

Chapter 16

IMPACTS OF BIOLOGICAL
INVASIONS ON
FRESHWATER
ECOSYSTEMS

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16.1 INTRODUCTION: A BRIEF HISTORICAL PERSPECTIVE

The human-assisted spread of non-indigenous fishes and aquatic invertebrates, microbes and plants has had strong ecological impacts in lakes and rivers worldwide (see, for example, Nesler & Bergersen 1991; Witte et al. 1992; Flecker & Townsend 1994; Hall & Mills 2000; Latini & Petrere 2004). Cumulative invasions have disproportionately transformed freshwater communities such that they are dominated by non-indigenous species to a greater extent than their terrestrial counterparts (Vitousek et al. 1997). Although some lakes and rivers have documented invasion histories spanning several decades (see, for example, Mills et al. 1996; Hall & Mills 2000; Ricciardi 2006; Bernauer & Jansen 2006), the ecological impacts of freshwater invasions were rarely studied until many years after the publication of Elton's (1958) influential book. Until the late 20th century, concern over freshwater invasions focused almost exclusively on the economic impacts of pest species, particularly those that threatened fisheries (Morton 1997). Earlier reports of impacts on freshwater biodiversity (for example, Rivero 1937; Sebestyen 1938) were rare and largely ignored. However, two dramatic examples were well documented. The first was the spread of a fungal pathogen that destroyed native crayfish populations throughout Europe starting in the 1870s and continuing for several decades (Reynolds 1988). The second was an example highlighted by Elton (1958): the invasion of the upper Great Lakes by the parasitic sea lamprey *Petromyzon marinus*, which contributed to the destruction of commercial fisheries (Mills et al. 1993).

Nevertheless, by the end of the 20th century it became apparent that freshwater fishes had been introduced to virtually everywhere on the planet and that the impacts of most of these introductions were completely unknown (Lever 1996), although cases were accumulating. In a landmark study, Zaret & Paine (1973) demonstrated cascading food-web effects of an introduced piscivore in a Panamanian lake; theirs is among the most highly cited of impact studies. The first syntheses of the impacts of introduced freshwater fishes indicated a wide array of ecological effects arising from predation, competition, hybridization, disease transfer and habitat modification (Moyle 1976; Taylor et al. 1984; Moyle et al. 1986). These negative effects were viewed as surprising at the time because, as Moyle and colleagues (1986) noted, fish introduc-

tions were generally made with the assumption that the new species filled a 'vacant niche' and thus would integrate into their communities without consequence. This assumption was further disputed by the 1990 international symposium 'The Ecological and Genetic Implications of Fish Introductions', which offered the first global perspective of the effects of fish introductions in case studies from Europe, Africa, Australasia, tropical regions of Asia and America, and North America (see Allendorf 1991, and references therein). It concluded that any beneficial effects of fish introductions were immediate, whereas detrimental effects were delayed and often overlooked, but could constitute a threat to the persistence of native populations (Allendorf 1991).

For decades, freshwater invertebrates were transplanted into lakes and rivers to supplement the diets of sport fishes. During the 1970s, the first negative impacts of non-indigenous freshwater mysid shrimp were documented in multiple countries and, as in other cases of introduced predators, revealed far-reaching effects on benthic communities, phytoplankton, zooplankton and the upper trophic levels of food webs in North American and Scandinavian lakes (Nesler & Bergersen 1991; Spencer et al. 1991). During the 1980s, surging interest in conservation provided further impetus for investigating the effects of invasions on freshwater biodiversity, spurred on by dramatic impacts of the Nile perch *Lates niloticus* in Lake Victoria (Witte et al. 1992) and the zebra mussel *Dreissena polymorpha* in the North American Great Lakes (MacIsaac 1996).

Indeed, there has been a rapid increase in studies on freshwater invasions over the past two decades (MacIsaac et al., this volume). Freshwater studies comprise approximately 15% of the entire invasion research literature published over the past 50 years, but, compared with terrestrial studies, they have made a disproportionately smaller contribution to classical Eltonian concepts such as biotic resistance, enemy release and disturbance (Fig. 16.1). They have made more substantive contributions to modern concepts such as propagule pressure and human vector dispersal, but their predominant focus has been on the effects of invasions on recipient communities and ecosystems. In a random sample of 100 journal articles on freshwater invasions published in 2008, over 40% of the articles specifically address ecological impacts of introduced species (A. Ricciardi, unpublished data). The number of published quantitative studies on the com-

