Parasites and marine invasions: ecological and evolutionary perspectives

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Abstract

Worldwide, marine and coastal ecosystems are heavily invaded by introduced species and the potential role of parasites in the success and impact of marine invasions has been increasingly recognized. In this review, we link recent theoretical developments in invasion ecology with empirical studies from marine ecosystems in order to provide a conceptual framework for studying the role of parasites and their hosts in marine invasions. Based on an extensive literature search, we identified six mechanisms in which invaders directly or indirectly affect parasite and host populations and communities: I) invaders can lose some or all of their parasites during the invasion process (parasite release or reduction), often causing a competitive advantage over native species; II) invaders can also act as a host for native parasites, which may indirectly amplify the parasite load of native hosts (parasite spillback); III) invaders can also be parasites themselves and be introduced without needing co-introduction of the host (introduction of free-living infective stages); IV) alternatively, parasites may be introduced together with their hosts (parasite co-introduction with host); V) consequently, these co-introduced parasites can sometimes also infest native hosts (parasite spillover); and VI) invasive species may be neither a host nor a parasite, but nevertheless affect native parasite host interactions by interfering with parasite transmission (transmission interference). We discuss the ecological and evolutionary implications of each of these mechanisms and generally note several substantial effects on natural communities and ecosystems via i) mass mortalities of native populations creating strong selection gradients, ii) indirect changes in species interactions within communities and iii) trophic cascading and knock-on effects in food webs that may affect ecosystem function and services. Our review demonstrates a wide range of ecological and evolutionary implications of

marine invasions for parasite-host interactions and suggests that parasite-mediated impacts should be integrated in assessing the risks and consequences of biological invasions.

Keywords:

Enemy release; co-evolution; emerging disease; co-introduction; trait-mediated indirect effects; density-mediated indirect effects

1. Introduction

The increase in marine aquaculture activities and global shipping during the last decades has resulted in the worldwide distribution of a multitude of invasive species (Bax et al., 2003). As a result, marine coastal systems are among the most heavily invaded ecosystems of the world (Grosholz, 2002). A potential role of parasites in the success and impact of marine invasions has been recognized and gained mainly attention in the form of the enemy release hypothesis, which refers to a loss of parasites in the invasion process, leading to potential competitive advantages for invasive species (see reviews by Blakeslee et al., 2013; Torchin et al., 2002). However, recent empirical studies and new conceptual frameworks beyond the marine realm have identified various additional ways of how parasites and their hosts can be involved in species invasions (e.g. Dunn, 2009; Tompkins et al., 2011). Here we review these recent theoretical developments in invasion ecology and link them with empirical studies from marine ecosystems in order to provide a conceptual framework for studying the role of parasites and their hosts in marine invasions.

We firstly summarize the different ways in which marine invaders directly or indirectly affect parasite and host populations and communities (section 2). Then we explain each mechanism, its direct ecological effects on the host and indirect effects on the surrounding community in more detail, including mechanisms where invasive species act as host (section 3.1 and 3.2), mechanisms in which parasites are introduced (section 3.3 - 3.5) and a mechanism where invaders are neither parasite or host, but nevertheless affect parasite-host interactions (section 3.6). We do so based on an extensive literature search using Google Scholar and Web of Science with the key words parasit*, parasit* AND spill*, invas* AND parasit*, parasit* AND "dilution effect", introduce* AND parasit*, "enemy release". To this initial literature database,

we added further studies by searching reference lists of publications and our own literature collections. This resulted in a comprehensive and up to date (December 2014) database of our current knowledge on parasites and marine invasions. In section 4, we discuss the evolutionary implications of all six ecological mechanisms highlighted in section 3. Finally, we provide a summary and outlook for future studies on ecological and evolutionary perspectives of parasites and marine invasions in section 5.

Throughout this review we use the term *parasite* for an organism that is living in or on another organism (the host), feeding on it and causing some degree of harm (*sensu* Poulin, 2006) and thereby refer to all microparasites, macroparasites and pathogens. In addition, we will use the term *introduction* when an organism is directly or indirectly moved by human activities beyond the limits of its native geographical range into an area in which it does not naturally occur (Falk-Petersen, 2006). Such introduced organisms we will call introduced or invasive species (*sensu* Blackburn et al., 2011; Lymbery et al., 2014) as most introduced hosts or parasites reported in the literature are in the state of spreading in invaded ecosystems.

2. Six mechanisms by which marine invaders affect parasite-host interactions

There are at least six mechanisms by which invaders directly or indirectly affect interactions between invasive and native parasite and host populations and communities. They differ in the invasive/native status of the host and/or the parasite and in their respective ecological implications (Fig. 1): I) the competitive ability of invasive species relative to native species in invaded ecosystems may be increased if an invasive species loses (some of) its native parasites in the process of introduction (*parasite release* or *parasite reduction*; Colautti et al., 2004; Keane and Crawley, 2002; Torchin, 2001, 2003; Torchin and Mitchell, 2004); II) invasive

species can act as a competent host for native parasites (*parasite acquisition*; Tompkins et al., 2011), thereby increasing host diversity and amplifying transmission dynamics of native parasite populations that can ultimately lead to increased infection levels in native hosts (*parasite spillback*; Kelly et al., 2009); III) invasive parasites can be introduced into a new habitat via a vector (e.g. ballast water, Ruiz et al., 2000) and infect native hosts, without needing the co-introduction of an invasive host species (*introduction of free-living infective stages*); and IV) invasive parasites can be introduced together with the introduction of a host and only infect the invasive host in the introduced range (*parasite co-introduction with host*), potentially giving native species a potential competitive advantage relative to the invader in the invaded range (Daszak et al., 2000; Taraschewski, 2006); V) invasive parasites can be co-introduced with their invasive host and spill over to naive native species (*parasite spillover*; Prenter et al., 2004; Kelly et al., 2009), potentially causing deleterious infections (*emerging disease*); VI) invasive species may be neither a host nor a parasite but can nevertheless potentially reduce the parasite burden in a system if an invader interferes with parasite transmission between native hosts (*parasite transmission interference*), e.g. by preying on free-living infective stages of parasites (Johnson et al., 2010).

It is important to realize that these six mechanisms are not mutually exclusive for a single invasive parasite or host species, but can act synergistically during an invasion process. For example, an invading host may be released from one species of parasite (parasite release), but at the same time co-introduce an invasive parasite (parasite co-introduction with host) that spills over to native species (parasite spillover).

3. Ecological implications

There are varying amount of empirical data supporting each of the six mechanisms. This includes mechanisms where invasive species act as host (sections 3.1, 3.2), mechanisms in which parasites are introduced (sections 3.3 – 3.5) and a mechanism where invaders are neither parasite nor host, but nevertheless affect local parasite-host dynamics (section 3.6).

3.1 Parasite release or reduction

When an invasive host species is introduced to a new ecosystem, it often leaves all or some of its co-evolved parasites behind in its native range (Fig. 1, *parasite release or reduction*), because introduced species must overcome barriers to introduction, establishment and spread before they become invasive (Colautti et al., 2004; Kolar and Lodge, 2011). Such barriers also act on parasites - either before, during or after the translocation phase. First, native parasites of introduced hosts are likely to be lost before or during translocation, because many introduced species arrive as larvae in the new environment and are therefore free of parasite species infecting juvenile or adult stages (Lafferty and Kuris, 1996; Torchin et al., 2002, but see Arzul et al., 2011). Moreover, parasites and/or infected hosts might die during transportation, reducing the likelihood of establishment. In addition, introduced aquaculture organisms can be treated with an anti-parasite treatment (e.g., copper sulphate to eliminate monogeneans of fish, Vignon et al., 2009a) before translocation to the new environments (Mitchell and Power, 2003) and translocations of stocks usually select only healthy individuals, reducing the possibility of translocating parasites (Colautti et al., 2004). Second, once infected hosts are translocated, their parasites may not find suitable hosts or vectors to complete their life cycle in the new environment (Blakeslee et al., 2013; Torchin et al., 2001) or the co-introduced parasites might suffer from local environmental conditions or predators (e.g., cleaner fish; Hatcher et al., 2012,

Vignon et al., 2009a). Finally, due to the mechanisms above, the propagule pressure (i.e., the number of individuals introduced into a new environment) of any surviving hosts and/or parasites after the translocation phase may be very low, resulting in a too low density for the introduced parasite to establish (Torchin et al., 2001; Hatcher et al., 2012).

Although host species may arrive without parasites or with a reduced parasite set in their new environments, they may also acquire native parasites in the introduced range, which ultimately determines the total parasite load of an invasive species (Fig. 1; Colautti et al., 2004). To successfully infect an invasive host, a native parasite must first encounter its new host species (encounter filter) and overcome any host barriers like the immune system (compatibility filter; *sensu* Combes, 2001). Host competence can vary greatly among host species and is often the result of co-adaptation over longer evolutionary time scales (Telfer and Brown, 2012). The lack of a co-evolutionary history may often render invasive species non-competent hosts and thus acquisition of native parasite species may not take place. For example, the invasive manila clam (*Ruditapes phillipinarum*) could not be artificially infected with the native trematode *Himastla elongata*, while in the native common cockle (*Cerastoderma edule*) infection success was high (Dang et al., 2011). Free-living infective stages of the parasite were not able to infiltrate the epithelium of the invasive bivalve and thereby the low infections in the lab and the field resulted from a host (tissue) barrier (Dang et al., 2011).

For marine and coastal ecosystems a recent review has shown that parasite release or reduction in invasive hosts is common (Blakeslee et al., 2013). Additionally, Torchin et al. (2002) showed that parasite richness (number of species) and prevalence (proportion of hosts infected) of invasive species are, on average, two to three times larger in the native than in the introduced range. The study of Blakeslee et al. (2013) revealed that most hosts generally show >

50% parasite reduction across parasite groups, but this depended on the parasite taxa. For example, Rhizocephala (Crustacea) were almost always lost while for other groups (e.g., Cestoda and Turbellaria) escape or reduction rates were lower (Blakeslee et al., 2013).

The level of parasite release or reduction may decrease with increasing residence time of invasive species in their new environments because they may acquire more and more native parasites over time (Colautti et al., 2004; Torchin and Lafferty, 2009). For example, the number of parasite species found in invasive populations of the common shore crab (*Carcinus maenas*) is positively correlated with the time since its introduction (Torchin and Lafferty, 2009). The same pattern was found in the swimming crab *Chrarybdis longicollis*, which was introduced in the Mediterranean in the 1950's (Innocenti and Galil, 2007; Innocenti et al., 2009). Here the crab was first released from its parasites, but in 1992 a native castrating parasite, the rhizocephalan *Heterosaccus dollfusi*, reached high prevalences (Innocenti et al., 2009). However, for other marine hosts the evidence for an increase in parasites with time since introduction is generally weak (Blakeslee et al., 2013).

A parasite reduction during an invasion process may lead to a competitive advantage for invasive species over native species (Keane and Crawley, 2002; Torchin et al., 2001, 2003; Mitchell and Power, 2003; Torchin and Mitchell, 2004). This is the case when the invasive host is negatively affected by its parasites in the native region so that a loss or reduction of parasite loads in the new area results in a direct fitness increase of the host population (regulatory release; Colautti et al., 2004). Additionally, the loss of parasites may release resources otherwise invested in parasite defence mechanisms (e.g. immune system), which may result in an increase in condition and reproduction rate (compensatory release; Colautti et al., 2004). It is important to note that both pathways are not mutually exclusive, but act on different time scales: regulatory

release is a more immediate effect, requiring plasticity of the host, while compensatory release will act on evolutionary time scales (Colautti et al., 2004; Dunn et al., 2009). Nevertheless, both individual pathways are theoretically expected to lead to fitness benefits and a competitive advantage for the invasive host (Keane and Crawley, 2002; Torchin et al., 2001, 2003; Mitchell and Power, 2003; Torchin and Mitchell, 2004).

