richness, mean prevalence, and mean intensity in marine amphipod hosts decrease with increasing latitude (Thieltges et al. 2009c). However, other across-species comparisons have failed to find such a latitudinal pattern. For example, Poulin and Mouritsen (2003) did not detect an effect of latitude across gastropod host species (but they found an effect at the sample level, i.e. when individual samples from locations were analysed). Likewise, Gutiérrez et al. (2017) did not detect any effect of latitude on parasite richness across shorebird species which often use mudflats as feeding grounds. These findings are in line with a recent meta-analysis on drivers of parasite richness, including terrestrial and freshwater environments (Kamiya et al. 2014), which emphasises that drivers of large-scale patterns in parasites of mudflats still remain to be identified.

3 Effects of Parasites on Mudflat Hosts and Ecosystems

3.1 Direct Effects on Individual Hosts and Host Populations

By definition, parasite-host interactions result in negative effects on infected hosts. These direct negative effects are inflicted on individual hosts, but they can also have knock-on effects on host populations. This is best illustrated in the case of parasite-

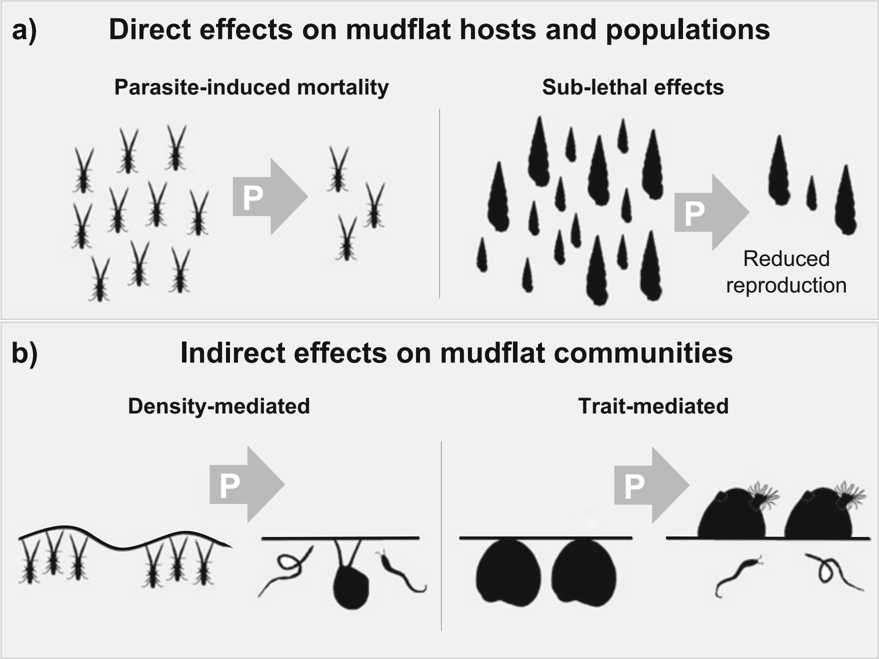


Fig. 9.5 Conceptual diagram illustrating direct and indirect effects of parasites on mudflat hosts, populations and communities. (**a**) Direct effects of parasites (P) include parasite-induced mortality and sub-lethal fitness effects such as reduced host reproduction on infected individual hosts which can have knock-on effects on host population sizes. (**b**) Indirect effects of parasites on mudflat communities occur when parasites alter the density (density-mediated indirect effects) or morphological, physiological or behavioural traits (trait-mediated indirect effects) of infected hosts such as the burrowing ability of cockles. In turn, this can affect other organisms living on mudflats, and ultimately affect community composition. For details, see text (Published with kind permission of © David Thieltges 2018. All Rights Reserved).

induced mortalities of infected hosts (Fig. 9.5a). Mortality induced by many parasites is intensity-dependent, i.e. host mortality increases with the infection intensity of a parasite (Fredensborg et al. 2004). If parasite infection levels are relatively high in a host population, this can result in the mortality of many infected hosts, and this in turn can affect the size and dynamics of the host population. For example, heavy trematode infections in populations of the amphipod *Corophium volutator* on mudflats have been reported to lead to significant decreases in population size, or even local extinction (Meissner and Bick 1997; Jensen and Mouritsen 1992). Such parasite-induced mortalities often coincide with other environmental stressors. In particular, temperature stress has been reported to be associated with mass mortalities of infected hosts. For example, in the amphipod *C. volutator*, mass mortalities of amphipods in the field have been associated with coinciding high temperatures, and elevated infection levels with trematode metacercariae (Jensen and Mouritsen 1992). In addition, laboratory experiments have confirmed the link between temperature stress and increased host mortality in infected amphipods (Mouritsen and Jensen 1997; Jensen et al. 1998; Meissner and Bick 1999; Larsen and Mouritsen 2014). Temperature stress does not only elevate host mortality in crustaceans, but has also been reported to increase mortality in infected gastropod (McDaniel 1969; Tallmark and Norrgren 1976) and bivalve hosts (Thieltges 2006a). However, in some cases, the resistance of trematode-infected gastropods to temperature stress and prolonged exposure is not different from that of non-infected ones, or is even higher (Riel 1975; Sousa and Gleason 1989; Berger et al. 2001; Bates et al. 2011). Besides temperature, other environmental stressors may also elevate parasite-induced mortality. For example, oxygen depletion reduces the survival of juvenile bivalves infected with metacercarial stages of trematodes (Wegeberg and Jensen 1999). Likewise, desiccation can lead to higher mortality in hydrobiid snails infected with trematodes (Jensen et al. 1996).

Instead of inducing direct host mortality, parasites can also have more subtle sub-lethal effects on hosts living on mudflats. Such sub-lethal effects on individual hosts may also have knock-on effects on host populations, just like the ones observed in the case of parasite-induced mortality. A good illustration for this is provided by the ubiquitous trematodes that can be found in many gastropods living on mudflats (Fig. 9.5a). These trematodes infect the gonadal tissue of their hosts and usually lead to partial or total castration, which strongly reduces the life-time fitness of infected individuals (Lauckner 1980; Huxham et al. 1993; Mouritsen and Jensen 1994). In host species that have pelagic larvae for dispersal, even the castration of the majority of individual hosts in a local population may not affect the size of the population much, since larval stages originating from elsewhere can supply the local recruitment. However, in host species that have direct development, parasitic castration of a large proportion of the host population may significantly lower local population size. Indeed, such population-level effects of parasite infections have been observed in several gastropod species with direct development (Lafferty 1993; Sokolova 1995; Fredensborg et al. 2005). Similar population-level effects have also been suggested in the case of the direct-developing amphipod *C. volutator*, in which metacercarial stages of trematodes reduce the brood size of infected females, which in turn likely reduces local abundance of the amphipods (Bick 1994; McCurdy et al. 1999).