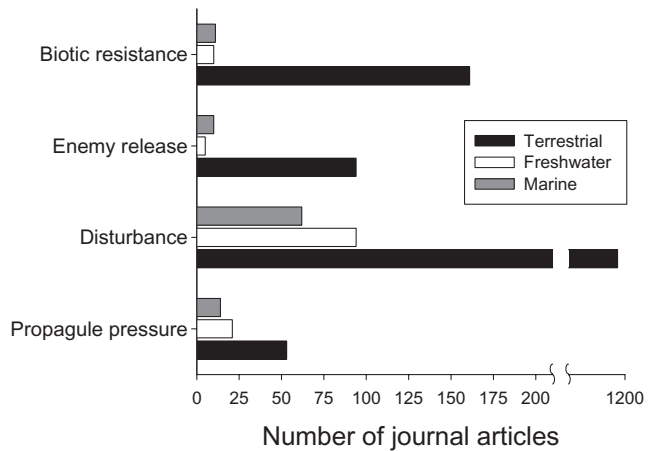


Fig. 16.1 Proportional contribution of published terrestrial, freshwater and marine studies to some key concepts in invasion ecology. Articles published between 1960 and 2008 were located using Web of Knowledge 4.0 (Thomson Institute for Science Information).

munity- and ecosystem-level impacts of freshwater fishes, for example, exceeds those for other individual groups such as terrestrial plants, terrestrial invertebrates and marine invertebrates (see Parker et al. 1999). It is not clear whether this overwhelming focus exists because the impacts of freshwater invasions are more conspicuous or more amenable to study in freshwater systems; in any case, it has enhanced our understanding of the context-dependent forces that structure communities and affect ecosystem processes. Herein, we evaluate the current state of knowledge of the impacts of invasions on freshwater biodiversity and food webs.

16.2 IMPACTS OF INVASIONS ON FRESHWATER BIODIVERSITY

Human activities have extensively altered freshwater ecosystems, whose species are disappearing at rates that rival those found in tropical forests (Ricciardi & Rasmussen 1999). Although biological invasions have been implicated as a principal cause of freshwater extinctions (Miller et al. 1989; Witte et al. 1992), researchers are confronted with the question of whether non-indigenous species are drivers or merely ‘passengers’ of ecological changes leading to biodiversity loss (Didham et al. 2005). Disentangling the respective roles of invasions and other anthropogenic stressors in causing major ecological impacts is a key challenge to invasion ecology. In freshwater systems,

this is made difficult by myriad stressors interacting with invasions. Habitat alteration facilitates invasions and exacerbates their impacts by increasing the connectedness of watersheds (for example through canalization), reducing native competitors and predators (through disturbance), and increasing habitat homogenization (through impoundment, reservoir construction and shoreline development) to the benefit of opportunistic invaders (see Moyle & Light 1996; Scott & Helfman 2001; Scott 2006; Johnson et al. 2008b). Impoundment and reservoir construction promote the replacement of endemic riverine species by cosmopolitan lentic species that would otherwise be poorly suited to natural river flows (Marchetti et al. 2004a). Further homogenization of fish communities results from the introductions of piscivores that reduce the abundance and diversity of littoral fishes, particularly in lakes where refugia have been removed by shoreline development (MacRae & Jackson 2001). Consequently, the interaction of invasion and land use has homogenized freshwater biota across multiple spatial scales (Duncan & Lockwood 2001; Rahel 2002; Clavero & García-Berthou 2006).

Nevertheless, invasions appear to be a principal contributor to biodiversity loss in some systems. A correlative analysis (Light & Marchetti 2007) suggests that introduced species, rather than habitat alteration, are the primary driver of population declines and extinctions of California freshwater fishes. Experimental studies are needed to confirm this result, but it is consistent with documented impacts of invasions

throughout the region (Moyle 1976). Elsewhere, another correlative study showed that zebra mussel invasion has added to the impacts of environmental stressors, resulting in a 10-fold acceleration in rates of local extinction of native mussels in the Great Lakes region (Ricciardi et al. 1998). In this case, there is ample experimental evidence that native mussel mortality is increased by zebra mussel activities (Ricciardi 2004). Recoveries of some native species after experimental removals of non-indigenous species provide further evidence of the significant role of invasions in freshwater biodiversity loss (see, for example, Vredenburg 2004; Lepak et al. 2006; Pope 2008).