Although many studies found evidence for parasite release or reduction in marine ecosystems by using a comparative approach comparing infection levels (see reviews Blakeslee et al., 2013; Torchin et al., 2002), only very few studies have actually used experiments to test whether the observed release or reduction actually leads to fitness differences between invasive and native hosts (Table 1). One of the few existing experimental studies was conducted in South Africa, where the invasive mussel *Mytilus galloprovincialis* is released from its parasites and is gradually outcompeting the native mussel *Perna perna* which is naturally infected with two trematode species (Calvo-Ugarteburu and McQuaid, 1998a, b). Experiments showed that these parasites negatively affect growth (trematode metacercariae which only infect juvenile stages of the mussel) or reproduction (bucephalid sporocysts which castrate the bigger mussels) in *P. perna* (Calvo-Ugarteburu and McQuaid, 1998b). *M. galloprovincialis*, by contrast, becomes not infected by either parasite and has lost its native parasites due to parasite release and this may be the reason for its high invasion success (Calvo-Ugarteburu and McQuaid, 1998b). Similar conclusions have been drawn for the invasive gastropod *Cyclope neritea* in Arcachon Bay in France and the Asian horn snail (*Batillaria attramentaria* (= *cumingi*)) at the Pacific coast of North America. Both species are infected with considerably fewer parasites than their native competitors (Bachelet et al., 2004; Torchin et al., 2005). *Cyclope neritea* outcompetes the native gastropod *Nassarius reticulatus* as it is more active and, therefore, shows a higher effectiveness

in utilizing resources, especially in still water conditions (Bachelet et al., 2004). Similarly, in comparison to the native California horn snail *Cerithidea californica*, the invasive Asian horn snail is more efficient in turning resources into growth (Byers, 2000).

To conclude, while parasite release or reduction have been widely reported in marine invading hosts, the number of studies experimentally investigating the ecological implications is limited. In particular, more studies are needed to investigate the actual competitive advantage of a parasite release or reduction for invasive species.

3.2 Parasite spillback

Invasive species can acquire native parasites in the introduced region, which may reduce the net effect of parasite release or reduction for the invasive host (see above). It may also amplify the transmission dynamics of native parasites, resulting in increased infection levels in native hosts (Fig. 1, *parasite spillback*). Whether an invasive host species accumulates native parasites is strongly influenced by its host competency (Kelly et al., 2009; Poulin et al., 2011). Utilizing new hosts will increase the basic reproduction number (R_0) of the parasite and thus the mean number of expected new infections caused by a single infected host (Telfer and Brown, 2012). When the invasive host is entirely unsuitable, the basic reproduction number of the parasite is zero ($R_0 = 0$) and the invasive species will act as a sink for parasites (Telfer and Brown, 2012). This happens when the parasites try to infect the new hosts but fail or if the invader interferes with the transmission otherwise (e.g. by preying on free-living infective stages of parasites) and it may ultimately reduce disease risk for native species (Telfer and Brown, 2012; see also section 3.6.). In contrast, when an invasive host is competent, the parasite generates more than one secondary case of infection (i.e. $R_0 > 1$), thereby amplifying the total

parasite population (Telfer and Brown, 2012). As a result of this amplification in the invasive hosts, the parasite may spill back to native hosts and thereby infection rates of native species increase (Kelly et al., 2009; Poulin et al., 2011). Hence, a parasite spillback effect occurs under the following conditions: 1) the invasive host species must acquire native parasites, 2) the invasive species must be a competent host for the parasites and amplify the parasite population ($R_0 > 1$), and 3) the native parasite must spill back from the invasive to native host species (Kelly et al., 2009).

Kelly et al. (2009) reviewed a potential spillback effect in 40 studies in terrestrial, freshwater and marine systems. They found that 70% of invasive host species acquired more than three native parasites, with 21% acquiring more than ten native parasites. The majority of native macroparasites acquired by the invasive hosts (38 out of 40) are generalist parasites (Kelly et al., 2009). Given the small sample size of marine species in the Kelly et al. (2009) study (only six out of 40), we conducted an updated literature review and found a total of 13 reported cases of marine invasive host species that are known to have acquired native parasites (Table 2). These consist of fish (seven), crustacean (three) and bivalve (three) host species. On average, invasive marine hosts acquired 3.2 (range 1-7) native parasite species, which is much lower than the mean of 6.3 (range 1-16) for all invaders reported by Kelly et al. (2009) and the overall average of 4.9 (range 1-15) for freshwater fish (Poulin et al., 2011). The reasons for the lower number of parasite species spilling back in marine hosts compared to freshwater and terrestrial hosts are unknown, but may be related to the open and three-dimensional nature of marine systems which may decrease contact rates between invaders and native parasites. The majority of acquired parasite taxa in marine hosts were native trematodes (29%) and cestodes (17%) (Table 2, Fig. 2a).

While the majority of the studies in Table 2 report on parasite acquisition (step 1 of the parasite spillback), there is little conclusive evidence for parasite amplification and/or spillback to native species (steps 2 and 3 of parasite spillback) from marine systems. We found only a single published study (Hershberger et al., 2010) that reports parasite amplification between the native marine protist *Ichtyophonus sp*. and the introduced American shad. After the introduction of the shad to the North American Pacific coast, the anadromous fish migrated from rivers to marine and coastal areas to feed, exposing increasing numbers of populations to the endemic protist *Ichtyophonus sp*.. Consequently, with the anadromous behaviour of its host, the parasite was transported into the Columbia River system, where it infected the native spring Chinook salmon (*Oncorhynchus tshawytscha*). Up to now, an efficient freshwater life cycle has not been established, but the authors suggest high potential for parasite spillback, because of low parasite-host specificity and previous establishments of *Ichtyophonus sp*. in freshwater systems (Hershberger et al., 2010).

The spillback effect can have several ecological implications for both native and invasive host species. For example, invasive and native species that do not directly compete for resources may still indirectly interact via a shared parasite, which is a form of apparent competition (Holt and Pickering, 1985). This can lead to exclusion of one of the two species, but also to co-existence, if, for example, the dominant competitor is more strongly affected by the parasite than the competitively inferior host (Hatcher et al., 2012). Such a scenario was investigated by Torchin et al. (1996), who studied the effect of a native nemertean egg predator on a native crab and its new invasive host, the common shore crab *Carcinus maenas*. Half a year after its introduction, the prevalence in the invader went from 11% to 98% versus the 74% to 79% in the native host, the yellow shore crab *Hemigrapsus oregonensis*, showing that the invasive common

shore crab is a competent host for the native parasite. However, in vitro egg predation rates of the nemertean of both invasive and native hosts were similar, suggesting little potential for apparent competition (Torchin et al., 1996). In addition to apparent competition, native parasites may also mediate the outcome of interactions between native and invasive host species through their effects on host behaviour or other traits (indirect trait-mediated effects; Dunn et al., 2012; Hatcher et al., 2006; Werner and Peacor, 1993). An example for this has been reported for native cestodes that modify the appearance, behaviour and fecundity of native species of brine shrimp (*Artemia spp.*; Amat et al., 1991; Sánchez et al., 2012; Thiéry et al., 1990), but not of the invasive brine shrimp *Artemia franciscana* in hypersaline wetlands of Portugal and Spain (Georgiev et al., 2014; Sánchez et al., 2012). Native cestodes colour the native brine shrimps bright red, induce positive phototaxis and increase surface time which makes the shrimps more visible for birds, the definitive host of the parasites (Georgiev et al., 2007; Sánchez et al., 2012). The prevalence of native cestodes is much higher in the native (47-89%) than in the invasive host (2-24%) and there is no evidence that the native cestodes are able to modify the behaviour of the invasive host (Georgiev et al., 2007). Therefore, differential parasite-mediated changes in behaviour in the native and the invasive hosts may underlie the observed replacement of the native populations of *Artemia spp.* by the invasive species *A. franciscana* (Georgiev et al., 2014).

The existing examples of acquisition of native parasites by invasive hosts indicate that spillback effects may exist in marine systems and that they could affect a range of interactions between native and invasive hosts. However, given the very limited number of existing studies on the actual magnitude of parasite spillback to native hosts, more research is needed to evaluate the relevance of spillback effects in marine invasions.

3.3 Introduction of free-living infective stages of parasites

Invaders cannot only affect native parasite-host interactions by serving as a host, but can also be invasive parasites themselves without needing the introduction of a host (Fig. 1, *introduction of free-living infective stages*). The introduction of free-living infective stages of especially microparasites is relatively common in marine ecosystems, with ship ballast water being a key vector (Carlton and Geller, 1993). However, not only the ballast water itself, but also the surfaces of the ballast water tanks can become covered with biofilms, organic matrices that can contain all sorts of microorganisms including pathogenic forms (Drake et al., 2005). In addition, sediment and water residuals in ballast water tanks can contain an assortment of bacteria and viruses (Drake et al., 2005, 2007). However, the majority of microorganisms is transported by ballast water, followed by sediment, water residuals and biofilms (Drake et al., 2007). Although introductions of marine microparasites with ballast water seem likely, only a relatively small number of studies has investigated the risk of introducing free-living bacteria and viruses with ballast water (Table 3). Many of these studies have quantified the abundance of infective stages in ballast water tanks and suggest a relatively high propagule pressure in many cases. For example, Drake et al. (2007) estimated an introduction in the order of 10^{20} microorganisms (3.9×10^{18} bacteria and 6.8×10^{19} viruses) in the Chesapeake Bay per year. In addition to microparasites, also life cycle stages of macroparasites may be found in ballast water tanks. For example, free-living stages of the parasitic isopod *Orthione griffenis* have been found in ballast water in North America, surviving a trip of 11-21 days from Japan (Carlton and Geller, 1993) and Chapman et al. (2012) suggested that ballast water traffic is the vector of introduction of *O. griffenis.*

The introduction of free-living infective stages of parasites can lead to *emerging diseases*, a term used for a disease that appears for the first time in a host population, or a previously existing disease that suddenly increases in incidence or geographic range, or that manifests itself in a new way (Daszak et al., 2000). Due to the lack of co-evolutionary history of native host and invasive parasites, native naive host species may be particularly vulnerable to invasive parasites, resulting in negative effects on native host species, communities and even ecosystems. For example, the collapse of the native mud-shrimp *Upogebia pugettensis* on the west coast of North America (Dumbauld et al., 2011) with major consequences for the ecosystem such as food reduction for fish (Chapman et al., 2012) has been attributed to the introduction of the parasitic isopod *Orthione griffenis* with ballast water as discussed above. Ballast water can also be a vector for human pathogenic microorganisms and epidemic outbreaks (McCarthy and Khambaty, 1994). For example, in January 1991, a human cholera epidemic caused by *Vibrio cholerae* O1 was reported in Peru and rapidly spread to other countries in South America (DePaola, 1992; McCarthy et al., 1992). Half a year later, a similar strain of *V. cholerae* O1 was recovered from oysters and fish collected in Alabama (North America; DePaola, 1992), which turned out to have been transported via ballast water from South America (McCarthy et al., 1992).