Besides host castration and reduced reproduction, other sub-lethal effects of parasites that have been observed in typical mudflat hosts include, among others, changes in growth rates of molluscs, both in a positive (Mouritsen and Jensen 1994; Probst and Kube 1999) and negative direction (Mouritsen et al. 1999; Thieltges 2006b; O'Connell-Milne et al. 2016), reduced condition of bivalves (Wegeberg and Jensen 2003; Stier et al. 2015; O'Connell-Milne et al. 2016), reduced filtration rates in bivalves (Stier et al. 2015), morphological changes such as the shape and ornamentation of shells in gastropods (Hay et al. 2005; Thieltges et al. 2009e), behavioural changes such as impaired burrowing ability in bivalves (Lauckner 1983; Thomas and Poulin 1998) and potential changes in animal personality such as reduced boldness in infected snails (Seaman and Briffa 2015). Many of these sub-lethal direct effects may also trigger knock-on effects on host population sizes and dynamics, and some of them may also trigger further indirect effects on other organisms and eventually affect entire mudflat communities, as discussed below.

3.2 Indirect Effects on Host Communities

Many of the direct effects that parasites inflict on their hosts can also lead to indirect effects on other species living next to the infected hosts, and ultimately affect entire mudflat communities. These indirect effects occur when parasites either alter the density of infected hosts (density-mediated indirect effects), or change morphological, physiological or behavioural traits of infected individuals (trait-mediated indirect effects; see Hatcher et al. (2006) and Hatcher and Dunn (2011) for a detailed account of indirect effects of parasites in general).

Density-mediated indirect effects of parasites are closely linked to the parasite-mediated mortalities discussed above. These mortalities can trigger indirect effects, particularly in host species that have strong impacts on local habitats and communities themselves. For example, parasites that affect ecosystem engineers (organisms that create or modify habitat for other organisms—Jones et al. 1997; see Chap. 10) may trigger particularly strong indirect effects on local communities (Thomas et al. 1999). A good example for this is the parasite-induced mortality of the amphipod *Corophium volutator* discussed above (Fig. 9.5b). With their tube-building activity, these amphipods can stabilise the sediment and lead to a typical mudflat topography of subtle hummocks and shallow puddles (Mouritsen and Poulin 2002). A parasite-induced mass mortality event of the amphipods on a mudflat in the Danish Wadden Sea lead to increased erosion, which altered the sediment grain size composition, and ultimately turned the mudflat topography into a flat surface (Mouritsen et al. 1998; Mouritsen and Poulin 2002). In turn, this change in habitat condition affected other organisms on the mudflat, leading to altered composition and abundance of macrofauna (Jensen and Mouritsen 1992; Larsen et al. 2011, and see Chap. 10). Similar indirect effects are likely to result from other parasite-induced host mortalities, but to date we lack information on the extent of such density-mediated indirect effects of parasites in mudflat ecosystems.

Examples for the other type of indirect effects induced by parasites, the so-called trait-mediated indirect effects, are also known from mudflat ecosystems. One of the prime examples comes from mudflats in New Zealand where the New Zealand cockle *Austrovenus stutchburyi* is infected by the trematode *Curtuteria australis* and other closely-related trematode species (Fig. 9.5b). These parasites infect the foot of the cockles, and compromise the burrowing ability of infected individuals, which normally live 1–2 cm beneath the sediment surface, so that infected cockles end up laying on the sediment surface (Thomas and Poulin 1998; Mouritsen 2002b). This behavioural alteration of the cockle is considered to be adaptive for the parasites, as it increases predation by birds, which serve as definitive host for the trematodes (Thomas and Poulin 1998). Besides increasing transmission for the parasites, the parasite-induced surfacing of cockles also indirectly affects other organisms. The cockles laying on the sediment surface change the local near-bed hydrodynamics and sedimentation rates by being obstacles, and they no longer act as bioturbators of the sediment. Together, these effects lead to an increase in general macrobenthic species richness and a higher abundance of many macrobenthic taxa and functional groups (Mouritsen and Poulin 2005). The parasite-induced surfacing of cockles has further been linked with changes in primary and secondary production on mudflats (Mouritsen and Poulin 2006). Similar trait-mediated effects have been observed in the mudsnail *Hydrobia ulvae* which serves as first intermediate host to a range of trematode species. Field experiments indicated that infected snails indirectly alter the abundance and composition of primary and secondary producers via direct effects of parasite infections on the snails' grazing behaviour (Mouritsen and Haun 2008). Other morphological, physiological or behavioural traits of hosts that are induced by parasites in infected hosts are likely common in mudflat ecosystems but, as in the case of density-mediated indirect effects, the extent and relevance of these indirect effects for mudflat ecosystems have yet to be determined.

3.3 Effects on Food Chains, Food Webs and Ecosystem Energetics

The various impacts of parasites on their hosts can also affect food chains, food webs and ecosystem energetics in mudflat ecosystems (Lafferty et al. 2008). One way of doing so is that parasites can mediate the strength of trophic interactions and thus alter the flow of energy in food chains. For example, trematode infections in periwinkles (*Littorina littorea*) can reduce the grazing activity of infected snails, so that they consume only about 2/3 of the macroalgal biomass compared to uninfected snails, thus altering the interaction strength between primary and secondary consumers (Clausen et al. 2008). Likewise, parasites can also mediate the interaction strength between secondary and tertiary consumers. Periwinkles (*L. littorea*) are often infected with the shell-boring polychaete *Polydora ciliata.* Infected snails have weaker shells caused by the burrowing activity of the worms, and this affects predation of snails by shore crabs (*Carcinus maenas*), a typical predator on mudflats along the North East Atlantic coast. Experiments have revealed that crab predation rates on infected snails are almost five times higher than on uninfected individuals (Buschbaum et al. 2007). Similar effects of increased predation by crabs on *P. ciliata*-infected hosts have also been observed in blue mussels *Mytilus edulis* (Ambariyanto and Seed 1991; Kent 1981). In some cases, such increased predation on infected individuals is associated with increased transmission of parasites to down-stream hosts if the predator serves as a host for the parasite. If the increased predation on infected hosts results from behavioural or other trait changes induced by the parasite, this is often considered to be an adaptive host manipulation by the parasite, as it increases its transmission (Poulin 2010). As parasite manipulation of host behaviour may be common in tropically transmitted parasites such as the ubiquitous trematodes occurring on mudflats, parasites may often alter the interaction strength between predators and infected prey in typical mudflat food chains. However, such parasite—mediated alterations of trophic interactions and energy flows are not well-studied in mudflat ecosystems to date.