Lakes and other insular systems are naïve to the effects of a broad range of invaders, owing to their evolutionary isolation (Cox & Lima 2006). In historically fishless lakes, introduced trout have caused the extirpation of native fauna that have evolved without selection pressures to adapt to large aquatic predators (see Knapp & Matthews 2000; Pope 2008; Schabetsberger et al. 2009). Major community-level impacts are often observed in species-poor systems such as alpine lakes, desert pools, isolated springs and oligotrophic waters (Moyle & Light 1996), but other studies have demonstrated that even species-rich freshwater systems are vulnerable to disruption. For example, North American rivers contain the planet's richest assemblage of freshwater mussels, which have no evolutionary experience with dominant fouling organisms like the zebra mussel. Intense fouling by the zebra mussel on the shells of other molluscs interferes with metabolic activities of native species and has led to severe rapid declines or extirpation of many native mussel populations (Ricciardi et al. 1998; Ricciardi 2004). In contrast, extirpations of native mussels have rarely been reported from invaded European lakes and rivers, whose fauna had a shared evolutionary history with an ancestral form of the zebra mussel in the geological past (Ricciardi et al. 1998). A more extreme example is Lake Victoria, in which the greatest vertebrate mass extinction in modern history followed the introduction of the Nile perch, a piscivore that grew to a maximum body size at least two orders of magnitude larger than any native resident in the lake. Its introduction has been implicated in the loss of nearly 200 endemic cichlid species that had no evolutionary experience with large piscivores (Witte et al. 1992).

These examples support the contention that invasions are more likely to alter communities that lack entire functional groups – such as large piscivores or

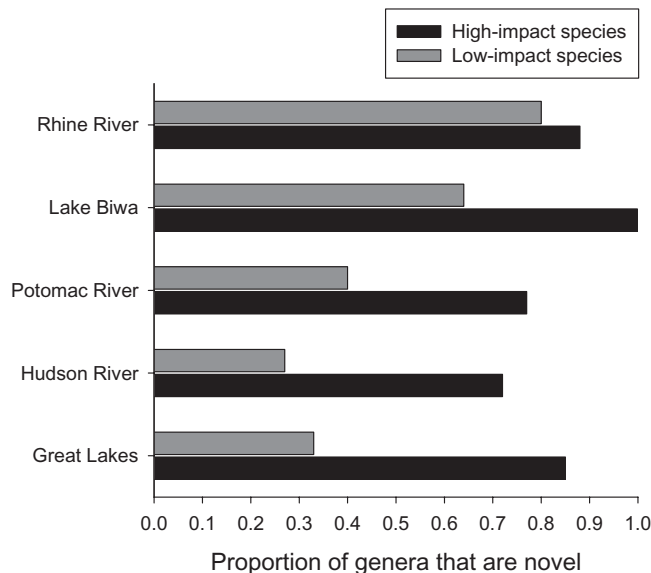
fouling bivalves – rather than high numbers of native species per se (Simberloff 1995). However, a community may be disrupted by any introduced species possessing sufficiently novel traits, particularly if such species are predators. The sea lamprey invasion of the Great Lakes contributed to the near total extirpation of lake trout *Salvelinus namaycush* from these waters and the extinction of some endemic salmonids (see Miller et al. 1989). The Great Lakes contain a few native species of lamprey, but these are smaller and lack the well developed jaws of the more predaceous sea lamprey; thus, the latter is ecologically distinct within the system. Ecologically distinct species are more likely to encounter naïve prey and less likely to encounter enemies that are adapted to them. Given that phylogenetically distant species tend to be ecologically distinct from each other, we expect that invaders that cause substantial declines in native populations will belong to novel taxa more often than low-impact invaders (Ricciardi & Atkinson 2004). Indeed, this appears to be the case in freshwater systems (Fig. 16.2).

Impacts on biodiversity can also result when invaders are brought into contact with closely related native species. Hybridization with introduced relatives appears to be at least partially responsible for over 30% of the North American freshwater fishes considered extinct in the wild; one example is the Amistad gambusia *Gambusia amistadensis*, which was hybridized to extinction when it interbred with introduced mosquitofish; such events can occur in only a few years (Miller et al. 1989). Although perhaps most widespread in fishes, hybridization and introgression have likely affected a broad range of freshwater taxa, but the global extent of these impacts remain unknown (Perry et al. 2002, and references therein).