To summarize, free-living infective stages of parasites are found in ballast water but to what extent these parasites are introduced and become invasive in new ecosystems is largely unknown. In addition, our knowledge about the impacts of introduction of free-living infective stages of parasites on native communities is very limited and more studies in this direction are needed.

3.4 Parasite co-introduction with host

Besides becoming introduced as free-living infective stages, parasites can also be co-introduced with an invasive host species (Lymbery et al., 2014). In some cases, the co-introduced parasites establish and spread with their invasive host, but do not infect other native species (Fig. 1, *parasite co-introduction with host*). In our literature survey, we found 48 cases of marine parasites reported to have been co-introduced with their invasive host (Tables 4 and 5). However, only a few of these parasites (n = 13, Table 4) have been documented to only use the invasive host species and no native host species in the introduced region (i.e. no spillover has occurred, see section 3.5). This low number can at least partly result from uncertainties on the status of many invasive host (Carlton, 1996) and parasite (Gaither et al., 2013) species, because it is often not known whether they are introduced or not. This makes it often difficult to assess whether a parasite species is native, co-introduced or has already spilled over (see section 3.5). Identifying the native range of cryptogenic parasites (parasites whose origin is unknown) is especially challenging as their taxonomy is poorly resolved and fossil and historical records are scarce (Vignon and Sasal, 2010). However, the cryptogenic status of parasites can be determined by combining population genetics, phylogeography and ecological survey data (Blakeslee et al., 2008; Gaither et al., 2013). For example, by using this multidisciplinary approach, Gaither et al., (2013) confirmed the invasive status of the nematode *Spirocamallanus istiblenni* in the Hawaiian archipelago where it was introduced with Bluestripe snappers (*Lutjanus kasmira*) from French Polynesia and now spills over to native hosts (Gaither et al., 2013).

Examples of co-introductions (without spillover) in marine ecosystems do, however, exist. For example, two snapper species (*Lutjanus spp.*) that were translocated from French Polynesia to the Hawaiian Islands in the 1950's to enhance local fisheries (Vignon et al., 2009a; Vignon and Sasal 2010) have co-introduced six monogenean species that have not (yet) infected native

hosts (Vignon et al, 2009a). Another example is the invasive Japanese mud snail, *Batillaria attramentaria* (=*cumingi*) that co-introduced the trematode *Cercaria batillariae* to the Pacific coast of North America. Torchin et al. (2005) compared the trematode diversity and prevalence of the invasive with the native mud snail *Cerithidea californica* and found that the invader was only infected with its co-introduced parasite, while the native mud snail was infected by ten native trematode species. While the parasite was using its introduced obligate host for the first part of the life cycle, it could still complete its life cycle in the introduced range via trophic transmission to native second intermediate and definitive hosts for which the relationship between host and parasite is less specific (Torchin et al., 2005).

Co-introductions are also likely to occur via frequent shellfish aquaculture translocations. The European flat oyster (*Ostrea edulis*) is a good example that shows how increasing shellfish trade between Europe and North America led to the extended spread of the infamous shellfish disease bonamiasis caused by the haplosporidian protist *Bonamia ostreae* (Chew, 1990). In the 1950s, healthy oyster stocks were introduced from the Netherlands and the UK to the Atlantic coast of North America (Balouet et al., 1983). As the population became established, the growing shellfish trade on the west coast of the USA triggered introductions of seed and adult oysters from the east coast to the Californian hatcheries. Presumably on the Pacific coast of North America, the oysters became infected with the blood cell parasite before being transported to France (Elston et al., 1986), introducing *Bonamia* to Europe, where it rapidly developed into an emerging infectious disease, killing large quantities of European flat oysters (Culloty et al., 1999). In Europe, the parasite did not spill over to native bivalves and these species could also not experimentally be infected, indicating that these species are not responsible for the spread of the disease in Europe (Culloty et al., 1999).

The example of bonamiasis shows that co-introductions of parasites without a spillover to native hosts may have important ecological implications, for example in the form of strong regulative effects on the population dynamics of the invader. Parasite co-introductions may also affect competitive interactions between native and invasive hosts. This will depend on the harmfulness (virulence) of the parasite that is co-introduced as this determines whether an invasive host will have a reduced fitness when infected. Also the infection levels of the native species with native parasites and the relative infection intensity and virulence of both invasive and native parasites in invasive and native hosts will determine the degree of competition and resulting impacts on native communities and ecosystems. However, these complex ecological implications of parasite co-introductions have not been studied.

In conclusion, while co-introductions of parasites without a spillover to native hosts are known to occur, in particular in the course of fishery and aquaculture activities, our knowledge on the ecological effects of such introductions for both invasive populations and native communities is very poor.

3.5 Co-introductions of parasites and spillover to native hosts

Besides infecting their original hosts, co-introduced parasites can also spill over to naive native species (Fig. 1, *parasite spillover*; Prenter et al., 2004; Kelly et al., 2009). To spill over, co-introduced parasites have to encounter a competent host to make a potential host switch to native species. Spillover events often lead to emerging diseases in native hosts (Daszak et al., 2000). From the known 35 co-introduced marine parasite species that have been reported to spill over to native host species (Table 5), 37% of the species are microparasites and 63% are macroparasites, originating from 14 different parasite taxa (Table 5; Fig. 2b). From the invasive

macroparasites, the Monogenea (20%) and Copepoda (17 %) where the most dominant taxa (Table 5; Fig. 2b). The majority of the parasite species (26) has a direct life cycle (Table 5), which makes invasion more likely, as these parasites do not depend on the presence of all hosts of their lifecycle to become established (Elsner et al., 2011). However, also parasites with indirect life cycles (9) succeed to infect native host species. These parasites manage to establish new life cycles in the introduced region in which they make use of co-introduced invasive hosts, but also new suitable native host species. For example, the acanthocephalan *Paratenuisentis ambiguus* was co-introduced with its crustacean intermediate host (*Gammarus tigrinus*) that was introduced to replenish depleted stocks of native gammarids in a river system in Europe (Taraschewski et al., 1987). Via the introduced intermediate host, the parasite infected the native European eel (*Anguilla anguilla*) that served as the definitive host of the parasite in the new region. Hence, this introduced host does not only serve as a source of infection, but also has a role in the newly established life cycle of the parasite and without this double role of the host, the parasite most likely would not have become established.

Looking at the introduction vector of the invasive parasites mentioned in Table 5 in more detail, most parasites were introduced with fish hosts (54%), followed by molluscs (34%: bivalves 23%, gastropods 11%) and crustaceans (11%) and, after spillover events, these host taxa were also the most infected in invaded habitats (fish 63%, molluscs 29%, crustaceans 6%). This pattern is probably related to the frequency of host introductions via aquaculture or fishing practices (80% of the host introductions; Table 5), such as re-stocking of wild populations, the moving of life organisms for aquaculture, life bait and human consumption. Because of these human-aided introductions, parasite spillover can affect both hosts in the wild and hosts in aquaculture settings (Dunn et al., 2009). For example, some aquaculture practices like net pen

farming facilitate the exchange of parasites between cultured and wild animal populations without direct contact between hosts (Kent, 2000). In general, parasite species were established via multiple introductions of one or multiple host species originating from similar or different taxa, but the total number of invasive hosts that co-introduced a parasite species never exceeded two (Table 5; Fig. 3). The number of native hosts infected per spillover event, in contrast, was higher: in some cases more than ten different native host species were infected by an introduced parasite species (Table 5; Fig. 3). A good example is the eel nematode *Anguillicola crassus* that has infected seven different eel species on four different continents via the global eel trade, causing severe damage to the swim bladder of the eels, which resulted in significant mortality in most eel species (Barse et al., 2001; Køie, 1991; Kvach and Skóra, 2007; Sasal et al., 2008).

Direct impacts on native species as a result of spillover events are frequently observed and often referred to as emerging diseases. One of the most frequently documented effects of spillover is mortality of native hosts, a direct impact of at least 15 parasites species on our list (Table 5). For example, the monogenean *Nitzschia sturionis* was co-introduced with the starry sturgeon (*Acipenser stellatus*) from the Caspian Sea to the Aral Sea and caused severe mass mortalities of the native bastard sturgeon (*Acipenser nudiventris*) in 1935-1936 and 1970. The parasite infected the gills of the fish, causing the fish to die on the beaches (Dogiel and Lutta, 1937 in Bauer, 2002). For more about disease related mass mortalities among natural populations of a variety of taxa in marine systems, see the reviews of Harvell et al. (1999) and Fey et al. (2015). Other parasite species that have spilled over have more subtle direct effects, such as impacting the health and fitness of the host, for instance by castrating the host (Farrapeira et al., 2008; Torchin et al., 2005), causing reductions in growth (Chew, 1990; Culver and Kuris, 2004) or damaging important tissues (Balseiro et al., 2006; Køie, 1991; Morozińska-Gogol, 2009). In

addition, infections can weaken the immune system, which can lead to secondary infections by parasites (Lahvis et al., 1995).

Introduced parasites that have spilled over to native hosts also exert indirect impacts on the native host community via density-mediated effects and can thereby determine co-existence outcomes for competing species (Hatcher et al., 2006; Dunn et al., 2012). For instance, the smooth cordgrass (*Spartina alterniflora*) originating from North America was intentionally introduced to the Yangtze River estuary of China to promote sediment accretion on the tidal flats. As a result, the fungus *Fusarium palustre* was co-introduced, spilled over to and caused die-off of native reed (*Phragmites australis*). In this system, the invasive plant acted as the source of infection and as a reservoir by maintaining the parasite population, resulting in apparent competition between both hosts (Li et al., 2014). Invasive parasites can also exert trait-mediated effects, for example by indirectly altering trophic relationships in the community. An example is the invasion of the rhizocephalan barnacle *Loxothylacus panopaei* that infects native flat back mud crabs (*Eurypanopeus depressus*). This parasite was presumably co-introduced with infected mud crabs (species unknown) in oyster batches that were translocated from the Gulf of Mexico to the Chesapeake Bay (North America) in the mid-1960s (van Engel, 1966). In a controlled lab experiment, parasitized crabs consumed significantly fewer mussels than unparasitized crabs. Eventually, this may result in trophic changes in intertidal oyster reef systems as predator-prey relationships in the system have been modified because of a release in crab predation intensity on mussels (O'Shaughnessy et al., 2014).

Direct and indirect effects of parasite spillover can also propagate to varying degrees through food webs and can thereby induce a trophic cascade, affecting the community and ecosystem on a large scale (Hatcher et al., 2012). An infamous example are the Australasian

pilchard (*Sardinops sagax*) mortalities in Australia and New Zealand in 1995 and 1998-1999 that were caused by a herpesvirus that was co-introduced with imported bait fish (10.000 tons per annum of *S. sagax* and a mix of bycatch species including clupeid fish from the Americas and Japan; Jones, 1997; Whittington, 1997, 2008). The Pilchard herpesvirus (PHV) caused lesions in the gills of the pilchards, causing them to swim slowly and erratically before sinking or washing ashore (Hyatt et al., 1997; Whittington, 1997). The virus spread with a speed of more than 12,000 km/year along the Australian coast, thereby exceeding the swimming speed of the pilchards, but making use of the ocean's three-dimensional nature, currents and eddies (McCallum et al., 2003). Pilchards used to represent ~60% of the diet of gannets, but after the mass mortality events (estimates ranged as high as 75%; Gaughan et al., 2000) only ~5% of the gannet diet consisted of pilchard (Bunce and Norman, 2000). As a result, gannets had to switch to a species of snake mackerel as main prey item, a food source that presumably has lower nutritional qualities than pilchard. The consequences are that greater foraging effort and food consumption are required, which may ultimately affect the reproductive success and survival of gannets (Bunce and Norman, 2000). This effect has already been shown for a different bird species in Australia, the little penguin *Eudyptula minor*. Pilchard is such an important food source for the penguins that there is indication that an early onset of egg laying is triggered by the abundance of pilchards in the diet of these birds (Cullen et al., 1992). The mass mortalities of pilchard therefore caused massive starvation of the penguins, leading to a two-week delay in breeding, a reduction in offspring numbers and increased mortality of the birds (Dann et al., 2000).

