Parasites and marine invasions

M. E. TORCHIN[1]*, K. D. LAFFERTY[2] *and* A. M. KURIS[1]

[1] *Marine Science Institute and Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA*
[2] *U.S. Geological Survey, Western Ecological Research Center, c/o Marine Science Institute, University of California, Santa Barbara, CA 93106, USA*

SUMMARY

Introduced marine species are a major environmental and economic problem. The rate of these biological invasions has substantially increased in recent years due to the globalization of the world's economies. The damage caused by invasive species is often a result of the higher densities and larger sizes they attain compared to where they are native. A prominent hypothesis explaining the success of introduced species is that they are relatively free of the effects of natural enemies. Most notably, they may encounter fewer parasites in their introduced range compared to their native range. Parasites are ubiquitous and pervasive in marine systems, yet their role in marine invasions is relatively unexplored. Although data on parasites of marine organisms exist, the extent to which parasites can mediate marine invasions, or the extent to which invasive parasites and pathogens are responsible for infecting or potentially decimating native marine species have not been examined. In this review, we present a theoretical framework to model invasion success and examine the evidence for a relationship between parasite presence and the success of introduced marine species. For this, we compare the prevalence and species richness of parasites in several introduced populations of marine species with populations where they are native. We also discuss the potential impacts of introduced marine parasites on native ecosystems.

Key words: Parasite, pathogen, disease, introduced species, biological invasion.

INTRODUCTION

Globalization of the world's economies has substantially increased the rate of biological invasions (Cohen & Carlton, 1998; Ewel *et al*. 1999) because most harmful exotic species arrive as hitchhikers on the vectors of international trade (Baskin, 1996). Advances in world-wide shipping and transportation have accelerated these processes, particularly in marine systems (Carlton, 1987). For example, ships regularly transit between biotic provinces and subsequently release up to hundreds of thousands of gallons of plankton-laden ballast water into new environments (Carlton, 1987). Carlton & Geller (1993) analyzed the ballast water of 159 Japanese cargo ships entering port in Coos Bay, Oregon, and found a minimum of 367 distinctly identifiable taxa. They estimated that, on any given day, ocean-going vessels transport over 3000 species. As international trade expands, so will the unintentional introduction of non-native species.

Introduced pests are a major threat to global biodiversity, ranked second only to habitat loss (Vitousek, 1990; Wilcove *et al*. 1998). The ecological and economic impacts of an introduced species are a direct result of its ecological success. Introduced species often attain unusually high population densities compared to both ecologically similar native species and to conspecific populations in their native region (for terrestrial examples see Elton, 1958; DeBach, 1974 – cottony cushion scale; Bird & Elgee, 1957 – European spruce sawfly; for aquatic and marine examples see Leech, 1992 – zebra mussel; Buttermore, Turner & Morrice, 1994 – northern Pacific seastar, Carlton *et al*. 1990 – Asian clam). In addition to increased population densities, introduced species often attain unusually large body sizes (Blaustein, Kuris & Alio, 1983; Crawley, 1987; Blossey & Notzhold, 1995; Torchin, Lafferty & Kuris, 2001). This suggests that introduced species are growing faster or surviving longer or both, compared to where they are native. What are the reasons for increased performance of introduced species relative to conspecifics in their native range? Is this correlated with invasion success? There are three main hypotheses for the success of introduced species relative to where they are native. The new habitat has (1) better environmental attributes, such as increased resources (Dobson, 1988), (2) fewer or poorer competitors (Crawley, 1986; Byers, 2000; Callaway & Aschehoug, 2000) and (3) a paucity of natural enemies, such as predators and parasites (Bird & Elgee, 1957; Elton, 1958; Baker & Stebbins, 1965; Huffaker, Messenger & DeBach, 1971; DeBach, 1974; Lawton & Brown, 1986; Dobson, 1988; Dobson & May, 1986; Lampo & Bayliss, 1996*a*, *b*; Meyer, 1996; Schoener & Spiller, 1995; Lafferty & Kuris, 1996; Torchin *et al*. 2001). Both (2) and (3) above may be characteristic of

* Corresponding author: Mark E. Torchin, Marine Science Institute, University of California, Santa Barbara, CA 93106, USA. Tel: 805-893-3998. Fax: 805-893-8062. E-mail: torchin@lifesci.ucsb.edu

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disturbed environments (Lafferty, 1997; Naeem *et al*. 2000). Disturbance can interact positively or negatively with parasites (Lafferty, 1997; Dove, 1998) and, thus, parasites and introduced species may interact with environmental disturbances in a number of ways. Although these hypotheses are sometimes treated as alternatives (Blossey & Notzhold, 1995), we stress that they are not mutually exclusive and can act synergistically (for example, Settle & Wilson, 1990).

Both the physical environment and biotic interactions will determine the success of an introduction. For intentional introductions, humans may knowingly choose suitable environments where species are introduced to fill an apparently open ecological niche (e.g. trout in mountain streams). In contrast, for unintentional introductions, new regions should not, on average, be better than the native range with respect to resources, competitors and generalist predators. However, on average, those invasions that are successful should be in areas where all aspects of the environment are suitable and some are favourable. In particular, new regions should almost always contain fewer specific, co-evolved natural enemies compared to the native range. While plants and animals are being introduced at an increasing rate (Cohen & Carlton, 1998), their parasites may never reach the new region.