16.3 CASCADING IMPACTS ON FOOD WEBS

Experimental studies on introduced aquatic predators have demonstrated that their effects extend beyond the replacement of native species. Such studies have enhanced our understanding of trophic cascades, wherein the biomass of primary producers is altered through indirect food-web effects (Flecker & Townsend 1994; Nyström et al. 2001; Schindler et al. 2001). A classic case involves European brown trout *Salmo trutta* in New Zealand streams, where their predation reduces invertebrate grazers, thereby releasing benthic

Fig. 16.2 Proportions of high-impact invaders (i.e. those implicated in a greater than 50% decline of a native species population) and low-impact invaders that belong to novel genera in independent freshwater systems with extensive invasion histories. The null hypothesis of no difference between proportions was tested with one-tailed Fisher exact tests and rejected for the Hudson River ($P = 0.0007$) and North American Great Lakes ($P = 0.00002$), but not for the Rhine River ($P = 0.49$), Lake Biwa ($P = 0.23$), and the Potomac River ($P = 0.07$). The null hypothesis was rejected by a meta-analysis of the entire data set (Fisher's combined probability test, $\chi^2 = 45.8$, $P < 0.0001$). Primary data sources: Mills et al. 1993, Ricciardi 2001 (Great Lakes), Mills et al. 1996 (Hudson River), Ruiz et al. 1999 (Potomac River), Hall and Mills 2000 (Lake Biwa), Bernauer and Jansen 2006 (Rhine River). Additional data were obtained from literature and online databases.



algae from herbivory; as a result, higher algal biomass is achieved in the presence of the brown trout compared with streams containing only native fishes (see Flecker & Townsend 1994). Through top-down effects and nutrient regeneration, trophic cascades generated in ponds, lakes and streams by introduced fish and crayfish have resulted in twofold to sixfold increases in algal biomass (Leavitt et al. 1994; Nyström et al. 2001; Herbst et al. 2009) and can lead to undesirable phytoplankton blooms (Reissig et al. 2006).

Cascading effects may extend beyond ecosystem compartments, particularly when they involve predators or omnivores that are not regulated by higher trophic levels. This was observed after the introduction of a piscivorous South American cichlid to Gatun Lake, Panama (Zaret & Paine 1973). Several native fishes were rapidly decimated through predation, which led to local declines of fish-eating birds such as kingfishers and herons. More significant was the loss of insectivorous fish, an entire guild, which was linked to an increase in the abundance of local mosquito populations in subsequent years and apparently affected the incidence and type of malaria infecting humans in the area. This phenomenon was noted decades earlier by Rivero (1937), who reported the decline of mosquitofish and a subsequent increase in malaria in Cuba

as a result of predation by introduced largemouth bass *Micropterus salmoides*.

In another spectacular case, the opossum shrimp *Mysis diluviana* (formerly *M. relicta*), a glacial relict species, was introduced deliberately by wildlife managers into Flathead Lake (Montana, USA) to supplement the diet of a non-indigenous landlocked salmon (kokanee, *Oncorhynchus nerka*). The shrimp is nocturnal, and during daylight hours it remained at the bottom of the lake while the salmon fed in shallower waters. Flathead Lake lacks upwelling currents that could have made the shrimp accessible to the salmon. Thus the shrimp avoided predation by the salmon and, moreover, outcompeted it for zooplankton prey, which subsequently became scarce. Consequently, the salmon population crashed, followed by the near disappearance of eagle and grizzly bear populations that depended on spawning salmon as a food resource (Spencer et al. 1991).

Cascading effects are also caused by introduced suspension feeders (see below) and aquatic plants. Being both autogenic engineers and primary producers, introduced aquatic plants have a great capacity to transform freshwater systems. Their impacts include altered habitat structure (Valley & Bremigan 2002), altered water quality (Rommens et al. 2003; Perna &

Burrows 2005) and reduced diversity (Boylen et al. 1999; Schooler et al. 2006). The replacement of natives by non-indigenous plants, even those that appear to be ecologically equivalent to the native, can have subtle negative effects on associated communities and food webs (Brown et al. 2006; Wilson & Ricciardi 2009).