To summarize, co-introductions of parasites with invasive hosts that then spill over from invasive to native hosts frequently occur. Parasite spillover events have been shown to pose

strong direct (i.e. mass mortalities) and indirect effects (i.e. parasite-mediated competition) that may even propagate through entire food webs. Of all the mechanisms discussed above, empirical evidence is strongest for parasite spillover and therefore this mechanism is of great importance in assessing the risk of invasive species introductions. However, more work is needed to quantify the diverse impacts of parasite spillover events on native ecosystems.

3.6 Interference with parasite transmission

Invasive species do not have to serve as a host or be a parasite to affect native parasite-host interactions. Instead, they can interfere with the transmission process between native hosts of parasites with complex life cycles (Kelly et al., 2009; Poulin et al., 2011). This mechanism has similarities with the dilution effect observed for parasites with frequency-dependent transmission, where an increase in the number of low-competent host species can reduce parasite establishment (Dobson, 2004). The dilution effect hypothesis was originally developed for vector-borne diseases like Lyme disease, suggesting that an increase in biodiversity could reduce disease risk for target host species (Keesing et al., 2006; Ostfeld and Keesing 2000). Two assumptions are crucial for this hypothesis: 1) the additional (i.e. invasive) host is not of higher competence than the main host species and 2) interspecific transmission is less than intraspecific transmission (Telfer and Brown, 2012). However, vector-borne diseases appear to be less common in marine than in terrestrial ecosystems, although this may partly be due to a scarcity in studies on potential marine vectors (McCallum et al., 2004).

For macroparasites with free-living infective stages in between sequential hosts, interference of invasive species with the transmission process can act via a variety of mechanisms, ultimately resulting in a reduction of disease risk for native species (Fig. 1,

transmission interference, Table 6). These mechanisms mainly work via reducing encounter rates with suitable hosts (Combes, 2001), but can also involve the compatibility of the host. First of all, invasive hosts can be completely unsuitable for the parasite ($R_0 = 0$), but still attract infective stages that fail to infect or to reproduce and thus act as a decoy, removing infective stages from the system (Johnson and Thieltges, 2010; see also section 3.2). Second, invasive species might act as a dead-end host for a parasite with a complex life cycle. In this case the invader can become infected but then the life cycle of the parasite is disrupted, as the invasive host is not consumed by native definitive hosts and thus trophic transmission is inhibited (Johnson and Thieltges, 2010). This is for example the case for the Pacific oyster (*Crassostrea gigas*) that is infected by the native trematode *Renicola roscovita* in northwest Europe, but is hardly consumed by native bird species that serve as definitive hosts for the parasite (Krakau et al., 2006). Other mechanisms act on the encounter probability by directly killing the parasites before they have the chance to infect the invader (Poulin et al., 2011). This is the case when invasive species prey on free-living stages of native parasites, including active predation as well as predation by filter and suspension feeders (Thieltges et al., 2008). For example, the invasive brush clawed shore crab *Hemigrapsus takanoi* can reduce the number of free-living infective stages of cercariae of the native trematode *Himastla elongata* by 55% via active predation (Welsh et al., 2014). Finally, invasive species can also interfere with transmission via physical and chemical barriers (Johnson and Thieltges, 2010). For example, parasites can get entangled in invasive algae, which reduce the encounter rates of the parasite with the host. This was shown for free-living stages of the trematode *H. elongata* that became entangled in the invasive seaweed *Sargassum muticum*, which in this way physically interfered with the transmission to the second intermediate host, the blue mussel *Mytilus edulis* (Welsh et al., 2014). Similarly,

native labrid fish that spend their whole life living in and around the invasive seaweed *Caulerpa taxifolia* are infected with fewer parasites than fish that live on sites that have not yet been invaded by this species of green algae, presumably due to secondary metabolites released by *C. taxifolia* (Bartoli and Boudouresque, 1997).

The interference of invaders with the transmission of native parasites can have important implications for native host and parasite species. For example, two invasive mollusc species, the Pacific oyster (*Crassostrea gigas*) and the American slipper limpet (*Crepidula fornicata*), significantly reduced parasite load in native blue mussels (*M. edulis*, Thieltges et al., 2009). By acting as a predator of free-living infective stages (cercariae) of trematodes, both species create a density-dependent transmission reduction: The higher the densities of invasive species the stronger the reductions in parasite loads in blue mussels, a situation that is of relevance in natural settings where invaders typically increase in numbers after their introduction (Thieltges et al., 2009). The native parasite species that naturally infects blue mussels as metacercariae (*H. elongata*), negatively affects its host by causing reductions in growth and filtration rates (Stier et al., 2015; Thieltges et al., 2006) and disruptions in byssus thread production, increasing the risk for mussels to be detached from their substratum (Lauckner, 1983). Furthermore, effects of metacercarial stages on hosts generally act in a density dependent matter (Fredensborg et al., 2004; Thieltges et al., 2006) and therefore dilution by invasive species directly reduces the disease risk for native species. How this mechanism indirectly mediates competition between native and invasive host species is still an open question.

In conclusion, invasive species do not have to serve as a host or be a parasite to affect native parasite-host interactions. Empirical evidence shows that invasive species can hamper transmission of native parasites with complex life cycles via a variety of mechanisms. However,

how this interference causes direct and indirect effects on parasite-host interactions is still a topic for future studies.

4. Evolutionary implications of parasite and host invasions

In addition to a multitude of ecological impacts, biological invasions will also alter the fitness landscapes of interacting species and should thus lead to evolutionary adaptation of both hosts and parasites. First of all, the initial translocation reduces genetic variation that can crucially influence invasion success (Roman and Darling, 2007), because lower genetic diversity limits the evolutionary potential to adapt to newly encountered environmental conditions (Barrett and Schluter, 2008). Despite reduced genetic variation, successful invasions may either still harbour sufficient amounts of genetic variation for invasive species to adapt (Facon et al., 2006) or show high phenotypic plasticity (Yeh and Price, 2004; Lucek et al., 2014). While a reduction in genetic variation has been generally observed for invasive species (Estoup et al., 2001), invasions in the marine realm are often not characterized by reduced genetic variation (Roman, 2006; Roman and Darling, 2007). Marine invasive species often establish through multiple introductions and are thereby 'diluting' initial founder effects (Rius et al., 2014).

However, much less is known about genetic diversity and structure of invasive parasites. While translocations of invasive species can, in principle, also homogenize genetic structure of parasite populations (Zarlenga et al., 2014), the genetic structure of invasive parasites has only rarely been studied – especially in marine ecosystems. On theoretical grounds, the effect of genetic bottlenecks should be amplified for co-introduced parasites unless parasite genetic diversity within each introduced host is high. An example showing reduced genetic variation of parasites in invaded ranges is the nematode *Anguillicola crassus*, which shows lower genetic

variation after spilling over to native European eels *Anguilla anguilla* infesting their swim bladders, supporting the assumption of reduced genetic variability in invaded ranges (Wielgoss et al., 2008). Similarly, ostreid herpesviruses show higher genotypic diversity in East Asia, presumably the region of origin, and a lower diversity in Europe (Mineur et al., 2014). Although both examples support reduced genetic variation in the invaded range, both species successfully spilled over after invasion, indicating that low genetic diversity in introduced ranges does not necessarily influence traits underlying host-parasite interactions or invasion success of parasites.

Once a host or parasite invasion is successful, it should alter selective pressures and different predictions for adaptive responses can be made depending on the role of parasites and hosts in the invasion (Fig. 1). Empirical evidence demonstrating such changes in selective regimes or adaptive responses resulting from them are however scarce in the context of invasions and especially in marine systems. For example, parasite release or reduction (I) relaxes selection pressure on the invasive host, while transmission interference (VI) relaxes selection on the native host, because both processes lead to lower infection rates. If expression of traits previously experiencing selection is costly, a loss of the trait is frequently observed (Lahti et al., 2009). If host resistance traits become neutral, direct responses to relaxed selection pressure will be hard to observe because they will mainly be subject to genetic drift. If host resistance traits are costly, however, compensatory release will potentially benefit invasive hosts via parasite release (Colautti et al., 2004) or transmission reduction. Such a shift in selective regimes may release other traits like fecundity or size from evolutionary canalization (Lee, 2002) as hosts do not need to allocate energy towards defence against parasites (Maron et al., 2004). For parasites, on the other hand, transmission reduction would select for avoidance of dead ends in unsuitable hosts, probably leading towards selection for generalism.

Parasite spillback (II) and spillover (V) on the other hand, should increase selection pressure on native hosts since infection rates will increase. Especially in spillover scenarios, native hosts will be confronted with new parasites that do not share any co-evolutionary history. If parasite spillover results in emerging diseases, the lack of co-evolutionary history before invasion can lead to strong effects on host populations, e.g. mass mortalities that are particularly common in the marine environment (Fey et al., 2015), but have only rarely led to research on associated evolutionary change (e.g. host adaptation: Wendling and Wegner, 2015; enemy release: Friedman et al., 2014).

Mass mortalities of infected hosts will not only lead to strong selection on native host populations, but can also result in selection on the invasive parasite. After spilling over into European eels, the nematode *Anguillicola crassus* rapidly evolved higher infectivity and faster development in its new host species, which could potentially explain the high levels of virulence that were observed after the invasion (Weclawski et al., 2014). Parasite induced mass mortalities will substantially reduce host density and limit the scope of future transmission. Maximizing transmission might therefore rather select for optimal host exploitation rather than maximal virulence. The initial mass mortalities associated with the invasion of the intestinal copepod parasite *Mytilicola intestinalis* (Korringa, 1968; Meyer and Mann, 1950; Cole and Savage, 1951; Theisen, 1966) in combination with low virulence and low mortality rates in contemporary host-parasite combinations could potentially reflect such an adaptive decrease in virulence, but tests of this hypothesis are lacking.

During parasite co-introductions with hosts (IV), interactions of host and parasite genotypes with the new environment (G x E interactions) will shape selective landscapes. Here, stronger G x E interactions could be expected for hosts, as they are more directly exposed to the

environment than parasites, for which the internal environment of the host changes to a lesser degree (Lazzaro and Little, 2009; Mitchell et al., 2005). However, during initial stages of a co-introduction, host density for the parasite might be too low, and may thus also select for more generalist parasite genotypes, potentially leading to spillover to native hosts. Again, empirical support for such changes in selective regimes is lacking in marine systems.