Besides mediating trophic interaction strength between predators and their resources in food chains, parasites may also act as a resource themselves (Johnson et al. 2010). One of the ways in which this can occur, is that the many free-living infective stages produced by parasites may be utilised by non-hosts as a resource. In particular, the production of cercarial stages of trematodes is known to be substantial in mudflat ecosystems (Kuris et al. 2008; Thieltges et al. 2008c), and many organisms that do not serve as host for these parasites are known to prey on these stages (Thieltges et al. 2008a, b; Welsh et al. 2014). Studies on parasite-inclusive food webs indicate that this predation on infective stages may be common, as this link type comprises 10–20% of the total number of trophic links in food webs of mudflat ecosystems (Thieltges et al. 2013b). However, whether the consumption of infective stages significantly contributes to the diet of consumers in mudflat ecosystems is largely unknown. Another mechanism through which parasites can become a resource themselves, is when parasites are consumed by a predator together with their host but when the predator is not a suitable host for the co-ingested parasites. This so-called concomitant predation of parasites is not well understood but studies on parasite-inclusive food webs indicate that it may actually be very common, as about 60–70% of the trophic links in food webs of mudflat ecosystems are concomitant predation links (Thieltges et al. 2013b). Besides potentially contributing additional nutritional value to predators in some cases, this type of predation on parasites may also have important consequences for parasite population dynamics (Lafferty et al. 2008). However, the magnitude and relevance of parasites as resources in mudflat food webs remain to be investigated.

Besides affecting predation strength and potentially serving as a resource to predators, parasites can also affect the general structure and topology of entire food webs (Lafferty et al. 2008; Dunne et al. 2013). When parasites are integrated into topological food webs, i.e. food webs that denote the presence or absence of trophic interactions but do not include information on interaction strength or energy flow, they generally increase food web size and the density of trophic interaction links (connectivity; Lafferty et al. 2008; Dunne et al. 2013). Many of these topological changes are probably not unique to parasites, but simply result from the addition of species to the webs (Dunne et al. 2013). However, the predation on parasites by predators discussed above seems to result in unique contributions to food web motifs, i.e. patterns of small interactive units of food webs (Dunne et al. 2013; Cirtwill and Stouffer 2015). However, it is largely unknown whether these changes in food web structure in topological webs, that denote only absence or presence of trophic interactions, also affect energy flows in food webs. The standing stock of some parasite groups can be high in mudflat food webs, e.g. the biomass of trematodes in gastropods equals that of birds in Californian estuaries (Kuris et al.

2008). However, the contribution of parasites to the flow of energy through entire food webs remains to be unravelled.

4 Parasites and Global Change

4.1 Species Invasions

Mudflats face a multitude of challenges in the course of ongoing global changes which also have repercussions for parasites and their hosts in mudflat ecosystems. Among these challenges are biological invasions. In marine ecosystems such as mudflats, species are mainly introduced via ballast water from large ships and by aquaculture practices such as oyster farming (Grosholz 2002; Bax et al. 2003, see also Chap. 14). Many introduced species do not spread much and remain at relatively low population levels, whereas others become invasive, disperse widely and cause considerable impacts on native ecosystems (Grosholz 2002, see also Chap. 11). Parasites can have various roles in the invasion process, and on the impacts of invasive species in mudflats and other marine ecosystems (see Goedknegt et al. 2016 for a recent review). First of all, invasive species are often released from parasite infection pressure in their recipient ecosystems and this may facilitate the establishment and spread of invasive species. Such a release from parasites results from the fact that introduced species often lose all or most of their own native parasites in the course of the introduction, due to various invasion barriers. For example, parasites may not survive the transport stage or do not find suitable intermediate and definitive hosts in the new environment (Torchin et al. 2003; Blakeslee et al. 2013). The resulting low parasite burden may give the invader a competitive benefit over native competitors, and thus facilitate its establishment and spread (Torchin et al. 2003; Blakeslee et al. 2013). However, once arrived in a new environment, invasive species may acquire local native parasite species. This may reduce their initial competitive advantage, but it may also affect native hosts of the parasites if the parasite species' population size is amplified by the invasive species, resulting in greater infection levels in native species (parasite spillback—Kelly et al. 2009). Invasive species may also co-introduce parasites which can affect native host species as well (parasite spillover—Prenter et al. 2004; Kelly et al. 2009). For example, Pacific oysters (*Crassostrea gigas*) that have been introduced to Europe for aquaculture purposes have co-introduced an intestinal parasitic copepod (*Mytilicola orientalis*) which has spilled over to native mussels, cockles and Baltic tellins (Goedknegt et al. 2017) and which has negative effects on host condition (Goedknegt et al. in review).

While such parasite spillover effects have negative effects for native host species, invasive species such as the Pacific oyster can also have positive effects on native hosts, by reducing their infection levels with native parasites. They can do so by the transmission interference mechanisms discussed above. For example, Pacific oysters are very efficient filter feeders, and can remove cercarial stages of trematodes from the water above mudflats (without becoming infected themselves), and thus reduce infection levels in native hosts such as mussels (Thieltges et al. 2009d). Other invasive species can also interfere with parasite transmission on mudflats (Welsh et al. 2014), but our understanding of the full range and magnitude of the effects of invasive species on parasites and their hosts in mudflat ecosystems is still very limited. With the globally increasing number of species introductions to coastal ecosystems, this will be an important future research field.

4.2 CO_2 Double Trouble: Temperature Increase and Ocean Acidification

Other global challenges affecting mudflat ecosystems include the effects of anthropogenic emissions of carbon dioxide (CO_2) which have increased atmospheric CO_2 levels by nearly 40% since the beginning of the industrial revolution (Salomon et al. 2007). The resulting effect on marine ecosystems is twofold: an increase in seawater temperature, and an increase in pH, due to the dissolution of CO_2 in seawater, leading to a phenomenon called ocean acidification (Doney et al. 2009; Orr et al. 2005; Hoegh-Guldberg and Bruno 2010). Based on the strong temperature-dependency of many parasite transmission processes such as in trematodes, a potential increase in infection levels under increasing water temperatures has been suggested (Poulin 2006; Poulin and Mouritsen 2006). For some host species that are sensitive to temperature stress and parasite infections, future temperature increases may thus have strong impacts on host population dynamics. For example, population dynamic modelling of trematode infections in amphipod hosts suggest strong population declines, and even local extinction at future elevated temperatures in mudflat ecosystems in Europe and New Zealand (Mouritsen et al. 2005; Studer et al. 2013a; Fig. 9.6).