Many introduced species appear to lack most or all of their native, presumably coevolved, natural enemies. Founding populations of introduced vertebrates in terrestrial systems often carry fewer or limited subsets of the parasites found in native regions (Dobson, 1988; Freeland, 1993). Likewise, introduced plants that arrive as seeds often lack natural enemies (Elton, 1958). For marine invasions, larval stages introduced via ballast water lack parasites that can infect adult stages (Lafferty & Kuris, 1996). If a species does not bring its natural enemies with it, it should experience a release in its new geographic range. This release will be of a magnitude proportional to the ecological importance of the natural enemies left behind. By comparing native and introduced populations (Lampo & Bayliss, 1996*a*, *b*; Calvo-Ugarteburu & McQuaid, 1998*a*; Torchin *et al*. 2001) and examining interactions between introduced species and ecologically similar native species (Calvo-Ugarteburu & McQuaid, 1998*b*; Byers, 2000; Callaway & Aschehoug, 2000; Torchin, Byers & Huspeni, unpublished observations), it is possible to evaluate these hypotheses. For example, in Australia, introduced cane toads achieve higher population densities compared to native South American populations. In contrast to the parasite-free introduced populations, native populations may be controlled by ticks which reduce frog biomass (Lampo & Bayliss, 1996*a*, *b*). Although evidence for this exists for terrestrial species, there have been few such comparisons made for marine systems (but see Calvo-Ugarteburu & McQuaid, 1998*a*; Torchin *et al*. 2001).

We focus on parasites because they are ubiquitous and have the potential to affect host growth, reproduction, and survivorship. Both empirical and theoretical evidence suggest that parasites can reduce host density and potentially control host populations (Anderson & May, 1986; Scott, 1987; Kuris & Lafferty, 1992). Parasites can interact directly (metabolically reducing host growth, reproduction, and survivorship) or indirectly (interacting with predation or competition or both) to affect community structure and, thus, are likely mediators of invasion success. Although invasion success is often attributed to an escape from natural enemies, there are only a few studies where this has been systematically examined and the evidence from these is consistent with this hypothesis (Lampo & Bayliss, 1996*a*, *b*; Torchin *et al*. 2001).

To assess the role of parasites in marine invasions, we review reasons why introduced species often leave their natural enemies behind. We define three types of invasion success and explore whether parasites can facilitate the success or failure of introduced marine species. For this, we use a theoretical framework developed to model invasion success. We then compare published studies of introduced species in both their native and introduced geographic ranges to examine the extent to which lack of parasites is a general phenomenon in marine invasions. We also review cases in which infected hosts invade new regions and explore the potential for introduced marine parasites and pathogens to impact native ecosystems. Finally, we discuss the importance of parasites as an indirect impact of invaders on food webs.

RELEASE FROM NATURAL ENEMIES

With Dogiel (1948), Bauer (1991), Kennedy (1994) and Dove (1998, 2000), we recognize that during the process of species invasions in a non-native region there will generally be a reduction in the parasite community and perhaps acquisition of native parasites. There are several reasons why introduced species may invade without their native parasites. Firstly, invasions often occur as a result of the introduction of relatively uninfected stages such as larvae or seeds. Although these stages sometimes harbour infectious agents and parasites, they are typically lost post-recruitment and do not affect other life-history stages (Polyanski, 1961; Rigby & Dufour, 1996; Cribb *et al*. 2000). In marine systems, invading species that arrived in ballast water, generally as larvae (Carlton, 1987), are rarely parasitized (Lafferty & Kuris, 1996). Secondly, even if adults are the source of the invasion, colonization by a low number of individuals reduces the prob-

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ability of introducing parasitized hosts. Thirdly, even if parasites do invade, host population bottlenecks after introduction may break parasite transmission. A fundamental principle of epidemiology is that the spread of a directly-transmitted infectious agent through a population increases with the density of susceptible and infectious hosts (Anderson & May, 1986). Empirical comparative studies support the prediction that intensity and prevalence tend to increase with host population density (Anderson, 1982; Anderson & May, 1986; Arneberg *et al*. 1998). Epidemiological models (McKendrick, 1940; Kermack & McKendrick, 1927; Bailey, 1957) indicate that there is a host-threshold density below which a parasite cannot persist in a host population. Therefore, low-density populations should be less subject to infection by a host–specific infectious disease agent. Observations of the epidemiology of morbillivirus (e.g. measles) of humans (Black, 1966) and cattle (Aune & Schladweiler, 1992) support this prediction, as do the experimental studies of Stiven (1964, 1968) and the field manipulation of host density by Culver & Kuris (2000). This suggests that in a recently introduced host–parasite system, host density will often be too low for the parasite to establish a self-sustaining population. This will be particularly true for inefficiently transmitted (most microbial) diseases. Finally, parasites often have complex life-cycles, which necessitate two or more host species. If suitable hosts for all life cycle stages are not present, establishment will not occur. For example, *Schistosoma mansoni*, introduced with infected humans, established in areas of Latin America where an appropriate first intermediate host snail, *Biomphalaria glabrata*, was present (Rollinson & Southgate, 1987). Although *S. haematobium* was also probably introduced, no suitable first intermediate host snails were present, and, thus, *S. haematobium* never established. Similarly, avian malaria was repeatedly introduced to the Hawaiian Islands, but it was not until the introduction of its mosquito vector that transmission and eventual establishment occurred (Warner, 1969; Van Riper *et al*. 1986).