While it is safe to assume that selection pressures will be asymmetric between hosts and parasites, the response of hosts and parasites will depend on how trait values of hosts (resistance, tolerance) and parasites (infectivity, transmission, virulence) can be translated into fitness in each specific case. Traits associated with infectivity (Weclawski et al., 2013; Weclawski et al., 2014) and transmission (Kelehear et al., 2012) were shown to evolve rapidly in invasive parasite populations. Evolution of both traits reflects selection pressures due to low host density (Phillips et al., 2010) that translates into longer periods of free-living infectious stages spent outside the host. Survival of infective stages can therefore evolve rapidly (Kelehear et al., 2012).

Besides co-introducing parasites to their new range, invasive hosts are also often confronted with native parasites in the introduced range that will exert selection on the invader (e.g. Kelehear et al. 2012). Rapid evolution of host resistance against these newly encountered parasites will increase host fitness and may be a decisive factor prolonging invasion success. Especially, when generalist parasites are encountered a fast evolutionary response will be adaptive (Roth et al., 2012). A prominent example for strong selection by opportunistic parasites are mass mortalities of invasive Pacific oysters (*C. gigas*) that are associated with bacterial infections of native *Vibrio* spp. (Lacoste et al., 2001; Wendling and Wegner, 2013). The rapid evolution of resistance against a wide variety of *Vibrio* bacteria within only a few generations in two independent invasions of Pacific oysters into the Wadden Sea, illustrates the rapid

evolutionary dynamics of host-parasite co-evolution during species invasions (Moehler et al., 2011; Wendling and Wegner, 2015).

Although the importance of evolutionary adaptation for biological invasion receives increasing attention (Colautti and Barrett, 2013), the limited numbers of studies discussed above indicate that the rapid evolutionary dynamics resulting from host-parasite interactions have largely been ignored. Especially in the marine realm that is characterized by frequent episodes of disease associated mass mortalities (Fey et al., 2015), these dynamics may play a decisive role and should be integrated into a coherent framework of eco-evolutionary implication of species invasions.

5. Summary and outlook

In order to provide a conceptual framework for studying the role of parasites and their hosts in marine invasions, we have reviewed recent theoretical developments in invasion ecology and linked them with empirical studies from marine ecosystems. This resulted in the identification of six mechanisms in which invaders directly or indirectly affect parasite-host interactions. These six mechanisms generally differ in their ecological and evolutionary consequences for invasive and native hosts and parasites (Fig. 4).

Invasive and native hosts are generally affected by parasites either via direct effects on individual hosts (and subsequently host populations) or via indirect effects that act on a community level (Dunn et al., 2012). In many of the studies reviewed here, parasites exerted a negative direct effect on the fecundity, body condition and/or survival of native and invasive individual hosts. This results in lower overall fitness and lower abundances of the affected host species (Tompkins et al., 2011) and thereby also in altered selective impacts and evolutionary trajectories. Alternatively, parasites can induce indirect effects with influence on the community

level in at least two ways: via density-mediated and via trait-mediated indirect effects (Dunn et al., 2012; Hatcher et al., 2006). Density-mediated indirect effects can be caused by parasites that mediate the (resource or interference) competition between a native and an invasive host (parasite-mediated competition), whereby the parasite negatively affects one host but not the other, thus altering the outcome of competition (Dunn et al., 2012; Hatcher et al., 2006). In addition, in some cases, when invasive and native species are not in direct resource competition, their shared parasite species may still mediate the interaction between both species via apparent competition (Holt and Pickering, 1985). This form of competition can lead to exclusion of one of the two species, but also to co-existence, for example if the dominant competitor is more strongly affected by the parasite than the competitively inferior species (Hatcher et al., 2012). Alternatively, parasites can also exert trait-mediated indirect effects (TMIEs; based on trait-mediated interactions, see Werner and Peacor, 1993) through their effects on host behavior or other traits that ultimately may modify the outcome of competitive and trophic interactions between invasive and native species (Dunn et al., 2012; Hatcher et al., 2006). For example, for parasites with complex life cycles that make use of trophic transmission, it has been shown that they often change their host's behavior in a way that increases their changes to be transmitted to the down-stream host (reviewed in Lefèvre et al., 2008). The relative role of these direct and indirect effects of parasites on their hosts conceptually differs among the six mechanisms and between native and invasive hosts (Fig. 4). However, at this stage the table remains largely conceptual as our review of the literature indicates that there is a strong lack in empirical studies on the more complex indirect effects of parasites in marine invasions. In particular, studies using experimental approaches will be needed to unravel the full magnitude of ecological and evolutionary implications of parasite-mediated effects in marine invasions.

The six different mechanisms also have different implications for native and invasive parasites (Fig. 4). While some mechanisms can result in an amplification of parasite populations (e.g. parasite spillback) others may lead to a reduced transmission and a decrease in parasite population size (e.g. transmission interference). Likewise, the evolutionary implications differ among the six mechanisms and between native and invasive parasites. However, like with the implications for hosts, the table currently remains largely conceptual as empirical studies are rare. More studies, in particular ones that integrate the evolutionary effects of altered selective landscapes on parasite-host interactions, are needed to understand the ecological and evolutionary implications of marine invasions for parasites and the subsequent effects on their host populations and communities.

In addition to affecting parasite and host populations and communities as well as their selective landscapes, invasions of parasites and hosts may also affect entire food webs. The role of parasites in food webs has recently gained increasing attention (Lafferty et al., 2006; Lafferty et al., 2008; Lafferty and Kuris 2009; Marcogliese and Cone, 1997; Thieltges et al., 2013a, b) and Britton (2013) suggested that introduced species and their parasites may increase connectivity and complexity of food webs via introducing new nodes and links, ultimately affecting entire ecosystems. For example, when an invader acts as a competent host for a native parasite, new links between the invader and parasites are formed, that might increase food web connectance and nestedness (Britton, 2013). In addition, via trait-mediated effects of the invader, feeding interactions and their strength might change, resulting in changes in the quantitative food webs (Britton, 2013). Indeed, the only existing study from a sub-arctic freshwater lake system suggests that the addition of two invasive pelagic fish species and their parasites to the food web has caused an increase in connectance and nestedness of the food web (Amundsen et al., 2013).

However, similar studies for marine food webs are non-existing, and new species invasions may create interesting research opportunities in food web topology for the future.

In conclusion, the manifold roles of parasites and their hosts in marine invasions can results in substantial effects on natural communities and ecosystems via i) catastrophic mass mortalities of native populations creating strong selection gradients (emerging diseases), ii) indirect changes in species interactions within communities and iii) trophic cascading and knock-on effects throughout the food web that may affect ecosystem functioning and services. Our review also demonstrates a wide range of other ecological and evolutionary implications of marine invasions for parasite-host interactions and suggests that parasite-mediated impacts should be integrated in assessing the risks and consequences of biological invasions.

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Figure captions

Fig. 1. Conceptual overview of the six mechanisms of how invaders can directly or indirectly affect parasite-host interactions. Grey semicircle = invasive host species, white semicircle = native host species, dark grey dot = invasive parasite species, white dot = native parasite species, grey environment = native range of invader, white environment = introduced range of the invader. For detailed explanation of the mechanisms see text.

Fig. 2. A) Proportion (%) of different taxa of native parasite species acquired by invasive hosts (n = 41; Table 2). Parasite species that were acquired by multiple invasive host species were only counted once. B) Proportion (%) of different taxa of invasive parasite species that were co-introduced and spilled over to native hosts (n = 35, Table 5). Parasite species that spilled over to multiple host species were only counted once.

Fig. 3. Frequency distribution of the number of introduced hosts that co-introduced a parasite species that spilled over to native hosts (black) and the number of native hosts the co-introduced parasite spilled over to (grey).

Fig. 4. Overview of ecological and evolutionary implications of the six mechanisms for invasive and native hosts and parasites. For legend of symbols, see Fig. 1.

