Chapter 11
Escape from Parasites

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11.1 Introduction

In betting circles, the odds-on favorite of a sporting match can depend on the health of the star players; a pulled hamstring or bad flu can determine the winner. Introduced species are often in contest with native species and their impacts are directly proportional to their demographic performance in the novel environment. Demographic performance can encompass population level parameters, such as densities, abundances, and biomass as well as individual level parameters, such as growth rate, survivorship and fecundity. One indication of an invader's demographic performance is size because individuals that grow fast or live long can become large. On average, marine invaders attain larger sizes compared to populations in their native range (Grosholz and Ruiz 2003). This increased performance, if it translates into increased standing biomass, should positively correlate with an invader's impact (Crivelli 1983). Exploring reasons for invasion success will not only accelerate our understanding of species interactions, but will strengthen our ability to manage invasions.

Debate as to what factors facilitate invasion success has led to quantitative evaluation of a long-standing explanation for successful introduced species: the enemy release hypothesis (ERH). One prediction of the ERH is that introduced populations lack natural enemies compared to populations within their original range (Williams 1954; Elton 1958). Another prediction of the ERH is that introduced species should benefit from enemy-mediated competition because they are less likely to be affected by natural enemies than their native competitors (Elton 1958; Keane and Crawley 2002). Here, the first prediction requires a comparison of the same species across native and introduced populations. The second prediction requires a comparison of populations of an introduced species with populations of one or more native species which coexist in the same community as the invader (generally competitors). These fundamentally different predictions are sometimes confused and lead to misleading evaluations of the ERH. The two predictions are not comparable or mutually exclusive. For example, a population of an introduced species might be similarly affected by natural enemies compared to sympatric pop-

ulations of native species. However, the invading population may still experience enemy release compared to conspecific populations in the native range. The effects of natural enemies on a species are a function of the total number of natural enemies, their mean abundance and their individual impacts at the population level (Torchin and Mitchell 2004). Therefore, release can occur through losing natural enemies (enemy escape), or having increased resistance or tolerance to existing natural enemies. Below, we consider parasites as the main category of natural enemies, recognizing that other natural enemies are important. We generally limit our comparisons to the number of parasite species per host species. Although the number of parasite species is the easiest metric to use for evaluating broad patterns, Torchin and Mitchell (2004) note that other aspects of parasitism such as pathology and the prevalence or intensity of infection can lead to important variation in the effects of parasitism among parasite species. Developing research strategies to broadly evaluate these factors will ultimately enable a more robust examination of the ERH.

The number of parasite species that attack an introduced species is a function of the number of parasites it has in its native range, minus the number it escapes during the introduction, plus the number it acquires in the introduced range. The difference between the number of parasite species in populations of hosts in the native and introduced ranges is perhaps the most simplistic measure of parasite release. A more comprehensive measure of parasite release is a function of number of parasite species, their mean abundance and their virulence, accounting for possible interspecific interactions amongst them (Torchin and Mitchell 2004). Evidence from plants (Fenner and Lee 2001; Wolfe 2002; Mitchell and Power 2003; DeWalt et al. 2004) and animals (Cornell and Hawkins 1993; Torchin et al. 2003) indicates that introduced populations experience a net reduction in parasitism (both in terms of species richness and prevalence within a host population) compared to conspecific populations from the native range. Studies of terrestrial species provide the bulk of the insight on how introduced species escape their parasites; based on a literature search using the ISI Web of Science,18 of the 19 recent papers specifically mentioning the enemy release hypothesis concerned terrestrial plants. Still, information is emerging for some marine invasions (Calvo-Ugarteburu and McQuaid 1998a, b; Torchin et al. 2001, 2002, 2005; Bachelet et al. 2004). Of the 26 animal species Torchin et al. (2003) examined, aquatic species (n = 15, both marine and freshwater) experienced a greater release from parasites than terrestrial species (Fig. 11.1). Release may not be permanent. Parasites can accumulate on introduced populations over time as more opportunities for parasites to invade or adapt to the invader increase (Cornell and Hawkins 1993).