INVASION SUCCESS

Both the physical environment and biotic interactions will determine the success of an introduction. Using biotic interactions as well as life-history and demographic parameters of an invader, we developed a theoretical framework to model invasion success (Fig. 1). This model illustrates how resources, competition, predation and parasitism can affect invasion success and, perhaps more importantly, how they can interact to do so. We define three types of invasion success for which this model can be used: (1) absolute success (AS) in which the equilibrial biomass of the invader is greater than zero, (2) relative conspecific success (RCS) in which the equilibrial biomass of the invader in its introduced range is greater than the biomass of the invader in its native range (controlling for area) and (3) relative interspecific success (RIS) in which the equilibrial biomass of the invader is greater than the biomass of native competitors in the introduced range (controlling for area). In this model, invasion success is quantified in terms of the biomass of the invader. Biomass is determined by both body size and population density. Growth and survival both positively affect body size while survival and natality both positively affect population density.

Direct effects are those in which a change in species A directly affects species B. Indirect effects are those, which are mediated through other species, for example if a change in species C affects species A, thereby affecting species B (Wootton, 1994). Direct effects are illustrated by arrows in Fig. 1 (and corresponding text). For example, invader growth, natality and survival directly increase with resources. Parasites can directly reduce invader growth and natality. Predators and some parasites directly reduce invader survival. Some parasites can directly negatively affect an invader's predators due to pathological effects of trophically-transmitted parasites on predators. An invader's predators will also directly positively affect some parasites by serving as hosts. Predators can directly reduce the abundance of some competitors. Some parasites can also directly reduce the abundance of an invader's competitors. Indirect effects are generally illustrated by the combination of two or more arrows (direct effects) operating in tandem. For example, resources are shared with competitors, so competitors indirectly decrease invader growth. Parasites and predators can also have an indirect positive effect on growth, survival and natality if they impact competitors, thereby releasing resources. Parasites can indirectly affect predation on the invader if they reduce predator density via pathology or increase predation efficiency by the effects of parasite-increased trophic transmission (Lafferty, 1999). Feedback in the model arises when the biomass of the invader becomes large enough to negatively impact resources and positively affect parasites and predators if the invader becomes a host or prey. Fig. 1 illustrates the potential importance and interconnectedness of resources, competition, predation and parasitism on invasion success. We point out that parasites, in particular, have the most linkages to life-history parameters either directly or through indirect routes via other biotic interactions. This feature contributes to their role in the stabilization of population dynamics, a role that is increasingly recognized (Price *et al*. 1986; Dobson, 1988; Freeland, 1993). Lacking parasites, introduced species may often perturb a system in unexpectedly powerful ways.

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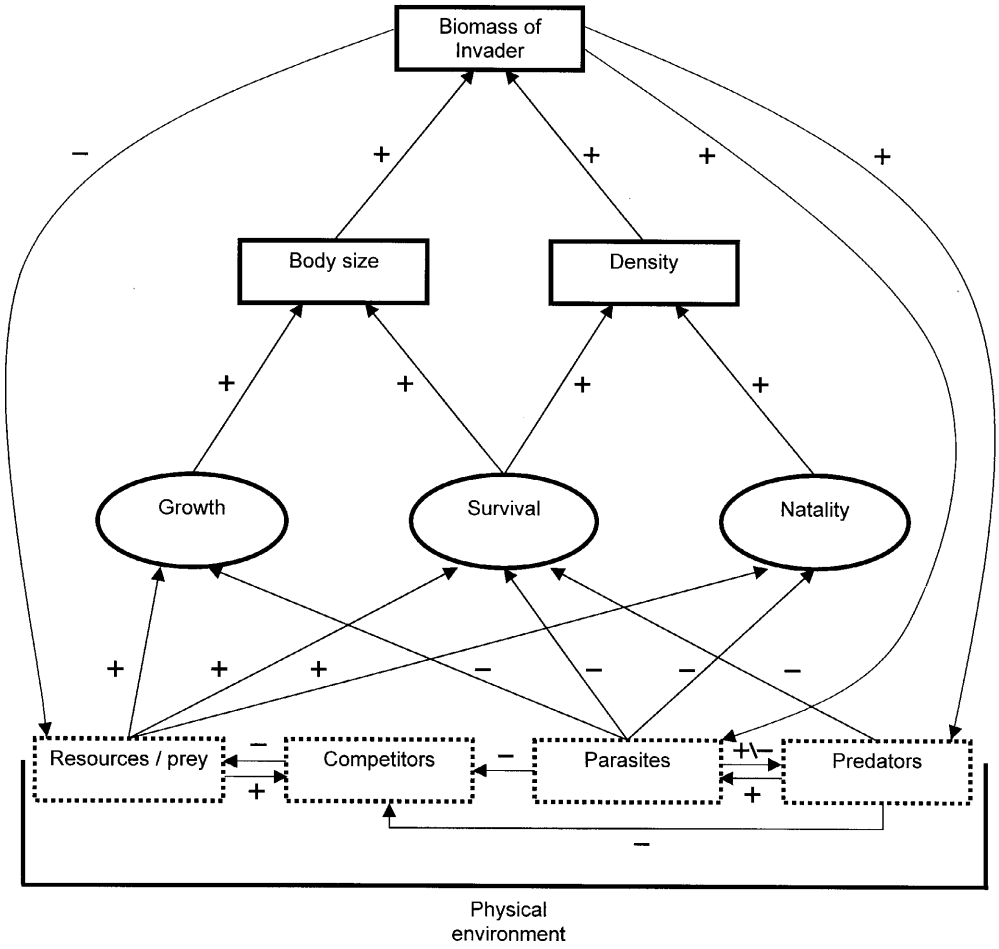


Fig. 1. In this theoretical framework, we consider invasion success to be proportional to invader biomass. This model represents a hierarchy of demographic parameters (solid boxes), life-history parameters (ovals) and biotic interactions (dashed boxes) of the invader. (+) indicates a positive effect, (−) indicates a negative effect and (+/−) indicates that the effect may be in either direction. Note that all biotic interactions are influenced by the physical environment which includes disturbances.