However, in other host species increased temperatures may offset negative effects of infections. For example, periwinkles (*Littorina littorea*) show reduced feeding rates when infected with trematodes at normal summer water temperatures (18 °C), but at elevated temperatures that are predicted to occur under climate change (21 °C), feeding rates did not differ between infected and uninfected periwinkles (Larsen and Mouritsen 2009). In other cases, increased temperatures may not lead to elevated infections levels in hosts in the first place as, for example, observed in cockles infected with trematode metacercariae where cercarial emergence is limited during hot days (de Montaudouin et al. 2016). Many trematode species may also exhibit a relatively high acclimation capacity, so that cercarial development, emergence and survival, as well as the survival of miracidia, will not be much influenced by temperature across a rather broad range of optimal temperatures (Morley 2011, 2012; Morley and Lewis 2013, 2015). Hence, the actual effects of climate change on parasites and their hosts will not be universal, but will most likely be parasite- and host-specific.

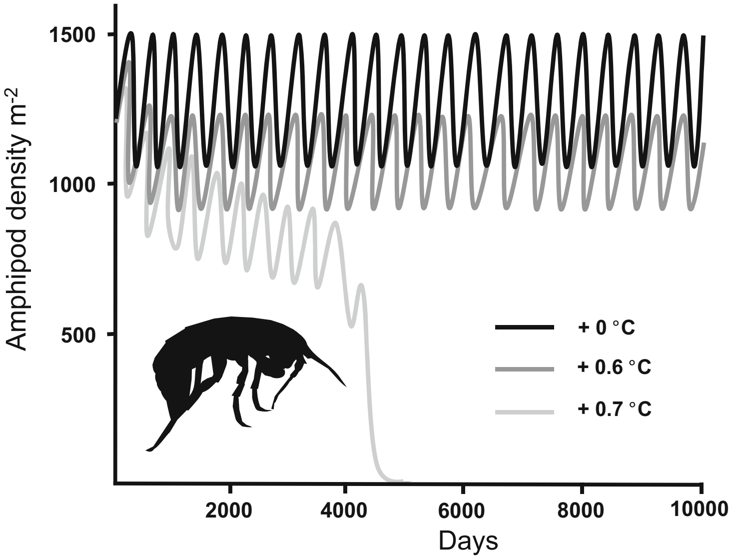


Fig. 9.6 Model simulation output of annual population fluctuations (density m^{-2}) of the amphipod *Paracalliope novizealandiae* infected with the trematode *Maritrema novaezealandensis* under various climate change scenarios: current conditions (+0 °C; black line), an increase in the mean temperature of 0.6 °C (dark grey line), and an increase of 0.7 °C (light grey line). Shown are the simplified population trajectories predicted for the first 10,000 days (≈27 years) of 80-year model runs. Data based on Studer et al. (2013a).

Parasites and hosts will not only be affected by temperature, but also by other environmental stressors, which may result in complex interactions. For example, a multifactorial experiment on the survival of cercariae of the intertidal trematode *Maritrema novaezealandensis* identified significant interactions among temperature, salinity and ultraviolet radiation (Studer and Poulin 2013), suggesting that the effects of future temperature increases on parasite-host interactions on mudflats will most likely be driven by a complex interplay of factors, rather than by simple temperature effects. Similar caveats with respect to predictions of future parasite infection levels on mudflats also apply to the effect of ocean acidification on marine parasites and their hosts. Here, the effects of increased seawater pH on parasites and their hosts also seem to be species-specific, and also interacting with other factors, such as temperature and salinity (Koprivnikar et al. 2010; MacLeod and Poulin 2015, 2016). Hence, more research will be necessary to characterize the complex interplay of major drivers of infection levels, and the resulting impacts on hosts in specific parasite-host interactions, to allow realistic predictions of changes in parasite infection levels under future temperature increases and ocean acidification.

Besides invasive species, temperature increases and ocean acidification, coastal mudflat ecosystems face other human-induced challenges such as habitat degradation, eutrophication and overfishing (see Chaps. 13 and 14). We do not know much about the impact of these various stressors, and more research will be needed to identify and quantify their effects on parasite-host interactions in mudflat ecosystems.

5 Conclusion and Outlook

In this chapter, we have illustrated and explored the many ways in which parasite-host interactions can affect host populations, communities and food webs in mudflat ecosystems, equalling in importance similar effects resulting from other species interactions such as predation and competition. However, although our knowledge of the ecology of parasites in mudflat ecosystems has grown considerably during the last two decades, there are still many aspects that await further investigation, as we have pointed out throughout the chapter. Possibly the greatest challenge preventing the full inclusion of parasites in ecological studies of mudflat ecosystems is, as we also stressed with respect to meiofauna in Chap. 5, the reluctance of marine ecologists to investigate small organisms whose identification and quantification have traditionally required expert taxonomical expertise. However, modern tools can facilitate rigorous studies of parasite diversity and abundance for non-parasitologists. For example, environmental DNA, or eDNA, approaches can allow the detection of parasite species and the estimation of their relative abundance with a non-invasive method based on samples of water or sediment (Bass et al. 2015). Similarly, in the future, the establishment of DNA barcode databases could be used for the quick and easy identification of multiple parasite taxa by non-experts, without the need for detailed morphological examinations (Leung et al. 2009). The rapidly-decreasing costs of gene sequencing should make such new technologies very attractive for future parasite-inclusive studies of mudflat ecosystems.

Acknowledgments We thank Peter Beninger and an anonymous reviewer for constructive comments on our chapter. Dörte Poszig is thanked for providing the drawings.