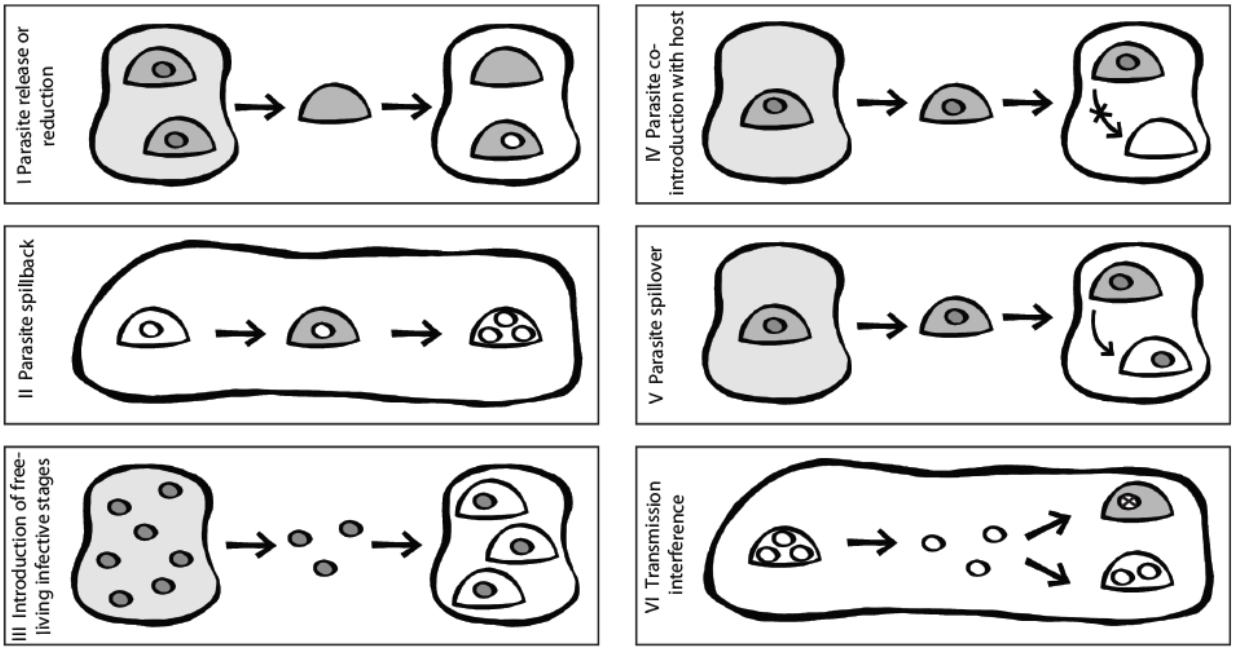

Figure 1

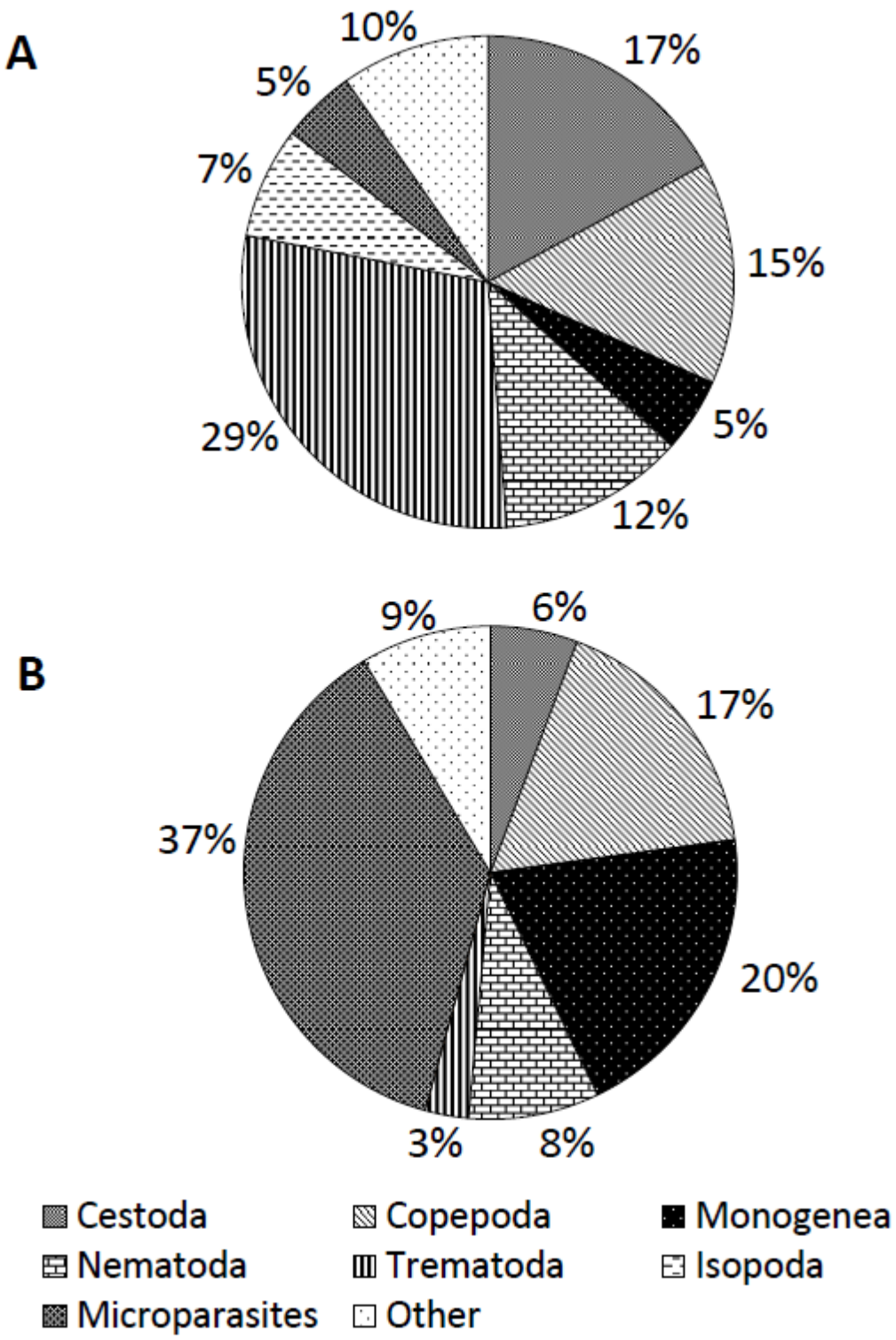

Figure 2

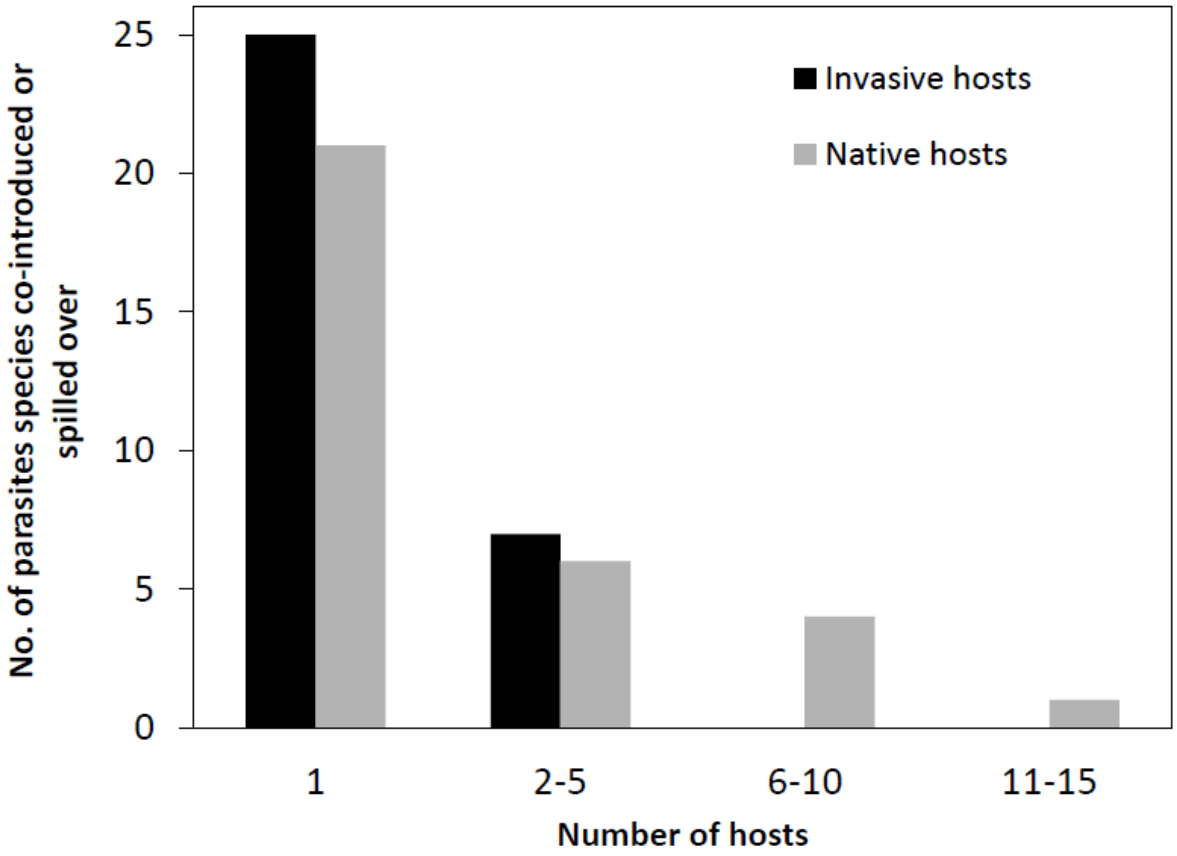

Figure 3

Mechanism	End result	Implication	Invasive host	Native host	Invasive parasite	Native parasite
I Parasite release or reduction		Eco.	Uninfected, hence no direct effects; indirect effects via potential competitive advantage	Direct effects of native parasite; indirect effects via parasite-mediated competition	NA	Potential for host switch to invasive host
		Evo.	Relaxed selection pressure	NA	NA	NA (if diluted see VI)
II Parasite spillback		Eco.	Direct effects of native parasite; indirect effects via apparent competition	Direct effect of native parasite (increased disease risk); indirect effects via apparent competition	NA	Amplification parasite population
		Evo.	Increased selection pressure	Increased selection pressure	NA	NA
III Introduction of free-living stages		Eco.	NA	Direct effect of invasive parasite: emerging disease	Potential to spread in introduced range	NA
		Evo.	NA	Increased selection pressure	Increased selection pressure to infect new potentially less suitable hosts	NA
IV Parasite co-introduction with host		Eco.	Direct effect by co-introduced parasite; indirect effects via parasite-mediated competition	Direct effects of native parasite; indirect effects via parasite-mediated competition	Potential to spread in introduced range	NA
		Evo.	Altered selective landscape due to new genotype by environment interactions of co-invading parasites	NA (if spillover, see V)	Altered selective landscape due to new genotype by environment interactions of co-invading host; with low host density selection for generalism	NA
V Parasite spillover		Eco.	Direct effect of invasive parasite; indirect effects via apparent competition	Direct effect of invasive parasite; indirect effects via apparent competition	High potential to spread in introduced range	NA
		Evo.	NA	Increased selection pressure	Selection for lower host specificity	NA
VI Transmission interference		Eco.	NA	Reduction disease risk by native parasite	NA	Reduced transmission
		Evo.	Adaptation to enemy shifts	Relaxed selection pressure	NA	Selection for lower host specificity to avoid dead ends

Figure 4

Tables

Table 1. Studies with evidence for parasite release or reduction in marine ecosystems with information on the taxa, the common and scientific name (in brackets), the native and invasive range of the invasive host, the number of native parasite species infecting the invasive host in the native range, the number of co-introduced invasive parasite species or acquired native parasite species by the invasive host in the invasive range, the common and scientific name (in brackets) of the native host, the number of native parasite species infecting native hosts, evidence for parasite release or reduction, results of tests for fitness differences between invasive and native host species and the respective literature sources.

Invasive host taxa	Invasive host species	Native range *	Invasive range*	# parasite species in native range	# parasite species in invasive range	Native host species	# parasite species native hosts	Evidence for parasite release or reduction	Fitness differences between invasive and native species	Ref.
Mollusca	Mediterranean mussel (*Mytilus galloprovincialis*)	MED	SAF	6	0	Brown mussel (*Perna perna*)	2	Parasite release in invasive host and does not acquire new parasites. Native host is infected with two native parasites.	Native parasites negatively affect growth and reproduction of native hosts.	1-3
	Mud snail *(Cyclope neritea)*	MED	EUR	6	2	Netted dog whelk *(Nassarius reticulatus)*	6	Parasite reduction in invasive host. Native host is infected with 6 native parasites, invasive host only with 2 parasites.	In still water conditions the invasive host reaches its prey faster than natives.	4
	Japanese mud snail (*Batillaria attramentaria* (= *cumingi*))	ASI	NAM	9	1	California hornsnail (*Cerithidea californica)*	18	Parasite reduction in invasive host. Native host is infected with >10 parasites, invasive hosts only with one that is co-introduced.	Invader is more efficient in turning resources into growth.	5-9
Crustacea	Common shore crab (*Carcinus maenas*)	EUR	NAM, SAF, AUS	10	0-3	-	-	Invasive shore crabs less parasitized compared	In invaded regions, crabs were larger and had a	10,11

									to native European populations.	greater biomass than in native regions. Parasitized crabs had significant lower testes weight, no effect of reproduction for other helminths.	
sh	**i**	Peacock grouper (*Cephalopholis argus*)	IO	PO	10	3	-	-	Significant reductions in richness and prevalence of parasites in introduced range.	Body condition of fish is not significantly different between native and introduced ranges.	12

* ASI = Asia , AUS = Australia, EUR= Europe, IO = Indian Ocean, MED = Mediterranean, NAM = North America, PO = Pacific Ocean, SAF = South Africa.

References: 1) Calvo-Ugartoburu and McQuaid, 1998a; 2) Calvo-Ugartoburu and McQuaid, 1998b; 3) Figueras et al., 1991; 4) Bachelet et al., 2004; 5) Byers, 2000; 6) Hechinger, 2007; 7) Martin, 1972; 8) Torchin et al., 2002; 9) Torchin et al., 2005; 7) ; 10) Torchin et al., 2001; 11) Zetmeisl et al., 2011; 12) Vignon et al. 2009b.

Table 2. Studies with evidence for acquisition of native parasites by invasive host species, with information on the taxa, the common and scientific name (in brackets), the native and invasive range of the invasive host species, the number of native parasite species that is acquired by the invasive host in the introduced range, the parasite taxa that are acquired by invasive hosts in the introduced range, the native host species that are infected with these native parasites in the introduced range and the respective literature sources.