PARASITES IN NATIVE AND INTRODUCED POPULATIONS

To examine the extent to which a release from parasites is a general phenomenon in marine invasions, we compared parasitological studies of invasive species (Table 1). We limited our comparison to a selection of introduced species for which there were readily available studies providing ecological data in both the native and introduced ranges of the invader. We excluded species under culture from our comparison because these species are introduced intentionally and are often medically treated for parasites or have their parasites intentionally manipulated. Cultured species are also typically grown at unnaturally high densities which promotes disease transmission.

Table 1 shows that in native regions there are twice as many studies of parasites and about four times as many hosts examined for parasites from native populations compared to introduced populations. This is a potential bias to detect more species of parasites in the native ranges. However, the large number of hosts examined in both regions makes it unlikely that rarefaction is the cause of detection of fewer species of parasites among the introduced populations. The species richness of parasites found in native regions (mean = 6) is on average three times greater than in introduced regions (mean = 2). The average prevalence of all parasites in the introduced range (30%) is over twice that in the native range (14%). Unlike species richness, prevalence is generally independent of sample size assuming that samples without infected individuals are included (Gregory & Blackburn, 1991). Other general patterns are that species presumably introduced via ballast water (*Hemigrapsus sanguineus*, *Mnemiopsis leidyi*, *Asterias amurensis*) tend to have the fewest parasites in the introduced range. The European green crab, *Carcinus maenas*, also has fewer parasites in regions where it was presumably introduced via ballast water (West Coast of North America, South Africa, Australia and Tasmania). On the East Coast of

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Table 1. Comparison of parasites reported from introduced marine species in both their introduced and native ranges. *Invader* is the introduced host species. *Number of studies* is the number of useable references found, *Number of individuals* is the combined sample size, *Species richness* is the total number of parasite species and *Prevalence* is the average prevalence of all parasite species across all studies examined. n is data for the native range and *i* is data for the introduced range. Grand total (sum) is the sum of the values for all host species. Grand total (avg) is the average of values for all host species. * *Poecilia latipinna* is predominantly a brackish water fish

		Number of studies		Number of individuals		Species richness		Prevalence		
Invader	Parasite group	n	*i*	n	*i*	n	*i*	n	*i*	References
Cancer novaezelandiae (Pie-crust crab)	Trematoda	1	1	37	50	1	0	17	0	1
Carcinus maenas (Green crab)	Fecampida	1	0		—	534	—	7	—	2
	Trematoda	2	3	372	725	2	1	81	25	3, 4, 5, 6
	Cestoda	1	1	372	606	1	2	10	13	1, 6
	Nemertea	3	1	554	1285	1	1	57	26	6, 7, 8
	Acanthocephala	2	2	2311	725	1	1	23	2	4, 6, 9
	Nematoda	2	1	372	606	1	1	—	0	6, 10
	Copepoda	1	1	14	—	1	1	29	—	10, 11
	Rhizocephala	5	1	29437	1442	1	0	21	0	6, 13, 14, 15, 16
	Isopoda	3	1	2401	606	1	0	4	0	6, 13, 14, 17
Total (sum)‡						10	7	225	66	
Total (avg)						1	1	32	9	
Hemigrapsus sanguineus (Japanese shore crab)	Trematoda	1	2	181	1000	1	0	55	0	6, 18
	Nematoda	1	2	181	1000	0	1	0	0	6, 18
	Rhizocephala	2	2	181	1000	1	0	17	0	6, 18, 19
	Isopoda	1	2	181	1000	0	0	0	0	6, 18
	Nemertea	0	2	—	1000	0	0	—	0	6, 18
Total (sum)‡						2	1	72	0	
Total (avg)						0	0	18	0	
Batillaria attramentaria (Japanese mud snail)	Trematoda	3	1	1289	955	7	1	24	24	20, 21, 22, 23, 24†
Ilyanassa obsoleta (Atlantic mud snail)	Trematoda	7	1	23631	3852	11	5	37	31	25, 26, 27, 28, 29, 30, 31
Littorina littorea (Periwinkle snail)	Trematoda	8	3	7943	1169	12	3	37	8	31, 32, 33, 34, 35, 36, 37, 38, 39, 40
Littorina saxatilis (Periwinkle snail)	Trematoda	6	2	6657	2453	19	8	36	26	33, 36, 41, 42, 43, 44, 45, 46
Asterias amurensis (Pacific seastar)	Ciliophora	3	1	1028	2000	1	0	59	0	47, 48, 49, 50
	Copepoda	2	0	381	—	1	—	7	—	47, 48
Total (sum)‡						2	0	66	0	
Total (avg)						1	0	33	0	