References

Ambariyanto A, Seed R (1991) The infestation of *Mytilus edulis* Linnaeus by *Polydora ciliata* (Johnston) in the Conwy Estuary, North Wales. J Mollusc Stud 57:413–424

Bass D, Stentiford GD, Littlewood DTJ, Hartikainen H (2015) Diverse applications of environmental DNA methods in parasitology. Trends Parasitol 31:499–513

Bates AE, Leiterer F, Wiedeback ML, Poulin R (2011) Parasitized snails take the heat: a case of host manipulation? Oecologia 167:613–621

Bax N, Williamson A, Aquero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: a threat to global biodiversity. Mar Policy 27:313–323

Berger VJ, Galaktionov KV, Prokofiev VV (2001) Influence of parasites on host adaptations to environmental factors: host-parasite system molluscs-trematode parthenitae. Parazitologiya 35: 192–200

Bick A (1994) *Corophium volutator* (Corophiidae: Amphipoda) as an intermediate host of larval Digenea – an ecological analysis in a coastal region of the southern Baltic. Ophelia 40:27–36

Blakeslee AMH, Fowler AE, Keogh CL (2013) Marine invasion and parasite escape: updates and new perspectives. Adv Mar Biol 66:87–169

Buschbaum C, Buschbaum G, Schrey I, Thieltges DW (2007) Shell-boring polychaetes affect gastropod shell strength and crab predation. Mar Ecol Prog Ser 329:123–130

Cardillo M (1999) Latitude and rates of diversification in birds and butterflies. Proc R Soc B Biol Sci 266:1221–1225

Cirtwill AR, Stouffer DB (2015) Concomitant predation on parasites is highly variable but constrains the ways in which parasites contribute to food-web structure. J Anim Ecol 84:734–744

Clausen KT, Larsen MH, Iversen NK, Mouritsen KN (2008) The influence of trematodes on the macroalgae consumption by the common periwinkle *Littorina littorea*. J Mar Biol Assoc U K 88:1481–1485

Combes C (2001) Parasitism: the ecology and evolution of intimate interactions. The University of Chicago Press, Chicago

de Montaudouin X, Blanchet H, Bazairi H, Nazik A, Desclaux-Marchand C, Bachelet G (2016) Cockle infection by *Himasthla quissetensis* – II. The theoretical effect of climate change. J Sea Res 113:108–114

Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean acidification: the other CO_2 problem. Annu Rev Mar Sci 1:169–192

Dunne JA, Lafferty KD, Dobson AP, Hechinger RF, Kuris AM, Martinez ND, McLaughlin JP, Mouritsen KN, Poulin R, Reise K, Stouffer DB, Thieltges DW, Williams RJ, Zander C-D (2013) Parasites affect food web structure primarily through increased diversity and complexity. PLoS Biol 11:e1001579

Fredensborg BL, Mouritsen KN, Poulin R (2004) Intensity-dependent mortality of *Paracalliope novizealandiae* (Amphipoda: Crustacea) infected by a trematode: experimental infections and field observations. J Exp Mar Biol Ecol 311:253–265

Fredensborg BL, Mouritsen KN, Poulin R (2005) Impact of trematodes on host recruitment, survival and population density in the intertidal gastropod *Zeacumantus subcarinatus*. Mar Ecol Prog Ser 290:109–117

Fredensborg BL, Mouritsen KN, Poulin R (2006) Relating bird host distribution and spatial heterogeneity in trematode infections in an intertidal snail: from small to large scale. Mar Biol 149: 275–283

Galaktionov KV (2017) Patterns and processes influencing helminth parasites of Arctic coastal communities during climate change. J Helminthol 91:38–408

Galaktionov KV, Dobrovolskij AA (2003) The biology and evolution of trematodes: an essay on the biology, morphology, life cycles, transmission, and evolution of digenetic trematodes. Kluwer Academic, Dordrecht

Goedknegt MA, Feis ME, Wegner KM, Luttikhuizen PC, Buschbaum C, Camphuysen KCJ, van der Meer J, Thieltges DW (2016) Parasites and marine invasions: ecological and evolutionary perspectives. J Sea Res 113:11–27

Goedknegt MA, Schuster A-K, Buschbaum GR, Jung AS, Luttikhuizen PC, van der Meer J, Troost K, Wegner KM, Thieltges DW (2017) Spillover but no spillback of two invasive parasitic copepods from invasive Pacific oysters (*Crassostrea gigas*) to native bivalve hosts. Biol Invasions 19:365–379

Groenewold S, Berghahn R, Zander CD (1996) Parasite communities of four fish species in the Wadden Sea and the role of fish discarded by the shrimp fisheries in parasite transmission. Helgländer Meeresun 50:69–85

Grosholz E (2002) Ecological and evolutionary consequences of coastal invasions. Trends Ecol Evol 17:22–27

Gutiérrez JS, Rakhimberdiev E, Piersma T, Thieltges DW (2017) Migration and parasitism: habitat use, not migration distance, influences helminth species richness in Charadriiform birds. J Biogeogr 44:1137–1147

Harland H, MacLeod CD, Poulin R (2015) Non-linear effects of ocean acidification on the transmission of a marine intertidal parasite. Mar Ecol Prog Ser 536:55–64

Harvell D, Altizer S, Cattadori IM, Harrington L, Weil E (2009) Climate change and wildlife diseases: when does the host matter the most? Ecology 90:912–920

Hatcher MJ, Dunn AM (2011) Parasites in ecological communities: from interactions to ecosystems. Cambridge University Press, Cambridge

Hatcher MJ, Dick JT, Dunn AM (2006) How parasites affect interactions between competitors and predators. Ecol Lett 9:1253–1271

Hay KB, Fredensborg BL, Poulin R (2005) Trematode-induced alterations in shell shape of the mud snail *Zeacumantus subcarinatus* (Prosobranchia: Batillariidae). J Mar Biol Assoc U K 85: 989–992

Hechinger RF, Lafferty KD (2005) Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. Proc R Soc B 272:1059–1066

Hechinger RF, Lafferty KD, McLaughlin JP, Fredensborg BL, Huspeni TC, Lorda J, Sandhu PK, Shaw JC, Torchin ME, Whitney KL, Kuris AM (2011) Food webs including parasites, biomass, body sizes, and life stages for three California/Baja California estuaries. Ecology 92:791

Høeg JT (1995) The biology and life cycle of the Rhizocephala (Cirripedia). J Mar Biol Assoc U K 75:517–550

Høeg JT, Lützen J (1995) Life cycle and reproduction in the Cirripedia Rhizocephala. Oceanogr Mar Biol Annu Rev 33:427–485

Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. Science 328:1523–1528

Hopper JV, Poulin R, Thieltges DW (2008) Buffering role of the intertidal anemone *Anthopleura aureoradiata* in cercarial transmission from snails to crabs. J Exp Mar Biol Ecol 367:153–156

Horn MH, Martin KLM, Chotkowski MA (1999) Intertidal fishes: life in two worlds. Academic Press, London

Huxham M, Raffaelli D, Pike A (1993) The influence of *Cryptocotyle lingua* (Digenea: Plathyhelminthes) infections on the survival and fecundity of *Littorina littorea* (Gastropoda: Prosobranchia); an ecological approach. J Exp Mar Biol Ecol 168:223–238

Jensen KT (1993) Density-dependent growth in cockles (*Cerastoderma edule*): evidence from interannual comparisons. J Mar Biol Assoc U K 73:333–342