Invasive host taxa	Invasive host species	Native range*	Invasive range*	# parasite species acquired	Parasite taxa	Native host species	Ref.
Bivalvia	Pacific oyster (*Crassostrea gigas)*	ASIR	EU	7	Trematoda (4), Copepoda (1), Polychaeta (1), Fungi (1)	Several mollusc species	1-4
	American razor clam (*Ensis americanus*)	NAM	EU R	5	Trematoda	Several mollusc species	1,2
	Asian date mussel (*Musculista senhousia*)	ASI	NZ	2	Crustacea, Copepoda	New Zealand mussel *(Perna canaliculus),* flea mussel (*Xenostrobus pulex*)	5
Crustacea	American brine shrimp (*Artemia franciscana*)	NAM	EU R	6	Cestoda	Two species of brine shrimp (*Artemia parthenogenetica* and *Artemia salina*)	6
	Common shore crab *(Carcinus maenas*)	EUR	NA M	2	Copepoda, Nemertea	Yellow shore crab *(Hemigrapsis oregonensis*), purple shore crab (*Hemigrapsus nudus*), Dungeness crab (*Cancer magister*)	7,8
	Asian paddle	ASI	NZ	1	Nematoda	New Zealand paddle crab (*Ovalipes*	9

	crab (*Charybdis japonica*)					*catharus*)	
Fish	Atlantic salmon (*Salmo salar*)	EU R/ASI	SA M	2	Copepoda, Nematoda	Chilean mussel blenny *(Hypsoblennius sordidus),* mote sculpin *(Normanichthys crokeri),* Chilean herring (*Strangomera Bentincki*), Chilean silverside (*Odontesthes regia*), Patagonian blenny (*Eleginops maclovinus*), Chilean jack mackerel (*Trachurus murphyi*)	10
	Bluestripe snapper (*Lutjanus kasmira*)	IO	PO	3	Monogenea, Copepoda, Trematoda	Tarry hogfish (*Bodianus bilunulatus*), small toothed jobfish *(Aphareus furca)*	11
	Blacktail snapper (*Lutjanus fulvus*)	IO	PO	3	Monogenea, Copepoda, Trematoda	Tarry hogfish (*Bodianus bilunulatus*), small toothed jobfish *(Aphareus furca)*	11
	Dusky spinefoot (*Siganus luridus*)	RS	ME D	2	Isopoda	Fish families: Labridae, Sparidae	12
	Marbled spinefoot (*Siganus rivulatus)*	RS	ME D	1	Isopoda	Fish families: Labridae, Sparidae	12

Round goby (*Neogobius melanostomus*)	BS, CS	BAS	6	Cestoda (1), Nematoda (3), Trematoda (1), Acanthocephala (1)	Black goby (*Gobius niger*), two-spotted goby (*Gobiusculus flavescens*), common goby (*Pomatoschistus microps*), sand goby (*Pomatoschistus minutes*)	13
American shad *(Alosa sapidissima)*	NA M-Atlantic	NA M-Pacific	1	Protista	Spring Chinook salmon (*Oncorhynchus tshawytscha*)	14

* ASI= Asia, BAS = Baltic Sea, BS = Black Sea, CS = Caspian Sea, EUR= Europe, IO = Indian Ocean, MED = Mediterranean, NAM = North America, NZ = New Zealand, PO = Pacific Ocean, RS = Red Sea, SAM = South America.

References: 1) Aguirre-Macedo and Kennedy, 1999; 2) Krakau et al., 2006; 3) Engelsma and Haenen, 2004; 4) Thieltges et al., 2006; 5) Miller et al., 2008; 6) Georgiev et al., 2007; 7) Johnson, 1957; 8) Torchin et al., 1996; 9) Miller et al., 2006; 10) Sepúlveda et al., 2004; 11) Vignon et al., 2009a, 12) Shakman et al., 2009; 13) Kvach and Skora, 2007; 14) Hershberger et al., 2010.

Table 3. Studies on introductions of free-living bacteria and viruses with ballast water, with information on the introduced region and the year(s) in which the ballast water was investigated, the number of vessels, ballast tanks per vessel and samples per ballast water tank sampled, the type of microorganism found in the ballast water, the percentage of ballast water samples that contained the microorganism (prevalence), the abundance of the microorganism found in positive ballast water samples and the respective literature sources.

Introduced region	Year	# vessels	# tanks per vessel	# samples per tank	Type of microorganism*	% Positive samples	Abundance**	Ref.
Brazil	2002-2003	105	1	1	*Vibro spp.*	32	<1-430 CFU/ml	1
					Vibrio cholerae	13.3	-	
Gulf of Mexico	2005	30	3	1	Total coliform bacteria	83.3	4-240 MPN/100 ml	2
					Fecal coliform bacteria	26.7	1-75 MPN/100 ml	
					Escherichia coli 0157	0.03	-	
					Other *Escherichia coli*	0.2	-	
					Enterococcus sp.	83.3	3-163 CFU/ml	
					Vibrio cholerae	0.03	-	
					Serratia marcescens	0.03	-	
					Sphingomonas spp.	0.03	-	
Mississippi,	1991-1992	19	NA	NA	Fecal coliform	62.5	3-5.1*10^2	3

Alabama, USA					bacteria		CFU/100 ml	
					Vibrio cholerae O1	31.2	-	
Chesapeake Bay, USA	NA	11	NA	NA	Bacteria	-	$8.3 * 10^8$ cell/l	4
		7	NA	NA	VLP's	-	$7.4*10^9$ cell/l	
			NA	NA	*Vibrio cholerae*	93.0	-	
		14	NA	NA	*Vibrio cholerae* O139	-	$1.4 * 10^4$ cell/l	
		15	NA	NA	*Vibrio cholerae* O1	-	$1.5*10^5$ cell/l	
Chesapeake Bay, USA	1996-2000	25	1-2	2	Bacteria	72.0	$0.06\text{-}15*10^9$ cell/l	5
		31	1	1	VLP's	53.3	$0.35\text{-}64*10^9$ cell/l	6
Chesapeke Bay, USA	1996-2001	53	1	1	Bacteria	-	$0.803*10^9$ cell/l	
		31			VLP's	-	$13.9*10^9$ cell/l	
Chesapeake Bay, USA	2002	1	1	4	Bacteria	-	$3.19*10^9$ cell/l	7
					VLP's	-	$2.96*10^{11}$ cell/l	
Qatar	2002-2003	1	12	6	Bacteria	-	$10 – 10^{4.7}$ CFU/ml	8
Brazil	2002-2003	105	1	1	*Vibro spp.*	32	<1-430 CFU/ml	1

					Vibrio cholerae	13.3	-	
Gulf of Mexico	2005	30	3	1	Total coliform bacteria	83.3	4-240 MPN/100 ml	2
					Fecal coliform bacteria	26.7	1-75 MPN/100 ml	
					Escherichia coli 0157	0.03	-	
					Other *Escherichia coli*	0.2	-	
					Enterococcus sp.	83.3	3-163 CFU/ml	
					Vibrio cholerae	0.03	-	
					Serratia marcescens	0.03	-	
					Sphingomonas spp.	0.03	-	
Mississippi, Alabama, USA	1991-1992	19	NA	NA	Fecal coliform bacteria	62.5	$3\text{-}5.1*10^2$ CFU/100 ml	3
					Vibrio cholerae O1	31.2	-	
Chesapeake Bay, USA	NA	11	NA	NA	Bacteria	-	$8.3 * 10^8$ cell/l	4
		7	NA	NA	VLP's	-	$7.4*10^9$ cell/l	
			NA	NA	*Vibrio cholerae*	93.0	-	
		14	NA	NA	*Vibrio cholerae* O139	-	$1.4 * 10^4$ cell/l	
		15	NA	NA	*Vibrio cholerae* O1	-	$1.5*10^5$ cell/l	

Chesapeake Bay, USA	1996-2000	25	1-2	2	Bacteria	72.0	0.06-15*10^9 cell/l	5
		31	1	1	VLP's	53.3	0.35-64*10^9 cell/l	6
Chesapeke Bay, USA	1996-2001	53	1	1	Bacteria	-	0.803*10^9 cell/l	
		31			VLP's	-	13.9*10^9 cell/l	
Chesapeake Bay, USA	2002	1	1	4	Bacteria	-	3.19*10^9 cell/l	7
					VLP's	-	2.96*10^{11} cell/l	
Qatar	2002-2003	1	12	6	Bacteria	-	$10 – 10^{4.7}$ CFU/ml	8

* VLP's = virus-like particles, ** CFU = colony forming units, MPN = most probable number

References: 1) Rivera et al., 2013; 2) Aguirre-Macedo et al., 2008; 3) McCarthy and Khambaty, 1994; 4) Ruiz et al., 2000; 5) Drake et al., 2001; 6) Drake et al., 2007; 7) Drake et al., 2005; 8) Mimura et al., 2005.

Table 4. Overview of marine parasites that have been co-introduced with invasive hosts, but not have been reported (yet) to spill over to native hosts. Shown are the taxa and the scientific name of the co-introduced parasite species, the common and scientific name (in brackets), the taxa, the native and invasive range of the invasive host that co-introduced the parasite, the stage that the invasive hosts occupies in the life cycle of the co-introduced parasite and the respective literature sources.

Parasite taxa	Co-introduced parasite species	Invasive host species	Invasive host taxa	Native range*	Invasive range*	Host life cycle stage	Ref.
Protista	*Bonamia ostreae*	European flat oyster (*Ostrea edulis*)	Bivalvia	EUR	EUR	Single host	1
Rhizocephala	*Heterosaccus dollfusi*	Swimming crab (*Charybdis longicollis*)	Crustacea	RS	MED	Single host	2,3
	Sacculina carcini	Green shore crab (*Carcinus maenas*)	Crustacea	EUR	ASI	Single host	4
Monogenea	*Polylabris cf. mamaevi*	Rabbit fish (*Siganus rivulatus*)	Fish	RS	MED	Single host	5
	Haliotrema longitubocirrus	Bluestripe and blacktail snapper (*Lutjanus spp.*)	Fish	PO	NAM	Single host	6,7
	Haliotrema patellacirrus	Bluestripe and blacktail snapper (*Lutjanus spp.*)	Fish	PO	NAM	Single host	6,7
	Haliotrema conf. anguiformis	Bluestripe and blacktail snapper (*Lutjanus spp.*)	Fish	PO	NAM	Single host	6,7
	Diplectanum fusiforme	Bluestripe and blacktail snapper (*Lutjanus spp.*)	Fish	PO	NAM	Single host	6,7
	Euryhaliotrem spirotubiforum	Bluestripe and blacktail snapper (*Lutjanus spp.*)	Fish	PO	NAM	Single host	6,7
	Euryhaliotrema	Bluestripe and blacktail	Fish	PO	NAM	Single host	6,7

	chrysotaeniae	snapper (*Lutjanus spp.*)					
Trematoda	*Cercaria batillariae*	Asian hornsnail (*Batillaria attramentaria (= cumingi*)	Gastropoda	ASI	NAM	1st int. host	8,9
	Cryptocotyle lingua	Common periwinkle (*Littorina littorea*)	Gastropoda	EUR	NAM	1st int. host	10
Virus	Osteroid herpes virus type I (OsHV-1 µvar)	Pacific oyster (*Crassostrea gigas*)	Bivalvia	ASI	NAM	Single host	11-15

* ASI = Asia, AUS = Australia, EUR = Europe, MED = Mediterranean, NAM = North America, NZ = New Zealand, PO = Pacific Ocean, RS = Red Sea.