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Mnemiopsis leidyi	Cnidaria	1	0	—	—	1	—	—	—	51
(Atlantic Ctenophore)	Trematoda	1	0	100	—	1	—	1	—	52
	Nematoda	0	1	—	—	—	1	—	1	53
	Amphipoda	1	0	—	—	1	—	—	—	54
Total (sum)‡						3	1	1	1	
Total (avg)						1	1	1	1	
*Poecilia latipinna**	Monogenea	1	0	—	—	1	—	—	—	55
(Sailfin molly)	Trematoda	2	1	60	40	15	1	100	85	55, 56
	Nematoda	2	1	60	40	1	0	2	0	55, 56
	Copepoda	2	1	60	40	1	0	28	0	55, 56
	Isopoda	2	1	60	40	1	0	—	0	55, 56
Total (sum)‡						19	1	130	85	
Total (avg)						6	0	65	34	
Grand total (sum)‡				77863	21635	85	27	634	241	
Grand total (avg)				3244	941	6	2	30	13	

References: (1) Kuris & Gurney, 1997; (2) Kuris, Torchin & Lafferty, unpublished; (3) Stunkard, 1956; (4) Brattley *et al*. 1985; (5) Castilho & Barandela, 1990; (6) Torchin *et al*. 2001; (7) Comely & Ansell, 1989; (8) Torchin *et al*. 1996; (9) Thompson, 1985; (10) Plotz, 1982; (11) Gallien & Bloch, 1936; (12) Johnson, 1957; (13) Bourdon, 1963; (14) Rasmussen, 1973; (15) Minchin, 1997; (16) Mathieson *et al*. 1998; (17) Bourdon, 1964; (18) McDermott, 1998; (19) Yamaguchi *et al*. 1994; (20) Shimura & Ito, 1980; (21) Rybakov & Lukomskaya, 1988; (22) Harada & Suguri, 1989; (23) Torchin *et al*. unpublished; (24) McDermott, 1996†; (25) Grodhaus & Keh, 1958; (26) Stambaugh & McDermott, 1969; (27) Curtis & Hubbard, 1990; (28) Curtis, 1997; (29) Curtis & Tanner, 1999; (30) McCurdy, Boates & Forbes, 2000; (31) Pechenick, Fried & Simpkins, 2001; (32) Hoff, 1941; (33) James, 1968; (34) Robson & Williams, 1970; (35) Williams & Ellis, 1975; (36) Pohley, 1976; (37) Hughes & Answer, 1982; (38) Mathews, Montgomery & Hanna, 1985; (39) Laukner, 1987; (40) Evans, Irwin & Fitzpatrick, 1997; (41) James, 1965; (42) Threlfall & Goudie, 1977; (43) Irwin, 1983; (44) Newell, 1986; (45) Bustness & Galaktionov, 1999; (46) McCarthy, 2000; (47) Kuris, Lafferty and Grygier, 1996; (48) Goggin & Bauland, 1997; (49) Byrne *et al*. 1997; (50) Goggin, 1998; (51) Bumann & Puls, 1996; (52) Martorelli, 1996; (53) Gayerskaya & Mordvinova, 1994; (54) Cahoon, Tronzo & Howe, 1986; (55) Hoffman, 1999; (55) Torchin, unpublished data. †We did not include data from McDermott (1996) because repeated assessments of the parasite fauna of introduced populations of *B. attramentaria* are inconsistent with his findings (Torchin *et al*. unpublished). ‡We have included the summed prevalence of all parasite species for a given host (*Total (sum)*) as an indicator of the cumulative impact of parasites on a host species.

North America, where green crabs were introduced over 200 years ago, and not likely via ballast water, introduced populations are more frequently parasitized compared to other introduced populations (Torchin *et al*. 2001.). This may be due to the introduction of adult crabs and the longer residence time of crabs on the East Coast of North America, which could provide a greater opportunity for native parasites to colonize the invader. Further, the East Coast of North America is faunistically quite similar to the Atlantic Coast of Europe and the parasites recovered from the East Coast populations are either conspecific with or closely similar to related European species (Stunkard, 1956; Brattey *et al*. 1985; Thompson, 1985). Although the very extensive geographic range of introduced green crabs (4 regions, 3 continents) compared to its native region (Europe) increases the overall likelihood of introduced crabs being colonized by parasites from those regions, the introduced populations' prevalences are generally lower for the same types of parasites where the green crab is native. Certain types of parasites (parasitic castrators, parasitoids), although locally prevalent in Europe, have never been documented from introduced regions.

Populations of snails introduced as biological contaminants with shellfish (oysters) imported for aquaculture (*Batillaria attramentaria* and *llyanassa obsoleta*) or those intentionally introduced for food (*Littorina littorea* and *L. saxatillis*) typically harbour a subset of the parasite species present in their native range. This suggests that some infected snails were introduced and some of their native parasites became established in the introduced regions. This is a relatively frequent occurrence despite the complex, multihost life cycles of the trematodes that parasitize them. Host specificity, while typically high for the snail first intermediate hosts, is relatively broad for second intermediate hosts and definitive hosts.

Although the rate of marine invasions is increasing dramatically (Zibrowius, 1991; Furlani, 1996; Ruiz *et al*. 1997; Cohen & Carlton, 1998), there are relatively few studies of the parasites of these invaders. A cautious interpretation of the data presented in Table 1 suggests that introduced populations of marine species are less affected by parasites compared to populations in their native range. However, more studies on the parasites of introduced species, both from native and introduced populations, are necessary to better evaluate the role of parasites in the invasion success of exotic marine species. Our preliminary examination of these species suggests a more comprehensive study of randomly-selected introduced species across a broader range of taxa and different environments might reveal important general patterns pertaining to how host specificity, lifecycle stages, trophic categories and methods of introduction relate to the success of exotic species.