Enemy release should usually benefit an invader in its new range, but for it to lead to a net demographic advantage relative to other species in the community depends on the direct and indirect effects of parasites on native competitors and the relative strength of competition. Both native and introduced parasite species can attack a native competitor (introduced parasites are an important consideration we do not explore in this chapter). The parasite advantage for an invader should be proportional to the impact of parasitism on a competing native host species minus
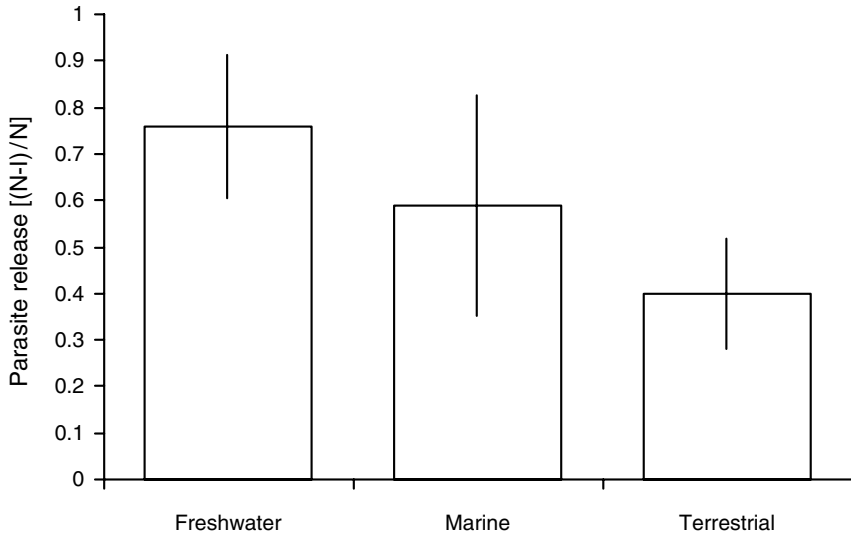
Fig. 11.1 Parasite release (species richness) experienced by introduced species in different habitats. Data are from Torchin et al. (2003). Release is the proportion (N−I)/N, where N is the number of parasite species in the native range and I is the number of parasite species in the introduced range. *Error bars* are 95% confidence intervals calculated using the standard deviation of the mean

the impact of parasites on the introduced host species (Torchin and Mitchell 2004). Sometimes, as evidenced by literature on plants, natural enemies can have similar impacts on sympatric native and introduced species (Blaney and Kotanen 2001; Agrawal and Kotanen 2003). This may be particularly true if invaders are sympatric with closely related native species, as host shifting may be more common, increasing the accumulation of parasites on invaders (Torchin and Mitchell 2004).

11.2   Reasons for Parasite Escape

The invasion process can filter out parasites in several ways (Fig. 11.2). First, species invasions, and the establishment of introduced populations, are often the result of a few colonists arriving and reproducing in the new environment. This, and the fact that parasites are generally not homogenously distributed among host populations, reduces the likelihood of introducing parasitized hosts (Fig. 11.2a). This is similar to the "bottle-necking" mechanism that can reduce the genetic diversity of invading population (Tsutsui et al. 2000). Second, even if parasitized hosts invade a new location, the low density of founder populations may impair parasite transmission. Thus, invaders may escape directly transmitted parasites, which require a minimum host density for transmission (Fig. 11.2b). Third, many
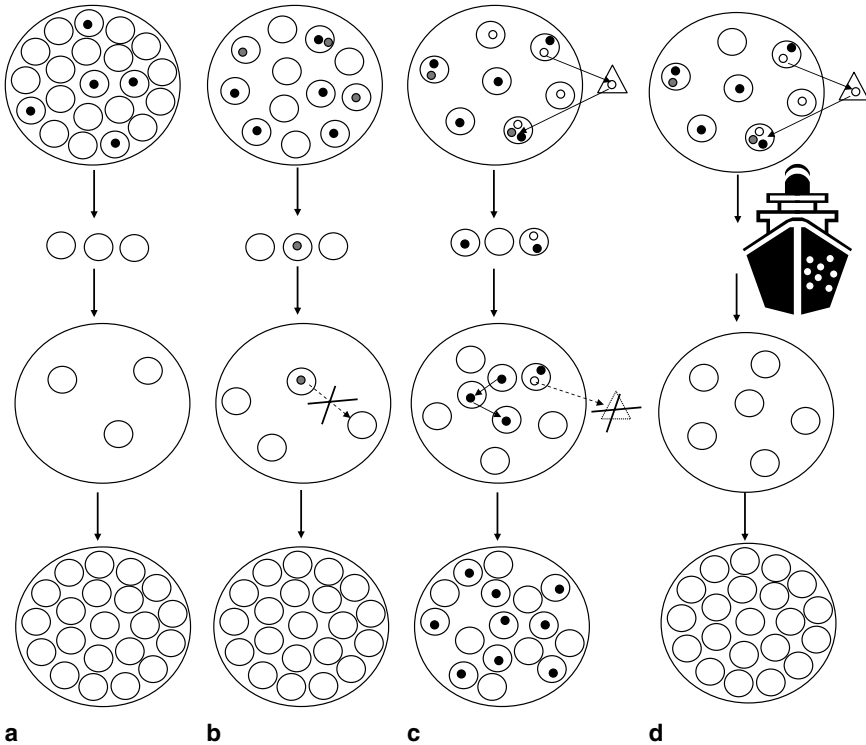
Fig. 11.2 Diagrammatic representation of the reasons (mechanisms) for parasite escape: *Large circles* are host populations, *medium circles* are host individuals, *small circles* represent parasite species: **a** few colonists and heterogeneously distributed parasites reduce the chances that parasitized hosts will be introduced; **b** small founder populations with host densities too low for parasite transmission prevent successful establishment of co-introduced parasites; **c** parasites with complex life cycles requiring more than one host (triangle is additional required host species) will not establish if suitable hosts are not present in new range – however, for directly transmitted parasites, when introduced population densities exceed the threshold for parasite transmission introduced parasites may establish; **d** introduction of uninfected larval stages, such as those introduced by ballast water will exclude parasites from transferring to novel location. Ballast water introduction may be particularly potent means for marine species to escape parasites