References: 1) Culloty et al., 1999; 2) Galil and Innconenti, 1999; 3) Galil and Lützen, 1995; 4) Boschma, 1972; 5) Pastenak et al., 2007; 6) Vignon et al., 2009a; 7) Vignon and Sasal, 2010; 8) Miura et al., 2006; 9) Torchin et al., 2005; 10) Blakeslee et al., 2008; 11) Engelsma et al., 2010; 12) Segarra et al., 2010; 13) Lynch et al., 2012; 14) Roque et al., 2012; 15) Mineur et al., 2014.

Table 5. Overview of co-introduced parasites that have spilled over from invasive to native hosts in marine and brackish systems. Shown are the taxa, the scientific name and the type of life cycle of the co-introduced parasite, the number of invasive host species that co-introduced the parasite, the taxa and the vector of introduction of the invasive host species, the native and invasive range of the invasive host and the co-introduced parasite species, the number of native host species where the co-introduced parasite spilled over to, the native host taxa to which the co-introduced parasite spilled over, mortality of the native host caused by the co-introduced parasite and the respective literature sources.

Parasite taxa	**Parasite species**	**Life cycle**	**# invasive hosts**	**Invasive host taxa**	**Vector**	**Native range***	**Invasive range***	**# native hosts**	**Native host taxa**	**ortality native host**	**I**	**ef.**	**R**
Acanthocephala	*Paratenuisentis ambiguus*	Indirect	2	Crustacea, Fish	Aquaculture, Stocking	NAM, ASI	EUR	1	Fish	o	I	,2	1
Annelida	*Terebrasabella heterouncinata*	Direct	1	Gastropoda	Aquaculture	SAF	NAM	8	Gastropoda	o	I		3
Bacteria	*Yersina ruckeri*	Direct	1	Fish	Fisheries	NAM	EUR	> 1	Fish	es	\	,5	4
	Aerococcus viridans	Direct	1	Crustacea	Aquaculture	NAM	EUR	1	Crustacea	es	\	,7	6
	Candidatus Xenohaliotis	Direct	1	Gastropoda	Aquaculture	NAM	EUR	1	Gastropoda	es	\		8

	californiensis											
	Nocardia crassostreae	Direct	1	Bivalvia	Aquaculture	ASI	EUR	1	Bivalvia	Strong suspicion		9
Cestoda	*Bothriocephalus claviceps*	Indirect	2	Fish	NA	NAM, EUR	IO	1	Fish	No	No	1
	Ligula intestinalis	Indirect	1	Fish	Aquaculture	EUR	OCA	1	Fish	No	1	1
Copepoda	*Clavellisa ilishae*	Direct	> 1	Fish	Immigrant	RS	MED	1	Fish	No	2	1
	Mitrapus oblongus	Direct	> 1	Fish	Immigrant	RS	MED	2	Fish	No	2	1
	Myicola ostreae	Direct	1	Bivalvia	Aquaculture	ASI	EUR	1	Bivalvia	No	3	1
	Mytilicola intestinalis	Direct	1	Bivalvia	Ship fouling	MED	EUR	1	Bivalvia	Yes	4-16	1
	Mytilicola orientalis	Direct	1	Bivalvia	Aquaculture	ASI	EUR, NAM	4	Bivalvia	No	3,17-19	1
	Nothobomolochus fradei	Direct	1	Fish	Immigrant	ASI	MED	1	Fish	No	2	1
Fungus	*Fusarium palustre*	Direct	1	Plantae	Conservation	NAM	ASI	1	Plantae	Yes	1	2
Monogenea	*Gyrodactylus anguillae*	Direct	> 1	Fish	Aquaculture	EUR	NAM, OCA	3	Fish	No	3	2
	Gyrodactylus nipponensis	Direct	1	Fish	Aquaculture	EUR	ASI	1	Fish	No	3	2
	Gyrodactylus salaris	Direct	1	Fish	Stocking	EUR	EUR	1	Fish	Yes	4,25	2

	Neobendenia melleni	Direct	1	Fish	Aquaculture	ASI	ASI	14	Fish		Yes	26
	Nitzschia sturionis	Direct	1	Fish	Stocking	CAS	ASI	1	Fish		Yes	27
	Pseudodactylogyrus anguillae	Direct	1	Fish	Aquaculture	ASI	EUR, NAM	2	Fish		Yes	1,28,29
	Pseudodactylogyrus bini	Direct	1	Fish	Aquaculture	ASI	EUR, NAM	2	Fish		No	1,28,29
Myxozoa	*Myxobolus cerebralis*	Indirect	2	Fish	Aquaculture	EUR	NAM	9	Fish		Yes	30-32
Nematoda	*Anguillicola crassus*	Indirect	> 1	Fish	Aquaculture	ASI,EUR	EUR,NAM,IO	7	Fish		Yes	29,33-40
	Paraquimperia africana	Direct	1	Fish	Stocking	SAF	IO	1	Fish		No	39
	Spirocamallanus istiblenni	Indirect	2	Fish	Stocking	PO	NAM	7	Fish		No	41,42
Protista	*Haplosporidium montforti*	Direct	1	Gastropoda	Aquaculture	NAM	EUR	1	Fish		No	8
Protozoa	*Trypanosoma murmanensis*	Indirect	1	Crustacea	Research	PO	EUR	1	Fish		No	43
	Haplosporidium nelsoni	Indirect	1	Bivalvia	Aquaculture	ASI	NAM	1	Bivalvia		Yes	7,44,45
	Marteilia refringens	Direct	1	Bivalvia	Aquaculture	ASI	EUR	1	Bivalvia		Yes	7,46
	Bonamia ostreae	Direct	2	Bivalvia	Aquaculture	NAM, ASI	EUR,NAM	2	Bivalvia		Yes	5,17,47-50
Rhizoceph	*Loxothylacus*	Direct	1	Crustac	Oyster	GOM	NAM,S	3	Crustac		No	5

ala	*panopaei*	t		ea	transloca tion, fisheries		AM		ea	o	1,52	
Trematoda	*Cercaria batillariae*	Indire ct	1	Gastro poda	Oyster transloca tion	ASI	NAM	> 1	Fish, Aves	o	3	5
Virus	Viral gill disease	Direc t	1	Bivalvia	Aquacult ure	ASI	EUR	1	Bivalvia	o	7	1
	Pilchard herpesvirus	Direc t	1	Fish	Fisheries	IO	OCA	1	Fish	es	4-57	5

* ASIA = Asia, CAS = Caspian Sea, EUR = Europe, GOM = Gulf of Mexico, IO = Indian Ocean, MED = Mediterranean Sea, NAM = North America, OCA = Oceania, PO = Pacific Ocean, RS = Red Sea, SAF = South Africa, SAM = South America.

References: 1) Morozińska-Gogol, 2009; 2) Taraschweski et al., 1987; 3) Culver and Kuris, 2004; 4) Michel, 1986; 5) Peeler et al., 2011; 6) Alderman, 1996; 7) Stebbing et al., 2012; 8) Balseiro et al., 2006; 9) Engelsma, 2008; 10) Sasal et al., 2008; 11) Pollard, 1974, 12) El-Rashidy and Boxshall, 2009; 13) Holmes and Minchin, 1995; 14) Elsner et al., 2011; 15) Minchin, 1996; 16) Stock, 1993; 17) Barber et a1., 1997, 8) Bernard, 1969; 19) Goedknegt et al., submitted; 20) His, 1977; 21) Li et al., 2014; 23) Hayward et al., 2001a; 24) Johnsen and Jensen, 1991; 25) Bakke et al., 1990; 26) Ogawa et al., 1995; 27) Bauer et al., 2002; 28) Hayward et al., 2001b; 29) Køie, 1991; 30) Arsan and Bartholomew, 2009; 31) O' Grodnick, 1979; 32) Hedrick et al., 1999; 33) Barse et al., 2001; 34) Hein et al., 2014; 35) Emde et al., 2014; 36) Knopf and Manke, 2004; 37) Barry et al., 2014; 38) Kirk, 2003; 39) Sasal et al., 2008; 40) Kvach and Skóra, 2007; 41) Gaither et al., 2013, 42) Vignon et al., 2009a; 43) Hemmingsen et al., 2005; 44) Burreson et al., 2000; 45) Burreson and Ford, 2004; 46) Cahour, 1979; 47) Culloty et al., 1999; 48) Elston et al., 1986; 49) Balouet et al., 1983, 50) Chew, 1990; 51) Farrapeira et al., 2008, 52)

Hines, 1997; 53) Torchin et al., 2005; 54) Hyatt et al., 1997; 55) Jones et al., 1997; 56) Whittington et al., 2008; 57) Whittington et al., 1997.

Table 6. Overview of invasive species that interfere with parasite transmission between native hosts. Shown are the common and scientific name (in brackets), the native range and invasive range of the invasive species, the native parasite species from which the transmission is interfered by the invasive host, the mechanism of interference, the resulting reduction in prevalence (proportion of hosts infected) of down-stream native hosts, the reduction in intensity (number of parasites per infected host in the sample batch) in down-stream native hosts, the reduction of free-living infective parasite stages, the type of scientific evidence and the respective literature sources.

Invasive species	**Native range***	**Invasive range***	**Native parasite**	**Mechanism**	**% Reduction prevalence**	**% Reduction intensity**	**% Reduction inf. stages**	**Evidence**	**ef.**
Pacific oyster (*Crassostrea gigas*)	ASIA	EUROPE	*Himastla elongata*	Dead-end host	-	91.5	67	Experimental	,2
			Renicola roscovita	Dead-end host	-	39.9-67.1	-	Experimental	
Slipper limpet (*Crepidula fornicata*)	ASIA	EUROPE	*Himastla elongata*	Dead-end host	-	87.6	-	Experimental	
Killer algae (*Caulerpa taxifolia*)	INDO	MED	Six digenean species	Toxic exudates	97	98	-	Observational	
Japanese knotweed	ASIA	EUROPE	*Himastla*	Physica	-	-	86.9	Experi	

(*Sargassum muticum*)	SI	UR		*elongata*	l barrier					mental	
Brush clawed shore		A	E	*Himastla*	Predati	-		-	54.9		Experi
crab (*Hemigrapsus takanoi*)	SI	UR		*elongata*	on					mental	
				Renicola	Predati	-		26.4	-		Experi
				roscovita	on					mental	
Australasian barnacle		O	E	*Renicola*	Filtrati	-		59.4-	-		Experi
(*Elminius modestus*)	CA	UR		*roscovita*	on		74.4			mental	
				Echinostephilla	Filtrati	33.5		23.8	-		Experi
				patellae	on					mental	

* ASI = Asia, EUR = Europe, IO = Indian Ocean, MED = Mediterranean, OCA = Oceania

References: 1) Welsh et al., 2014; 2) Thieltges et al., 2008; 3) Goedknegt et al., 2015, 4) Bartoli and Boudouresque, 1997; 5) Prinz et al.; 2009.

Highlights

- We identified six mechanisms in which invasive species directly or indirectly affect parasite host populations and communities: I) parasite release or reduction, II) parasite spillback, III) introduction of free-living infective stages, IV) parasite co-introduction with host, V) parasite spillover, VI) transmission interference.
- All mechanisms are not mutually exclusive for a single invasive host species, but can act synergistically during an invasion process.
- Ecological and evolutionary implications of these mechanisms note several substantial effects on natural communities and ecosystems via i) mass mortalities, ii) indirect changes in species interactions and iii) trophic cascading and knock-on effects in food webs that may affect ecosystem function and services.
- This wide range of implications suggests that parasite-mediated impacts should be integrated in assessing the risks and consequences of biological invasions.