INTRODUCED PARASITES

If infected hosts invade a new locale and their parasites become established, these invasive parasites may impact native species if they can recruit to novel hosts. Table 2 illustrates parasite introductions in marine systems. The rhizocephalan barnacle, *Loxothylacus panopaei*, is native to the Gulf of Mexico and southern Florida. It was first discovered in Chesapeake Bay in 1964, presumably introduced with infected mud crabs associated with oysters transplanted from the Gulf of Mexico (Van Engel *et al*. 1965). It now parasitizes three crab species in its introduced range, including two which only appear to be infected within the introduced range (Hines, Alvarez & Reed, 1997). Another rhizocephalan barnacle, *Heterosaccus dollfusi*, followed its portunid host crab, *Charybdis longicollis*, from the Red Sea through the Suez Canal to the Mediterranean Sea. However, while *C. longicollis* invaded the Mediterranean before 1954 and is now well established, its parasite has only recently arrived (Galil & Lützen, 1995; Galil & Innocenti, 1999). This parasite has not been recovered from any species of native crab, nor from other introduced species of portunids, including *C. hellerii*, also native to the Red Sea. Other reports of rhizocephalans introduced with their hosts are anecdotal and lack confirmation (e.g. Boschma, 1972, Kinzelbach, 1965).

Parasitic copepods that infect shellfish have been widely introduced with the transport and culture of bivalves. *Mytilicola orientalis* and *Myicola ostrae* are both parasitic copepods of the Pacific oyster, *Crassostrea gigas*, in Asia, where they are native. *Mytilicola orientalis* has been accidentally introduced to Europe and the Pacific Coast of North America, while *Myicola* has only been reported from Europe (His, 1997; Stock, 1993; Holmes & Minchin, 1995; Minchin, 1996). They were likely introduced with infected oysters imported for culture. Both species infect native bivalves and *M. orientalis* is considered a serious pest (Holmes & Minchin, 1995). *Mytilicola intestinalis*, which was presumably introduced to northern Europe from blue mussels originating in the Mediterranean Sea, may have been transported in its host, *Mytillus galloprovincialis*, on the hulls of ships (Minchin, 1996). In the early 1950s an epidemic of *M. intestinalis* caused considerable damage to mussel fisheries and infections spread to other native bivalve species in the Netherlands (Stock, 1993).

Although exotic monogeneans have been reported more commonly from freshwater fish species than from marine fishes, we briefly review a few examples of monogeneans introduced with catadromous and anadromous fish species. These monogeneans are typically restricted to the freshwater portions of their hosts's life cycles. *Gyrodactylus salaris*, a monogenean of Atlantic salmon, has been introduced to,

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Table 2. Introduced parasites. Asterisks indicate possible introductions

Parasite taxon	Parasite	Introduced region	Native region	Method of introduction	Impacts	References
Rhizocephala	*Loxothylacus panopaei*	ANA	GOM	Aquaculture	Natives	1, 2
	Heterosaccus dolfusi	MED	RED	Migrant	Unknown	3
Copepoda	*Mytilicola orientalis*	EUR, PNA	ASI	Aquaculture	Aquaculture/Natives	4, 5, 6, 7
	Mytilicola intestinalis	N. EUR	MED	Fouling	Fisheries	8, 9
	Myicola ostrae	EUR	ASI	Aquaculture	Aquaculture/Natives	8
Monogenae	*Gyrodactylus anguillae*	AUS, ASI, ANA	EUR?	Aquaculture	Aquaculture/Natives	10, 11
	Pseudodactylogyrus anguillae	EUR, ANA	ASI	Aquaculture	Aquaculture/Natives	12
	Pseudodactylogyrus bini	EUR, ANA	ASI	Aquaculture	Aquaculture/Natives	12
	Gyrodactylus salaries	NOR	—	Stocking	Aquaculture/Natives	13, 14
	**Neobenedenia melleni*	JAP	HKG, HAN	Aquaculture	Aquaculture	15
	Nitzschia sturionis	ARA	CAS	Stocking	Natives	16, 17
Nematoda	*Anguillicola crassus*	EUR, ANA	ASI	Aquaculture	Aquaculture/Natives	18
Trematoda†	*Cercariae batillariae*	PNA	ASI	Aquaculture	Natives	19
Protozoa	Haplosporidia	PNA	JAP	Aquaculture	UnKnown	20
	**Haplosporidium nelsoni*	ANA	ASI	Aquaculture	Aquaculture/Natives	21, 22
	**Bonamia ostreae*	EUR	PNA	Aquaculture	Aquaculture/Natives	9, 23
	**Perkinsus marinus*	N. ANA	S. ANA	Aquaculture	Aquaculture/Natives	24
	**Paramoeba invadens*	N. ANA	Unknown	Unknown	Natives	25
Polychaeta	*Terebrasabella heterouncinata*	PNA	SAF	Aquaculture	Aquaculture/Natives	26, 27