parasites have complex life cycles requiring the presence of more than one host. If suitable hosts are not present in the novel environment, complex life cycle parasites will not establish (Fig. 11.2c). Finally, introduction of uninfected life-history stages, such as larvae or seeds, will preclude most parasites which are infectious to adults. While these stages can harbor parasites, parasites of larvae are often lost post-recruitment and generally do not infect adult stages (Rigby and Dufour 1996; Cribb et al. 2000). This mechanism may be particularly important for marine and aquatic species that arrive as larvae in ballast water (Fig. 11.2d) (Lafferty and Kuris 1996).

11.3   Consequences of Parasite Release

For parasite release to confer an advantage requires that parasites negatively affect host populations. Mathematical models indicate that the spread and impact of a directly transmitted infectious disease agent through a population increases with the density of susceptible and infectious hosts. This means that parasites can be density-dependent sources of mortality or reproductive impairment – a prerequisite for being able to regulate populations (Anderson and May 1979). Laboratory experiments where parasites are added to an uninfected host population or where parasites are removed from an infected host population have demonstrated that parasites can limit host populations (Greenwood et al. 1936; Park 1948; Stiven 1964; Keymer 1981; Lanciani 1982; Anderson and Crombie 1984; Scott and Anderson 1984 Scott 1987). Experiments with a parasitic nematode and red grouse (Hudson and Dobson 1989; Dobson and Hudson 1992; Hudson et al. 1998) demonstrate that parasites can regulate host populations in nature. The importance of parasites in driving host population demographics and ecosystem function is becoming evident (reviewed in Hudson et al. 2006). Understanding the role of parasites in natural systems is a key step in determining the importance of their absence for some invasive species.

11.4   Fishes

Although limited, studies examining parasitism in introduced and native populations of marine and estuarine fishes are beginning to emerge. The rabbitfish, *Siganus rivulatus*, provides one example of the potential for fish to escape natural enemies and experience enemy release. Twenty-two species parasitize the rabbitfish in its native Red Sea (Diamant et al. 1999). Rabbitfish have migrated to the Mediterranean through the Suez Canal, and the lack of genetic differentiation between introduced and native rabbitfish populations suggests that many individuals made the trip (Bonhomme et al. 2003; Hassan et al. 2003). It is no surprise, therefore, that eight species of rabbitfish parasites (mostly protozoans) have also invaded the Mediterranean. None of these have complex life cycles (Diamant et al. 1999), suggesting that a lack of appropriate intermediate hosts may limit some Red Sea parasites from establishing in the Mediterranean (Fig. 11.2c). Only one new parasite (a ciliate) has successfully colonized rabbitfish in the Mediterranean (Diamant et al. 1999). The rabbitfish is now abundant in the Mediterranean (Bonhomme et al. 2003), perhaps thanks to an escape from parasitism.