Jensen KT, Mouritsen KN (1992) Mass mortality in two common soft-bottom invertebrates, *Hydrobia ulvae* and *Corophium volutator* – the possible role of trematodes. Helgoländer Meeresun 46:329–339

Jensen KT, Latama G, Mouritsen KN (1996) The effect of larval trematodes on the survival rates of two species of mud snails (Hydrobiidae) experimentally exposed to desiccation, freezing and anoxia. Helgoländer Meeresun 50:327–335

Jensen T, Jensen KT, Mouritsen KN (1998) The influence of the trematode *Microphallus claviformis* on two congeneric intermediate host species (*Corophium*): infection characteristics and host survival. J Exp Mar Biol Ecol 227:35–48

Johnson PTJ, Thieltges DW (2010) Diversity, decoys and the dilution effect: how ecological communities affect disease risk. J Exp Biol 213:961–970

Johnson PTJ, Dobson A, Lafferty KD, Marcogliese DJ, Memmott J, Orlofske SA, Poulin R, Thieltges DW (2010) When parasites become prey: ecological and epidemiological significance of eating parasites. Trends Ecol Evol 25:362–371

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957

Kaiser MJ, Attrill MJ, Jennings S, Thomas DN, Barnes DKA (2011) Marine ecology: processes, systems, and impacts. Oxford University Press, Oxford

Kamiya T, O'Dwyer K, Nakagawa S, Poulin R (2014) What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. Biol Rev 89:123–134

Kelly DW, Paterson RA, Townsend CR, Poulin R, Tompkins DM (2009) Parasite spillback: a neglected concept in invasion ecology? Ecology 90:2047–2205

Kent RML (1981) The effect of *Polydora ciliata* on the shell strength of *Mytilus edulis*. J Cons Int Explor Mer 39:252–255

Koch W, Boer P, Witte JIJ, van der Veer HW, Thieltges DW (2014) Inventory and comparison of abundance of parasitic copepods on fish hosts in the western Wadden Sea (North Sea) between 1968 and 2010. J Mar Biol Assoc U K 94:547–555

Koehler AV, Poulin R (2010) Host partitioning by parasites in an intertidal crustacean community. J Parasitol 96:862–868

Koprivnikar J, Lim D, Fu C, Brack SHM (2010) Effects of temperature, salinity, and pH on the survival and activity of marine cercariae. Parasitol Res 106:1167–1177

Kuris AM, Hechinger RF, Shaw JC, Whitney KL, Aguirre-Macedo L, Boch CA, Dobson AP, Dunham EJ, Fredensborg BL, Huspeni TC, Lorda J, Mababa L, Mancini FT, Mora AB, Pickering M, Talhouk NL, Torchin ME, Lafferty KD (2008) Ecosystem energetic implications of parasite and free-living biomass in three estuaries. Nature 454:515–518

Lafferty KD (1993) Effect of parasitic castration on growth, reproduction and population dynamics of the marine snail *Cerithidea californica*. Mar Ecol Prog Ser 96:229–237

Lafferty KD, Kuris AM (2002) Trophic strategies, animal diversity and body size. Trends Ecol Evol 17:507–513

Lafferty KD, Porter JW, Ford SE (2004) Are diseases increasing in the ocean? Annu Rev Ecol Evol Syst 35:31–54

Lafferty KD, Allesina S, Arim M, Briggs CJ, De Leo G, Dobson AP, Dunne JA, Johnson PTJ, Kuris AM, Marcogliese DJ, Martinez ND, Memmott J, Marquet PA, McLaughlin JP, Mordecai EA, Pascual M, Poulin R, Thieltges DW (2008) Parasites in food webs: the ultimate missing links. Ecol Lett 11:533–546

Larsen MH, Mouritsen KN (2009) Increasing temperature counteracts the impact of parasitism on periwinkle consumption. Mar Ecol Prog Ser 383:141–149

Larsen MH, Mouritsen KN (2014) Temperature–parasitism synergy alters intertidal soft-bottom community structure. J Exp Mar Biol Ecol 460:109–119

Larsen MH, Jensen KT, Mouritsen KN (2011) Climate influences parasite-mediated competitive release. Parasitology 138:1436–1441

Latham ADM, Poulin R (2002) New records of gastrointestinal helminths from the southern black-backed gull (Larus *dominicanus*) in New Zealand. N Z J Zool 29:253–257

Lauckner G (1980) Diseases of mollusca: gastropoda. In: Kinne O (ed) Diseases of marine animals, General aspects, protozoa to gastropoda, vol I. Wiley, New York, pp 311–424

Lauckner G (1983) Diseases of mollusca: Bivalvia. In: Kinne O (ed) Diseases of marine animals, Introduction, Bivalvia to Scaphopoda, vol 2. Biologische Anstalt Helgoland, Hamburg, pp 477–961

Lei F, Poulin R (2011) Effects of salinity on multiplication and transmission of an intertidal trematode parasite. Mar Biol 158:995–1003

Leung TLF, Donald KM, Keeney DB, Koehler AV, Peoples RC, Poulin R (2009) Trematode parasites of Otago Harbour (New Zealand) soft-sediment intertidal ecosystems: life cycles, ecological roles and DNA barcodes. N Z J Mar Freshw Res 43:857–865

MacLeod CD, Poulin R (2012) Host–parasite interactions: a litmus test for ocean acidification? Trends Parasitol 28:365–369

MacLeod CD, Poulin R (2015) Differential tolerances to ocean acidification by parasites that share the same host. Int J Parasitol 45:485–493

MacLeod CD, Poulin R (2016) Parasitic infection alters the physiological response of a marine gastropod to ocean acidification. Parasitology 143:1397–1408

McCurdy DG, Forbes MR, Boates JS (1999) Testing alternative hypotheses for variation in amphipod behaviour and life history in relation to parasitism. Int J Parasitol 29:1001–1009

McDaniel JS (1969) *Littorina littorea*: lowered heat tolerance due to *Cryptocotyle lingua*. Exp Parasitol 25:13–15

Meissner K, Bick A (1997) Population dynamics and ecoparasitological surveys of *Corophium volutator* in coastal waters in the Bay of Mecklenburg (southern Baltic Sea). Dis Aquat Org 29: 169–179

Meissner K, Bick A (1999) Mortality of *Corophium volutator* (Amphipoda) caused by infestation with *Maritrema subdolum* (Digenea, Microphallidae) ± laboratory studies. Dis Aquat Org 35: 47–52