Other food-web effects include diet shifts, which have substantive consequences for ecosystem processes such as contaminant cycling and secondary production. In a California lake, competition with an introduced planktivore (threadfin shad, *Dorosoma petenense*) caused three native planktivores to shift their diets from zooplankton to nearshore benthos, resulting in elevated mercury concentrations in each species (Eagles-Smith et al. 2008). In Canadian Shield lakes, introduced bass reduce the abundance and diversity of littoral fishes, the preferred prey of a native piscivore, lake trout (Vander Zanden et al. 1999). To mitigate such competition, lake trout change their foraging behaviour and shift their diets towards pelagic zooplankton in lakes where pelagic fishes are absent, and suffer reduced growth rates as a result (Vander Zanden et al. 1999, 2004; Lepak et al. 2006). In a Japanese woodland stream, introduced rainbow trout *Oncorhynchus mykiss* monopolized terrestrial invertebrate prey that fell into the stream. The loss of this prey subsidy caused native fish to shift their diet to stream insects that graze on benthic algae, thereby increasing algal biomass and reducing the biomass of adult insects that emerge from the stream; the latter effect led to a 65% reduction in the density of riparian spiders (see Baxter et al. 2004).

16.4 COMPLEX INTERACTIONS AMONG SPECIES

A major contributor to spatial variation in impact is the interaction between the invader and the invaded community. Antagonistic interactions, such as predation, can limit the impact of an invader by regulating its abundance or by constraining its behaviour (Robinson & Wellborn 1988; Harvey et al. 2004; Roth et al. 2007). Several case studies from freshwater systems also demonstrate synergistic interactions among invading species (Ricciardi 2001), such as when one invader indirectly enhances the success and impact of another by releasing it from predation. An experimental study in western North America revealed

that local invasions of the bullfrog *Rana catesbeiana* are facilitated by the presence of introduced bluegill sunfish *Lepomis macrochirus*. The latter indirectly enhance survival of tadpoles by reducing densities of predatory macroinvertebrates (see Adams et al. 2003). Similarly, the population collapse of the historically dominant piscivore in the Great Lakes as a result of sea lamprey predation that targeted lake trout apparently facilitated the invasion of the alewife *Alosa pseudoharengus*, an introduced planktivorous fish that was previously sparse or absent in Lakes Michigan, Huron and Superior when lake trout populations were intact. Subsequent population explosions of alewife triggered changes in the composition and abundance of zooplankton and abrupt declines of native planktivores (see Kitchell & Crowder 1986).

A bottom-up food-web effect that is rarely studied in freshwater systems is hyperpredation, in which an introduced prey indirectly facilitates the decline of a native species by enabling a shared predator to increase its abundance. This has been observed in lakes of the Klamath Mountains, California, where introduced trout have reduced populations of a native frog both through their own predation and by facilitating predation by an introduced aquatic snake (Pope et al. 2008).

Freshwater studies have also highlighted an important synergistic interaction between introduced suspension-feeding bivalves and both native and non-indigenous plants. Through their filtration activities, dreissenid mussels (the zebra mussel and quagga mussel *D. rostriformis bugensis*) have increased water clarity, thereby stimulating the growth of vegetation that includes non-indigenous species such as Eurasian watermilfoil *Myriophyllum spicatum* and curly pondweed *Potamogeton crispus* in the Great Lakes region (MacIsaac 1996; Vanderploeg et al. 2002), which in turn provide settlement surfaces for juvenile mussels. In Lake St. Clair, a formerly turbid system, zebra mussels stimulated macrophyte growth to unprecedented levels, which caused a major shift in the fish community by reducing the abundance of species adapted to turbid waters (for example walleye, *Sander vitreus*) and favouring species adapted to foraging in weed beds (smallmouth bass, *Micropterus dolomieu*, and northern pike, *Esox lucius*) (Vanderploeg et al. 2002). Similar cascading effects were observed after the invasion of the Potomac River estuary by the Asiatic clam *Corbicula fluminea*. Water clarity in the estuary tripled within a few years of the clam's discovery, and coincided with the development of submerged

macrophyte beds that had previously been absent for 50 years. These beds included the non-indigenous species *Hydrilla verticillata* and *Myriophyllum spicatum*, and supported an increased abundance of fishes, including introduced bass and waterfowl. The overwhelming influence of the clam on these changes was confirmed after it suffered a major decline that precipitated reductions in submerged aquatic vegetation and associated populations of birds and fish (Phelps 1994).