A euryhaline invader, the round goby, *Neogobius melanostomus*, is native to the Ponto-Caspian region where it is parasitized by 50 species with typical prevalences of 100% and intensities of 1000 parasites per fish (Pronin et al. 1997; Corkum et al. 2004). It has now invaded the Baltic Sea and the Laurentian Great Lakes, presumably via ballast water or movement through shipping lanes (Corkum et al. 2004). Goby

populations in the Great Lakes have fewer parasites (10 species, 76% prevalence) compared to native populations (Pronin et al. 1997). Baltic populations have even fewer parasites (four species, 4–20% infection prevalence). Pronin et al. (1997) suggests the lack of parasites in the Great lakes may be partly due to limited parasitic infections in the zebra mussel (*Dreissena polymorpha*), another introduced species originating from the same location as the round goby. The zebra mussel serves as an intermediate host for several of the parasites infecting the round goby in its native range (Pronin et al. 1997), but introduced populations are generally less parasitized compared to native populations (Molloy 1998). This situation may not be stable. Co-invasion by two potential hosts opens the door to a variety of Ponto-Caspian parasites with complex life cycles.

11.5   Molluscs

Marine species introduced via aquaculture provide a unique vector for accidental introductions, including parasites. Historic aquaculture practices often introduced large quantities of adult individuals of many species (both wanted as well as unwanted hitchhikers) (Naylor et al. 2001; Chap. 5, Minchin et al.). Large quantities and repeated introductions likely facilitate transfer and establishment of introduced parasites better than other introduction pathways (Torchin et al. 2002, 2003, 2005).

The Asian mud snail, *Batillaria attrementaria* is one such aquaculture introduction. Introduced to the west coast of North America as a byproduct of Pacific oyster (*Crassostrea gigas*) aquaculture from Japan (Bonnot 1935; Barrett 1963), *B. attrementaria* populations now occur from Southern Canada to Central California (Byers 1999). While in its native range, *B. attrementaria* is infected with at least eight different morphologically distinct trematode species (Shimura and Ito 1980; Rybakov and Lukomskaya 1988; Harada and Suguri 1989; Torchin et al. 2005), only a single trematode species (apparently from Japan) infects introduced populations in North America (Torchin et al. 2005). This introduced trematode was the most geographically widespread and abundant species within Japan (Torchin et al. 2005; Miura et al. 2005), evidence that common parasite species are the ones most likely to invade (Torchin et al. 2003). In some invaded locations, *B. attrementaria* encounters a very similar native competitor, *Cerithidea californica* (Byers 2000). This native snail has a rich trematode fauna, including a species that uses it as a first and second intermediate host (*B. attrementaria* only serves as a first intermediate host to its introduced parasite) (Torchin et al. 2005). None of these species are able to infect *B. attrementaria*.

Batillaria attrementaria is outcompeting the native *C. californica* where they co-occur (Byers 2000). From a traditional food-web perspective, replacement of one species by an ecological analog should have no detectable effect on food-web topology. However, Torchin et al. (2005) posit that the replacement of the native snail would also result in the replacement of ten or more native trematodes with one

Japanese trematode. This has implications for parasite diversity and could also reduce parasitism in the invertebrate community. For example, the trematodes that parasitize the native snail have life cycles that use crabs, polychaetes, mollusks and fishes as second intermediate hosts, while the Japanese trematode only uses fishes. In a food web that considers parasites and their effect on trophic interactions, Lafferty and Kuris (in press) found that the high host specificity of trematodes for the snail hosts, the low diversity of trematodes in the introduced snail and the local extirpation of the native snail results in a large decrease in connectance in the estuarine food web.

As an aside, it is worth noting that the ability to document parasite release can be a function of the capability to find and identify parasites. Recent molecular investigations found multiple cryptic trematode species in *B. attrementaria* in Japan (Miura et al. 2005) and a complex of three cryptic species in North America (Miura et al. 2006). Regardless, compared to native populations in Japan, introduced populations still experience a significant reduction in parasite species richness.

Another snail to invade California along with oysters is the Atlantic mud snail, *Ilyanassa obsoleta* (Demond 1952; Carlton 1999). Similarly, this snail has escaped many of its parasites. There are five trematode species reported to infect *I. obsoleta* in its introduced range (Grodhuas and Keh 1958) – about half the number recorded from populations where this snail is native (Stunkard 1983; Curtis 1997). One of these is probably an introduced trematode, *Austrobilharzia variglandis*, which causes swimmer's itch in humans (Miller and Northup 1926; Stunkard and Hinchliffe 1952; Grodhuas and Keh 1958). The remaining four unidentified species (Grodhuas and Keh 1958) are possibly a subset of *I. obsoleta's* native suite of parasites as well (Torchin et al. 2002; Torchin and Kuris 2005), but this awaits study.