Regions are: ANA Atlantic North America, MED Mediterranean, EUR Europe, PNA Pacific North America, AUS Australia, ASI Asia, NOR Norway, JAP Japan, ARA Aral Sea, GOM Gulf of Mexico, RED Red Sea, HKG Hong Kong, HAN Hainan, CAS Caspian Sea, SAF South Africa. References: (1) Van Engel *et al*. 1965; (2) Hines *et al*. 1997; (3) Galil & Lutzen, 1995; (4) His, 1977; (5) Stock, 1993; (6) Bernard, 1969; (7) Holmes & Minchin, 1995; (8) Stock, 1993; (9) Minchin, 1996; (10) Hayward *et al*. in press; (11) Ernst *et al*. 2000; (12) Hayward *et al*. 2001; (13) Johnsen & Jensen, 1991; (14) Hastein & Lindstad, 1991; (15) Ogawa *et al*. 1995; (16) Osmanov, 1971; (17) Zholdasova, 1997; (18) Barse & Secor, 1999; (19) Torchin, Byers & Huspeni, unpublished data; (20) Friedman, 1996; (21) Barber, 1997; (22) Andrews, 1980; (23) Chew, 1990; (24) Ford, 1996; (25) Scheibling & Hennigar, 1997; (26) Kuris & Culver, 1999; (27) Culver & Kuris, 2000. †Grodhaus & Keh (1958) report the invasive *Ilyanassa* (=*Nassarius*) *obsoletus* in San Francisco Bay, California to be infected with five larval trematode species (See Table 1). We suspect that they are likely introduced as well.

and now infects, wild salmon stocks in Norway. It causes heavy mortality in salmon parr (Johnsen & Jensen, 1991). It appears to have been introduced to Norway by stocking rivers with infected fish from Sweden (Johnsen & Jensen, 1991). *Gyrodactylus salaris* was geographically isolated in rivers because it could not survive in brackish or marine water. However, it was spread by the movement of infected fish among hatcheries (Johnsen & Jensen, 1988). Another monogenean, *Neobenedenia melleni* (= *girellae*), is a pest of marine fishes. Ogawa *et al*. (1995) suggest that this parasite was introduced to Japan with amberjack, *Seriola dumerili*, imported from Hainan and Hong Kong. This parasite has spread from the imported amberjack to cultured local marine fishes and causes mortality in heavily infected fish. Introduced monogeneans are pests in the eel trade. They often cause mortality and are capable of infecting native eel species (Hayward *et al*. 2001, in press). *Pseudodactylogyrus anguillae* and *P. bini* were introduced from Asia to North America and Europe with the importation of the Japanese eel, *Anguilla japonica* (Hayward *et al*. 2001). Both species now infect wild populations of the native North American eel, *Anguilla rostrata* (Cone & Marcogliese, 1995; Hayward *et al*. 2001) and wild populations of the native European eel, *Anguilla anguilla* (Gelnar *et al*. 1996; Hayward *et al*. 2001). Another probable invader, *Gyrodactylus anguillae*, occurs on four continents. It was likely introduced from Europe through the importation of infected European eels (Hayward *et al*. in press).

Another serious pest of eels is the swim bladder nematode, *Anguillicola crassus*. Native to Asia, *A. crassus* has been introduced to Europe and North America where it now infects native eels in both natural and cultured conditions (Barse & Secor, 1999). *Anguillicola crassus* can reach high prevalences in native eel populations and it can cause severe pathology in European and North American eels (Barse & Secor, 1999). Yet another parasite introduced with the importation of fish is the gill monogenean, *Nitzschia sturionis*. The first stocking of the stellate sturgeon from the Caspian to the Aral Sea introduced this monogenean. It caused massive mortality of the native ship sturgeon in the 1930s (Osmanov, 1971; Zholdasova, 1997).

The Japanese mud snail, *Batillaria attramentaria*, was accidentally introduced to the West Coast of North America with the importation of oysters for aquaculture (Bonnot, 1935). It now has a disjointed distribution: populations occur in Boundary Bay, British Columbia; Padilla Bay, Washington; Tomales Bay, California; Drakes Estero, California; Bolinas Lagoon, California and Elkhorn Slough, California (Byers, 1999). Although introduced populations of *B. attramentaria* are not infected with native trematodes, they are often infected, sometimes at high prevalences, with an exotic trematode (Torchin, Byers & Huspeni, unpublished observations). This trematode, *Cercaria batillariae*, whose adult form has still not been described nor is its life cycle fully known (Shimura & Ito, 1980), likely parasitized some of the *B. attramentaria* associated with imported oysters. On the West Coast of North America, this trematode uses native fishes as second intermediate hosts and native birds as final hosts.

There are several marine protozoan parasites that are apparently introduced. Most are parasites of oysters, presumably introduced with infected aquaculture stocks. *Haplosporidium nelsoni*, agent of MSX disease, which caused massive mortalities of native oysters in Delaware and Chesapeake Bay may be introduced from Asia (Andrews, 1980; Barber, 1997). Undocumented introductions of the Japanese oyster, *Crassostrea gigas*, may have been the source of the invasion (Barber, 1997). Haplosporidian infections, that closely resemble *H. nelsoni*, were also found in *C. gigas* imported to California from Japan (Friedman, 1996). *Bonamia ostrae* which infects native European oysters may have been introduced from California (Chew, 1990). It was presumably introduced to France with a shipment of *Ostrea edulis*, cultured in California from broodstock originating in the Netherlands (Barber, 1997). It has since spread throughout Europe. The argument that it is introduced and not native to Europe stems from the fact that epizootics of *B. ostrae* were not recorded in Europe until 1979, soon after the introduction of oysters from California (Barber, 1997). There is also some evidence that the recent range extension of the oyster parasite, *Perkinsus marinus*, is a result of repeated introductions of infected native oysters to the northeastern USA (Ford, 1996). Recent outbreaks of the marine amoeba, *Paramoeba invadens*, have caused mass mortalities in the sea urchin, *Strongylocentrotus droebachiensis*, in the North Atlantic coast of Canada. *Paramoeba invadens* may be an exotic species, but further research is needed to determine its origin (Scheibling & Hennigar, 1997). The sabellid worm, *Terebrasabella heterouncinata* was accidentally imported from South Africa with infested abalone and became a major pest in abalone mariculture facilities in California in the early 1990s (Kuris & Culver, 1999). Although it does not derive any nutrition from its host, it infests the host's shell causing abnormal shell growth and heavily infested abalones do not grow (Kuris & Culver, 1999). This worm became established in nature near a mariculture facility where it infested abalone and other susceptible native gastropods. It has since been apparently eradicated by manually reducing the densities of potential host snails to levels too low for transmission to occur (Culver & Kuris, 2000).