Particular combinations of invaders, especially co-adapted species, can also produce strong synergistic impacts. In western Europe, multiple invasions by Ponto-Caspian species completed the parasitic life cycle of the trematode *Bucephalus polymorphus*. The introductions of the trematode's first intermediate host, the zebra mussel, and its definitive host, the pike-perch *Sander lucioperca*, allowed *B. polymorphus* to become established in inland waters and cause high mortality in local populations of cyprinid fishes that served as secondary intermediate hosts (Combes & Le Brun 1990). Interactions among Ponto-Caspian species introduced to the Great Lakes have also produced synergistic impacts (Ricciardi 2001). A new food-web link composed of the Eurasian round goby *Neogobius melanostomus* and its natural prey, dreissenid mussels, created a contaminant pathway that has increased the heavy-metal burden of piscivorous fish (Hogan et al. 2007). Furthermore, the prolific growth of benthic plants and algae in response to the filtration effects of dreissenid mussels has resulted in the build-up of excessive decaying vegetation that periodically depletes oxygen levels in bottom waters, generating conditions that promote the proliferation of botulism bacteria. Outbreaks of type E botulism have occurred in the Great Lakes every summer since 1999, and are responsible for die-offs of over 90,000 waterfowl, primarily fish-eating and scavenging species. The botulin toxin occurs in the mussels and in their principal predator, the round goby, which itself is commonly found in the stomachs of fish-eating birds. Therefore it is hypothesized that the round goby is transferring toxin from the mussels to higher trophic levels (Yule et al. 2006).

16.5 PREDICTABILITY OF IMPACT

Predictive methods are needed to prioritize invasion threats, but progress in predicting impact has been modest, largely because of the moderating influence of local environmental conditions such as those men-

tioned above (Parker et al. 1999; Ricciardi 2003). So far, very few general hypotheses have related impact to physical habitat conditions, although some researchers have observed that invaders are more likely to extirpate native species in nutrient-poor aquatic systems with low species diversity and extremely high or extremely low environmental (for example flow, temperature) variability or severity (Moyle & Light 1996).

The context-dependent nature of impact has been explored by studies correlating the impact of introduced species to variation in physicochemical variables. Freshwater studies on amphipod crustaceans and fishes have demonstrated that the magnitude and direction of antagonistic interactions (such as intra-guild predation) that determine whether an introduced species replaces or is inhibited by a resident species can vary along environmental gradients such as conductivity, salinity, oxygen and temperature (Taniguchi et al. 1998; Alcaraz et al. 2008; Piscart et al. 2009; Kestrup & Ricciardi 2009). These studies demonstrate that although impacts are highly context dependent, only a few key environmental variables might be important for prediction. Such is the case for the zebra mussel's impact on native mussel populations, which is largely driven by their level of fouling on the shells of native species. Their fouling intensity is positively correlated with calcium concentration and negatively correlated to the mean particle size of surrounding sediments (Jokela & Ricciardi 2008), suggesting that the most vulnerable native mussel populations can be identified from these two habitat variables before invasion.

Only a few introduced organisms in a given region appear to cause severe ecological impacts (Ricciardi & Kipp 2008) and tools are needed to identify these high-impact species. The use of species traits to predict high-impact aquatic invaders has lagged behind terrestrial studies. Predictive traits vary across different stages of invasion (Kolar & Lodge 2002; Marchetti et al. 2004b) and the invasiveness, or colonizing ability, of a species is an inadequate predictor of impact for terrestrial and aquatic organisms (see Ricciardi & Cohen 2007); even poor colonizers (for example Atlantic salmon, *Salmo salar*) may have strong local impacts, whereas widely successful colonizers (for example freshwater jellyfish, *Craspedacusta sowerbyi*) do not necessarily disrupt ecosystems. However, there is intriguing evidence that the relative risk posed by introduced species to their invaded communities may be predicted by a

comparison of their functional responses. Comparing native and non-indigenous amphipod crustaceans, Bollache et al. (2008) suggested that high-impact invasive predators have a higher functional response (*sensu* Holling 1959) than more benign species. Moreover, they argue that this comparative analysis can be extended to other trophic groups. A similar approach uses bioenergetics modelling to estimate predator consumptive demand, and thus compares the relative threats of introduced piscivores in a given system (Johnson et al. 2008a).