Another recently established gastropod species, *Cyclope neritea* in the Bay of Biscay, was likely accidentally introduced through shellfish culture practices (Bachelet et al. 2004). In its native range in the Mediterranean, *C. nerita* can be heavily parasitized by trematodes (Bachelet et al. 2004), but appears to have escaped parasitism in the introduced range (1% prevalence with one trematode species). This likely gives it a parasite advantage over a native competitor, *Nassarius reticulatus*, (6–18% prevalence with six trematode species) because infected *N. reticulatus* exhibit reduced survivorship (Bachelet et al. 2004).

Introduced to South Africa, the Mediterranean mussel, *Mytilus galloprovincialis* competes with the native mussel, *Perna perna* and has a parasite advantage. While two pathogenic trematode species infect the native mussel, the introduced mussel remains uninfected (Calvo-Ugarteburu and McQuaid 1998a, b). These parasites reduce the native mussel's competitive ability against the invader and may partly explain the invasion success of the Mediterranean mussel in South Africa (Calvo-Ugarteburu and McQuaid 1998a, b). Despite the parasite advantage, it is not clear whether this an example of escape from natural enemies. Although native populations of *M. galloprovincialis* harbor trematodes (Cheng 1967), they are not com-

mon in northern Spain (Calvo-Ugarteburu and McQuaid 1998b) where the invasion may have originated.

11.6   Crabs

In its native Japan, the intertidal crab, *Hemigrapsus sanguineus*, is infected by a parasitic castrator (rhizocephalan barnacle, up to 64% prevalence) (Yamaguchi et al. 1994) and trematode metacercariae (A. Kuris and K. Lafferty, unpublished data). The crab recently invaded the East Coast of the USA where it is large and abundant (Lohrer et al. 2000). Parasitological examination of over 1000 introduced crabs from New Jersey failed to recover any parasites (McDermott 1998) from introduced *H. sanguineus*, but, Torchin et al. (2001) found one out of 27 introduced crabs from New England infected with a nematode. A similar parasitological comparison of the New Zealand pie crust crab, *Cancer novaezelandiae*, found abundant trematode metacercariae in a native New Zealand population and no parasites in Tasmania where the crab has been introduced (Kuris and Gurney 1997).

   The European green crab, *Carcinus maenas* has invaded several locations around the world. Torchin et al. (2001) examined several populations of the green crab both in its native range in Europe and introduced populations around the world. In Europe, the crab's demographic performance (individual size and biomass) declines with the prevalence of parasitic castrators (which block reproduction and stop growth). Parasitic castrators explain 64% of the variation in crab size and 36% of the variation in crab biomass. Parasitic castrators do not infect introduced populations. As one would expect from the association between parasitism and performance in Europe, introduced populations of the green crab are significantly larger in body size and population biomass than native populations with parasites. The introduced populations are most similar to the few European populations where parasitism is rare. A few generalist and relatively non-pathogenic parasite species infect some of the introduced populations. This tends to occur in the populations that invaded a relatively long time ago. Parasite species richness increases in older introductions (Table 1 in Torchin et al. 2001) and time since introduction accounts for over 80% of the variance in the number of parasite species found in the introduced populations (Fig. 11.3).

11.7   Conclusion

Evidence that introduced marine species escape parasites is emerging. The extent to which they accumulate parasites in the novel region generally does not make up for the loss on ecological time scales. This leads to enemy release and makes it more likely that they will have a parasite advantage over competitors. The extent to
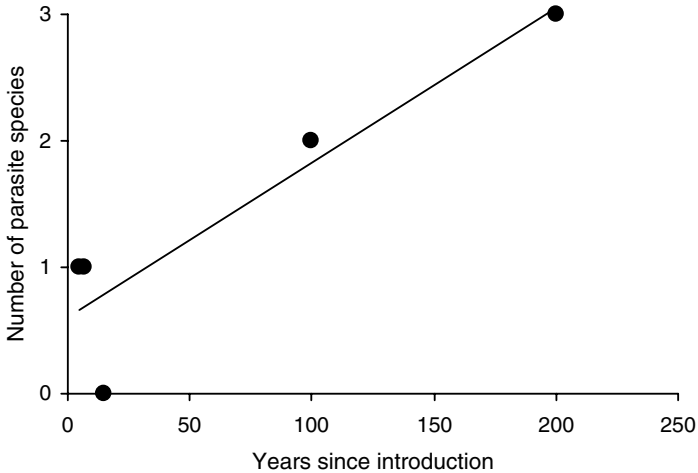
Fig. 11.3 Association between number of parasites found (Torchin et al. 2001) and time since introduction for introduced populations of the European green crab, *Carcinus maenas*. y= 0.01x + 0.6, R^2 = 0.83, P = 0.03

which this facilitates their demographic expansion and success in their introduced range remains an important question.

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