Epizootics of previously undocumented parasites should not, *de facto*, be considered introduced species just because they are associated with the introduction of exotic hosts. If previously rare local

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infectious agents are eventually able to colonize introduced hosts that have already achieved a high abundance, this could fuel epizootics of such infectious agents. For putative parasite introductions associated with exotic hosts, examining hosts in the native range for parasites is the key to understanding the source of newly discovered parasites. Considering the number of introduced marine species (Zibrowius, 1991; Furlani, 1996; Ruiz *et al*. 1997; Cohen & Carlton, 1998), it is notable that there are relatively few reports of introduced marine parasites (and they are not included in the lists cited above). There are two probable explanations for this. Introduced parasites are understudied and it is rare that parasites accompany accidentally introduced hosts. We believe that both factors likely operate. An overwhelming majority of the exotic parasites in Table 2 have been introduced along with intentionally introduced hosts cultured by the aquaculture industry. The introduction of adult hosts from high host density to another region where hosts are kept at high densities is likely to facilitate the introduction and transmission of exotic parasites and diseases. Recently, recognition of this problem, with inspections and quarantine, has led to more cautious husbandry practices, and we predict that the role of aquaculture as a vector for unwanted introductions will decline. We also note that introduced parasites are more likely to be discovered in cultured species which are rigorously examined for diseases.

INDIRECT IMPACTS OF INVADERS ON NATIVE PARASITES AND HOSTS

Parasites may indirectly influence the impact of an introduced species in a novel environment. For example, when exotic species exclude native species, parasites specific to these native species will be excluded as well. If parasites with complex life cycles are excluded from the ecosystem there may be indirect effects on the suite of former hosts. As previously discussed, the Japanese mud snail *Batillaria attramentaria*, was introduced to the West Coast of North America. At the southern end of its introduced range, it overlaps with the California horn snail, *Cerithidea californica*. Both snails compete intensely for food (Whitlatch & Obrebski, 1980; Byers, 2000) and *B. attramentaria* appears to be competitively excluding *C. californica* (Carlton, 1975; McDermott, 1996; Byers, 2000; Byers & Goldwasser, 2001). *Cerithidea californica* serves as first intermediate host for at least 18 native trematode species throughout its range in California (Martin, 1972). Most of these trematodes are trophically-transmitted through the marsh community, infecting multiple hosts during their life cycle. If *C. californica* is excluded where it overlaps with *B. attramentaria*, its parasites will become locally extinct since none are known to infect alternative first intermediate hosts, including *B. attramentaria*. Although the precise manifestations of these local extinctions on the marsh community remain unclear, the removal of several native trematode species due to local extinction of their first intermediate host will consequently eliminate infection by the trematodes in the second intermediate host molluscs, crustaceans and fishes. Because some trophically transmitted parasites markedly increase the likelihood of predation of infected second intermediate hosts by final hosts (Holmes & Bethel, 1972; Lafferty & Morris, 1996; Lafferty, 1999), we predict that the loss of trematodes will reduce predation rates on these second intermediate hosts. This may then have a cascading effect, potentially altering the foraging strategies and abundances of the shore birds that serve as final hosts (Lafferty, 1992; Lafferty & Morris, 1996).

Another example of an invader with indirect effects in a native ecosystem is the introduced alga, *Caulerpa taxifolia*. In areas of the western Mediterranean Sea, *C. taxifolia* appears to be interfering with parasite transmission (Bartoli & Boudouresque, 1997). Trematodes which normally infect a native fish are absent in areas where *C. taxifolia* is present, yet they are prevalent in control sites without *C. taxifolia*. Bartoli & Boudouresque (1997) propose that the secondary metabolites produced by *C. taxifolia* may be responsible for the disappearance of these trematodes, rather than a reduction in the number of first intermediate hosts. It is also possible that the reduction in abundance and biodiversity of hosts other than molluscan first intermediate hosts could interrupt transmission of trematode life cycles in the *C. taxifolia* beds.

CONCLUSION

The pervasiveness of parasites calls for our increased attention to their role in the success and impacts of exotic species as well as their potential impacts as invaders. Our analysis of Table 1 supports the hypothesis that introduced species are typically released from specific natural enemies, namely, parasites. This calls for an additional comparison of the parasites of introduced species with those of sympatric and ecologically equivalent native species to further evaluate the role of parasites in invasion success, as well as, the impacts of the invader in the novel environment. While our focus is on the role of parasites in marine invasions, we recognize the importance of other biotic interactions and hope to illustrate the broader context in which parasites are embedded in these. As economic globalization continues, the unintentional introduction of exotic marine species will increase. Understanding pathways of accidental introductions will help reduce

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unwanted introductions. However, once established, understanding the reasons for the success of exotic species may help reduce the impacts of these invaders. The available evidence indicates that the release of introduced species from their native natural enemies, particularly parasites, is a significant contributor to their pest status.

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