Melzner F, Thomsen J, Koeve W, Oschlies A, Gutowska MA, Bange HW, Hansen HP, Körtzinger A (2013) Future ocean acidification will be amplified by hypoxia in coastal habitats. Mar Biol 160:1875–1888

Morley NJ (2011) Thermodynamics of cercarial survival and metabolism in a changing climate. Parasitology 138:1442–1452

Morley NJ (2012) Thermodynamics of miracidial survival and metabolism. Parasitology 139: 1640–1651

Morley NJ, Lewis JW (2013) Thermodynamics of cercarial development and emergence in trematodes. Parasitology 140:1211–1224

Morley NJ, Lewis JW (2015) Thermodynamics of trematode infectivity. Parasitology 142:585–597

Mouritsen KN (2002a) The *Hydrobia ulvae-Maritrema subdolum* association: influence of temperature, salinity, light, water-pressure and secondary host exudates on cercarial emergence and longevity. J Helminthol 76:341–347

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

Mouritsen KN, Haun SCB (2008) Community regulation by herbivore parasitism and density: trait-mediated indirect interactions in the intertidal. J Exp Mar Biol Ecol 367:236–246

Mouritsen KN, Jensen KT (1994) The enigma of gigantism: effect of larval trematodes on growth, fecundity, egestion and locomotion in *Hydrobia ulvae* (Pennant) (Gastropoda: Prosobranchia). J Exp Mar Biol Ecol 181:53–66

Mouritsen KN, Jensen KT (1997) Parasite transmission between soft-bottom invertebrates: temperature mediated infection rates and mortality in *Corophium volutator*. Mar Ecol Prog Ser 151: 123–134

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

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

Mouritsen KN, Poulin R (2006) A parasite indirectly impacts both abundance of primary producers and biomass of secondary producers in an intertidal benthic community. J Mar Biol Assoc U K 86:221–226

Mouritsen KN, Mouritsen LT, Jensen KT (1998) Changes of topography and sediment characteristics on an intertidal mud-fat following mass-mortality of the amphipod *Corophium volutator*. J Mar Biol Assoc U K 78:1167–1180

Mouritsen KN, Gorbushin A, Jensen KT (1999) Influence of trematode infections on in situ growth rates of *Littorina littorea*. J Mar Biol Assoc U K 79:425–430

Mouritsen KN, McKechnie S, Meenken E, Toynbee JL, Poulin R (2003) Spatial heterogeneity in parasite loads in the New Zealand cockle: the importance of host condition and density. J Mar Biol Assoc U K 83:307–310

Mouritsen KN, Tompkins DM, Poulin R (2005) Climate warming may cause a parasite-induced collapse in coastal amphipod populations. Oecologia 146:476–483

Mouritsen KN, Poulin R, McLaughlin JP, Thieltges DW (2011) Food web including metazoan parasites for an intertidal ecosystem in New Zealand. Ecological Archives E092–173. Ecology 92:2006

O'Connell-Milne SA, Poulin R, Savage C, Rayment W (2016) Reduced growth, body condition and foot length of the bivalve *Austrovenus stutchburyi* in response to parasite infection. J Exp Mar Biol Ecol 474:23–28

Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, Feely RE, Gnanadesikan A, Gruber N, Ishida A, Joos F, Key RM, Lindsay K, Maier-Reimer E, Matear R, Monfray P, Mouchet A, Najjar RG, Plattner G-K, Rodgers KB, Sabine CL, Sarmiento JL, Schlitzer R, Slater RD, Totterdell IJ, Weirig M-F, Yamanaka Y, Yool A (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681–686

Pechenik JA, Fried B, Simpkins HL (2001) *Crepidula fornicata* is not a first intermediate host for trematodes: who is? J Exp Mar Biol Ecol 261:211–224

Peoples RC (2013) A review of the helminth parasites using polychaetes as hosts. Parasitol Res 112:3409–3421

Peoples RC, Randhawa HS, Poulin R (2012) Parasites of polychaetes and their impact on host survival in Otago Harbour, New Zealand. J Mar Biol Assoc U K 92:449–455

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

Poulin R (2007) Evolutionary ecology of parasites. Princeton University Press, Princeton

Poulin R (2010) Parasite manipulation of host behavior: an update and frequently asked questions. Adv Study Behav 41:151–186

Poulin R, Cribb TH (2002) Trematode life cycles: short is sweet? Trends Parasitol 18:176–183

Poulin R, Mouritsen KN (2003) Large-scale determinants of trematode infections in intertidal gastropods. Mar Ecol Prog Ser 254:187–198

Poulin R, Mouritsen KN (2006) Climate change, parasitism and the structure of intertidal ecosystems. J Helminthol 80:183–191

Prenter J, MacNeil C, Dick JTA, Dunn AM (2004) Roles of parasites in animal invasions. Trends Ecol Evol 19:385–390

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

Raffaelli D, Hawkins SJ (1999) Intertidal ecology. Springer, Berlin

Raffel TR, Martin LB, Rohr JR (2008) Parasites as predators: unifying natural enemy ecology. Trends Ecol Evol 23:610–618

Reise K (1985) Tidal flat ecology. Springer, Berlin

Rhode K (1993) Ecology of marine parasites: an introduction to marine parasitology. CAB International, Wallingford

Rhode K (ed) (2005) Marine parasitology. CSIRO Publishing, Melbourne and Wallingford

Riel A (1975) Effect of trematodes on survival of *Nassarius obsoletus* (Say). Proc Malacol Soc Lond 41:527–528

Schmid-Hempel P (2011) Evolutionary parasitology: the integrated study of infections, immunology, ecology, and genetics. Oxford University Press, Oxford

Seaman B, Briffa M (2015) Parasites and personality in periwinkles (*Littorina littorea*): infection status is associated with mean-level boldness but not repeatability. Behav Process 115:132–134

Shaw DJ, Dobson AP (1995) Patterns of macroparasite abundance and aggregation in wildlife populations: a quantitative review. Parasitology 111:S111–S127

Sokolova IM (1995) Influence of trematodes on the demography of *Littorina saxatilis* (Gastropoda: Prosobranchia: Littorinidae) in the White Sea. Dis Aquat Org 21:91–101

Solomon S, Quinn D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) (2007) Climate change 2007: the physical science basis: contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

Sousa WP, Gleason M (1989) Does parasitic infection compromise host survival under extreme environmental conditions? The case for *Cerithidea californica* (Gastropoda : Prosobranchia). Oecologia 80:456–464

Stier T, Drent J, Thieltges DW (2015) Trematode infections reduce clearance rates and condition in blue mussels Mytilus edulis. Mar Ecol Prog Ser 529:137–144