A burgeoning number of case studies tentatively suggest that the most severe ecological impacts are caused by aquatic invaders with the following characteristics: (i) they tend to have a higher fecundity and abundance than related native species (Hall & Mills 2000; Keller et al. 2007); (ii) they are often generalist predators or omnivores (Moyle & Light 1996; Hall & Mills 2000) and, in the case of crustaceans, are highly aggressive (Gamradt et al. 1997; Dick 2008); (iii) they are introduced to systems where functionally similar species do not exist (Ricciardi & Atkinson 2004); (iv) they use resources differently from resident species such that they can alter the availability of critical resources such as light, nutrients, food or habitat space, for example through ecosystem engineering (Phelps 1994; Rodriguez et al. 2005) or by building or breaking trophic links between different ecosystem compartments (Simon & Townsend 2003; Baxter et al. 2004); (5) their physiological requirements are closely matched to abiotic conditions in the invaded environment (the intensity of impact is higher in environments that are optimal to the invader (see, for example, Jokela & Ricciardi 2008)); and (6) they have a history of strong impacts in other invaded regions (Marchetti et al. 2004b). Invasion history, when sufficiently documented, provides a valuable basis for developing quantitative predictions (for example using synthetic tools such as meta-analysis) of the impacts of widespread aquatic invaders such as zebra mussels (Ricciardi 2003; Ward & Ricciardi 2007), common carp (Matsuzaki et al. 2009) and various species of crayfish (McCarthy et al. 2006; Matsuzaki et al. 2009). These studies have shown that although the magnitude of an impact is often quite variable, the types and direction of impacts might exhibit patterns that are consistent, and thus predictable, across a range of invaded habitat types and geographic regions.

On the other hand, some impacts are so idiosyncratic that they defy prediction. For example, the mass

die-offs of Great Lakes' waterfowl linked to the mussel–goby–botulism interaction described above could not have been predicted from the literature because similar events involving these species have not been previously recorded, despite the extensive invasion histories of zebra mussels and round gobies in Europe. Such unpredictable synergies are likely to accrue in systems that are heavily invaded (Ricciardi 2001). Furthermore, the effects of introduced species can vary substantially over time, owing to shifts in resident species composition (for example other invasions), changes to abiotic variables and evolutionary processes; such long-term feedbacks between introduced species and their invaded environments have rarely been studied and present a challenge to predicting the chronic effects of an invasion (Strayer et al. 2006).

16.6 ARE FRESHWATER SYSTEMS MORE SENSITIVE TO THE IMPACTS OF INTRODUCED SPECIES?

To our knowledge, no one has explicitly compared the impacts of invasions in freshwater, terrestrial and marine systems. In particular, it would be interesting to determine if differences between freshwater and terrestrial trophic interactions contribute to differential sensitivity to the effects of introduced consumers. Top-down control of plant biomass is stronger in water than on land (Shurin et al. 2006), thus the indirect effects of consumers may be larger in freshwater systems. Furthermore, the insularity of lakes and small rivers may result in a greater naiveté of their biota compared with continental terrestrial and marine biota (Cox & Lima 2006). This is evident in contrasting patterns of impact by terrestrial mammals and freshwater fishes; invasions by mammals are more likely to contribute to extirpations of native species when they involve dispersal between continents than within continents, whereas invasions by fishes are just as likely to cause extirpations whether they occur intra-continentially or inter-continentially (Fig. 16.3). Strong negative impacts of invasions on native species appear to be more frequent in freshwater systems than in marine systems (Ricciardi & Kipp 2008). Freshwater systems tend to have a higher proportion of invaders that are reported to have caused native species declines (Fig. 16.4). On average, high-impact invaders comprise 11% (95% confidence limits 0.069–0.154) of the total number of invaders in a freshwater system and

Fig. 16.3 Data on the percentage of invaders with strong negative impacts, i.e. those implicated in the severe (greater than 50%) decline of a native species population. For freshwater fishes in California and the Great Lakes, intra-continental and inter-continental invaders had similar proportions of species with strong negative impacts (Fisher's exact test, $P > 0.05$). For terrestrial mammals, inter-continental invasions had much stronger impacts than intra-continental invasions ($P < 0.05$). After Ricciardi and Simberloff (2009).