Studer A, Poulin R (2012) Seasonal dynamics in an intertidal mudflat: the case of a complex trematode life cycle. Mar Ecol Prog Ser 455:79–93

Studer A, Poulin R (2013) Cercarial survival in an intertidal trematode: a multifactorial experiment with temperature, salinity and ultraviolet radiation. Parasitol Res 112:243–249

Studer A, Thieltges DW, Poulin R (2010) Parasites and global warming: the net effect of temperature on an intertidal host-parasite system. Mar Ecol Prog Ser 415:11–22

Studer A, Poulin R, Tompkins DM (2013a) Local effects of a global problem: modelling the risk of parasite-induced mortality in an intertidal trematode-amphipod system. Oecologia 172: 1213–1222

Studer A, Widmann M, Poulin R, Krkošek M (2013b) Large scale patterns of trematode parasitism in a bivalve host: no evidence for a latitudinal gradient in infection levels. Mar Ecol Prog Ser 491:125–135

Tallmark B, Norrgren G (1976) The influence of parasitic trematodes on the ecology of *Nassarius reticulatus* (L.) in Gullmar Fjord (Sweden). Zoon 4:149–154

Thieltges DW (2006a) Parasite induced summer mortality in common cockles *Cerastoderma edule* by the trematode *Gymnophallus choledochus*. Hydrobiologia 559:455–461

Thieltges DW (2006b) Effect of infection by the metacercarial trematode *Renicola roscovita* on growth in intertidal blue mussel *Mytilus edulis*. Mar Ecol Prog Ser 319:129–134

Thieltges DW (2007) Habitat and transmission – effect of tidal level and upstream host density on metacercarial load in an intertidal bivalve. Parasitology 134:599–605

Thieltges DW (2008) Effect of host size and exposure on metacercarial infection levels in the intertidal cockle *Cerastoderma edule*. J Mar Biol Assoc U K 88:613–616

Thieltges DW, Poulin R (2016) Food-web-based comparison of the drivers of helminth parasite species richness in coastal fish and bird definitive hosts. Mar Ecol Prog Ser 545:9–19

Thieltges DW, Reise K (2007) Spatial heterogeneity in parasite infections at different scales in an intertidal bivalve. Oecologia 150:569–581

Thieltges DW, Rick J (2006) Effect of temperature on emergence, survival and infectivity of cercariae of the marine trematode *Renicola roscovita* (Digenea: Renicolidae). Dis Aquat Org 73:63–68

Thieltges DW, Krakau M, Andresen H, Fottner S, Reise K (2006) Macroparasite community in molluscs of a tidal basin in the Wadden Sea. Helgol Mar Res 60:307–316

Thieltges DW, Jensen KT, Poulin R (2008a) The role of biotic factors in the transmission of free-living endohelminth stages. Parasitology 135:407–426

Thieltges DW, Donas-Botto Bordalo M, Hernández C, Prinz K, Jensen KT (2008b) Ambient fauna impairs parasite transmission in a marine parasite-host system. Parasitology 135:1111–1116

Thieltges DW, de Montaudouin X, Fredensborg BL, Jensen KT, Koprivnikar J, Poulin R (2008c) Production of marine trematode cercariae – a potentially overlooked path of energy flow in benthic systems. Mar Ecol Prog Ser 372:147–155

Thieltges DW, Ferguson MAD, Jones CS, Noble LR, Poulin R (2009a) Biogeographical patterns of marine larval trematode parasites in two intermediate snail hosts in Europe. J Biogeogr 36: 1493–1501

Thieltges DW, Fredensborg BL, Poulin R (2009b) Geographical variation in metacercarial infection levels in marine invertebrate hosts–parasite species character versus local factors. Mar Biol 156:983–990

Thieltges DW, Fredensborg BL, Studer A, Poulin R (2009c) Large-scale patterns in trematode richness and infection levels in marine crustacean hosts. Mar Ecol Prog Ser 389:139–147

Thieltges DW, Reise K, Jensen KT (2009d) Invaders interfere with native parasite-host interactions. Biol Invasions 11:1421–1429

Thieltges DW, Saldanha I, Leung TLF, Poulin R (2009e) Contribution of parasites to intra- and inter-site variation in shell morphology of a marine gastropod. J Mar Biol Assoc U K 89: 563–568

Thieltges DW, Reise K, Mouritsen KN, McLaughlin JP, Poulin R (2011) Food web including metazoan parasites for a tidal basin in Germany and Denmark. Ecological Archives E092–172. Ecology 92:2005

Thieltges DW, Engelsma MY, Wendling CC, Wegner KM (2013a) Parasites in the Wadden Sea food web. J Sea Res 82:122–133

Thieltges DW, Amundsen P-A, Hechinger RF, Johnson PTJ, Lafferty KD, Mouritsen KN, Preston DL, Reise K, Zander C-D, Poulin R (2013b) Parasites as prey in aquatic food webs: implications for predator infection and parasite transmission. Oikos 122:1473–1482

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

Thomas F, Poulin R, de Meeus T, Guegan J-F, Renaud F (1999) Parasites and ecosystem engineering: what roles could they play? Oikos 84:167–171

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. Nature 421:628–630

Torchin ME, Miura O, Hechinger RFG (2015) Parasite species richness and intensity of interspecific interactions increase with latitude in two wide-ranging hosts. Ecology 96:3033–3042

Turner JRG, Gatehouse CM, Corey CA (1987) Does solar-energy control organic diversity—butterflies, moths and the British climate. Oikos 48:195–205

Wegeberg AM, Jensen KT (1999) Reduced survivorship of *Himasthla* (Trematoda, Digenea)-infected cockles (*Cerastoderma edule*) exposed to oxygen depletion. J Sea Res 42:325–331

Wegeberg AM, Jensen KT (2003) In situ growth of juvenile cockles, *Cerastoderma edule*, experimentally infected with larval trematodes (*Himasthla interrupta*). J Sea Res 50:37–43

Welsh JE, van der Meer J, Brussaard CPD, Thieltges DW (2014) Inventory of organisms interfering with transmission of a marine trematode. J Mar Biol Assoc U K 94:697–702

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annu Rev Ecol Evol Syst 34:273–309

Wilson WH (1991) Competition and predation in marine soft-sediment communities. Annu Rev Ecol Syst 21:221–241

Zander CD, Josten N, Detloff KC, Poulin R, McLaughlin JP, Thieltges DW (2011) Food web including metazoan parasites for a brackish shallow water ecosystem in Germany and Denmark. Ecological Archives E092–174. Ecology 92:2007