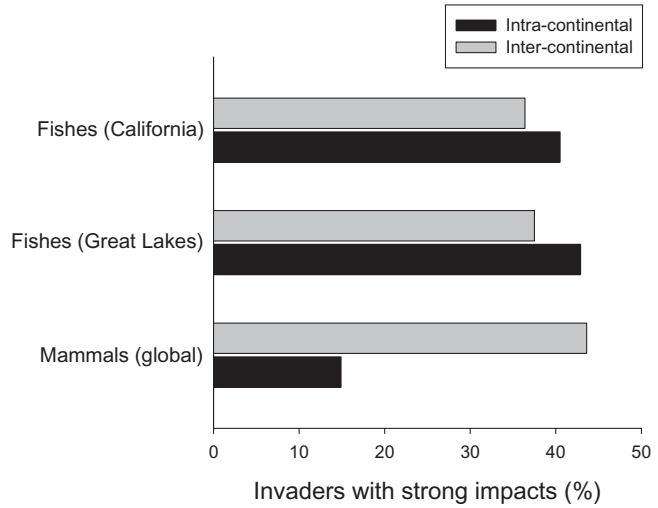
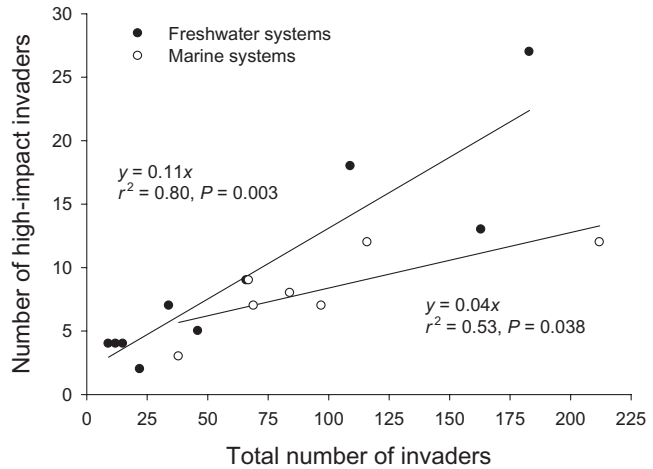


Fig. 16.4 Relationships between the number of high-impact invaders (i.e. those implicated in the severe decline of a native species population) and the total number of invaders in freshwater and marine systems. After Ricciardi and Kipp (2008), with data from Marsden and Hauser (2009).



4% (95% confidence limits 0.004–0.084) in a marine system.

In terms of their well-defined boundaries, their insularity, and the generally limited diversity and size of the populations that inhabit them, lakes and small river basins can be thought of as analogous to oceanic islands. Therefore, it might be more appropriate and useful to compare freshwater systems to islands when testing the generality of concepts across biomes.

16.7 CONCLUSIONS AND FUTURE PROSPECTS

Lakes and river basins offer well-defined, replicated model systems for studying the effects of non-indigenous species (see, for example, Vander Zanden et al. 2004; Rosenthal et al. 2006; Sharma et al. 2009). Freshwater ecosystems are among the most invaded in the world, and have revealed patterns and problems

that have added substantially to our knowledge of the population-, community- and ecosystem-level effects of introduced species. Yet research has only glimpsed the extent to which invasions have transformed these ecosystems. There is a dearth of impact studies in regions where introductions of aquatic species are most prevalent (for example Asia (Leprieur et al. 2009)). Even in the North American Great Lakes, which have an extensive history of invasion involving over 180 non-indigenous species (see Mills et al. 1993; Ricciardi 2006), the effects of most invasions remain unknown. The identification of general patterns has been hindered by taxonomic biases in impact studies, which focus more often on fishes than invertebrates (see Parker et al. 1999). Furthermore, although an invader can potentially affect different levels of ecological organization – including individuals (for example behaviour, morphology), populations (abundance, genetic structure), communities (richness, evenness, food-web structure) and ecosystems (habitat structure, primarily production, nutrient dynamics, contaminant cycling), few impact studies have examined multiple levels simultaneously (Simon & Townsend 2003).

Notwithstanding the challenge it poses to prediction, the context-dependent variation of the effects of an invader across a set of lakes or rivers offers valuable opportunities to identify environmental conditions that enhance or inhibit impact. The scarcity of pre-invasion data sets impedes efforts to measure impacts against a background of temporal variation and multiple stressors; but in cases where long-term data exist, the effects of non-indigenous species may be isolated from other anthropogenic perturbations (Yan & Pawson 1997).

The risk of a highly disruptive invasion will increase as more non-indigenous species are added to a system, or as the same species invade more systems (Ruesink 2003; Ricciardi & Kipp 2008). An important insight is that many introduced species, if widely distributed, can become highly disruptive in at least some systems (Ruesink 2003). Given (i) the complexity of direct and indirect interactions between introduced species and other stressors (Didham et al. 2007), (ii) the insularity and acute sensitivity of freshwater ecosystems and (iii) our current level of understanding of impact, we conclude that humans cannot engage safely in deliberate introductions of freshwater species, and that management plans to conserve freshwater biodiversity must include strategies for preventing invasions. Fortunately, this view seems to be better appreciated by biologists

and wildlife managers today than it was during Elton's time.

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