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Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future

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SUMMARY

1. Biological invasions are numerous in fresh waters around the world. At least hundreds of freshwater species have been moved outside of their native ranges by vectors such as ballast water, canals, deliberate introductions, and releases from aquaria, gardens, and bait buckets. As a result, many bodies of fresh water now contain dozens of alien species.
2. Invasions are highly nonrandom with respect to the taxonomic identity and biological traits of the invaders, the ecological characteristics of the ecosystems that are invaded, and the geographical location of the ecosystems that supply and receive the invaders.
3. Some invaders have had deep and pervasive effects on the ecosystems that they invade. Classes of ecologically important invaders in fresh waters include molluscs that are primary consumers and disrupt the food web from its base, fishes that disrupt the food web from its apex or centre, decapods that act as powerful omnivores, aquatic plants that have strong engineering effects and affect the quality and quantity of primary production, and diseases, which probably have been underestimated as an ecological force.
4. The number of alien species in freshwater ecosystems will increase in the future as new aliens are moved outside of their native ranges by humans, and as established aliens fill their potential ranges. Alien species create ''no-analogue'' ecosystems that will be difficult to manage in the future. We may be able to reduce future impacts of invaders by making more serious efforts to prevent new invasions and manage existing invaders.
5. *Thematic implications*: interactions between alien species and other contemporary stressors of freshwater ecosystems are strong and varied. Because disturbance is generally thought to favour invasions, stressed ecosystems may be especially susceptible to invasions, as are highly artificial ecosystems. In turn, alien species can strongly alter the hydrology, biogeochemical cycling, and biotic composition of invaded ecosystems, and thus modulate the effects of other stressors. In general, interactions between alien species and other stressors are poorly studied.

Keywords: alien species, exotic species, introduced species, invasive species, no-analogue ecosystems

Introduction

Introductions of alien species are among the most important, least controlled, and least reversible of human impacts on the world's ecosystems, strongly affecting their biodiversity, biogeochemistry, and economic uses (e.g., Cox, 1999; Lockwood, Hoopes & Marchetti, 2007). Indeed, the ecological, economic, and evolutionary changes caused by alien species are so profound that some biologists have suggested that we are entering a new era, the Homogocene (a term apparently coined by Gordon Orians in the mid-1990s

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– Rosenzweig, 2001), in which all of the continents are connected into a ''New Pangaea'' through human activities. The ecosystems of the Homogocene will be different from the ecosystems that freshwater ecologists have become familiar with, and will pose important challenges to both scientists and managers (Olden, 2006).

The goal of this paper is to briefly summarise the state of knowledge about the ecological effects of alien species in fresh waters, and to highlight important scientific and management challenges. My treatment is necessarily brief and selective, and focuses solely on ecological effects, although the economic effects of freshwater invaders can be varied and substantial (e.g., Pimentel *et al.*, 2000; Lovell, Stone & Fernandez, 2006; Connelly *et al.*, 2007; Keller *et al.*, 2009). The paper contains three parts. First, I will review briefly what we know, showing that alien species are numerous, a highly nonrandom subset of the freshwater biota, travel around the world by more or less well known vectors, and are capable of effects that are as strong and far-reaching as any human-caused stressor on freshwater ecosystems. Second, I will describe the strong interactions between species invasions and other multiple stressors of freshwater ecosystems. Third, I will consider what the future holds for freshwater ecosystems in the Homogocene, highlighting management issues that may be especially difficult.

For the purposes of this discussion, I define a species as ''alien'' as if human activities (deliberate or inadvertent) moved it outside of its native range. Other authors call such species exotic, introduced, or non-indigenous (Colautti & MacIsaac, 2004). This definition does not imply or require that an alien species is harmful in any sense.

What we know

Alien species are common and widespread in fresh water

Comprehensive inventories of aliens have been attempted for just a few freshwater ecosystems (Mills *et al.*, 1993, 1996a; Ricciardi, 2006), which contain tens to hundreds of alien species (Table 1). Comprehensive regional inventories of alien species in fresh waters also are scarce and incomplete (García-Berthou, Boix & Clavero, 2007; USGS, 2008; Gherardi *et al.*, 2009), but support the idea that the world's fresh waters have been heavily invaded (Table 2). Inventories of specific, well-studied parts of the biota, usually fishes (e.g., Whittier & Kincaid, 1999; Leprieur *et al.*, 2008), are more common than comprehensive inventories, and confirm that aliens often constitute a large fraction of the species, individuals, or biomass of freshwater ecosystems (Fig. 1). Finally, range maps of well-known freshwater alien species (Fig. 2; see Table 3 for additional examples of widely distributed aliens) show that high-profile invaders now occupy countless sites beyond their original ranges. Very few freshwater sites are beyond the current or projected range of at least one high-profile invader.

Table 1 Numbers of known or suspected alien species in the Laurentian Great Lakes (Ricciardi, 2006) and Hudson River (updated from Mills *et al.*, 1996a and Waldman *et al.*, 2006) basins. Figures in parentheses are the percentage of species in the basin that are alien. Except perhaps for fishes and molluscs, the numbers of alien species probably are underestimated, sometimes severely

Taxon	Great Lakes	Hudson River
Fishes	26	34 (33%)
Crustaceans	19	7 (63%)*
Molluscs	18	22 (23%)
Other invertebrates	18	ND†
Vascular plants	61	33
Algae	26	ND†
Other	14	ND†

*Decapods only.
†No data.

Alien species are a highly nonrandom subset of the freshwater biota

Although existing inventories of freshwater alien species are scarce and incomplete, it is clear that introduced species are a highly nonrandom subset of the freshwater biota (Fig. 3; see also García-Berthou *et al.*, 2007; Gherardi *et al.*, 2009). In particular, although insects dominate the world's freshwater fauna, they are almost unrepresented in lists of alien species. Vertebrates and molluscs, on the other hand, are overrepresented among alien species.

There are several possible reasons for the very uneven representation of different animal groups among freshwater aliens. First, some groups may be undersampled by invasion ecologists (e.g., Demoor, 1992). Surely invasion ecologists have not adequately

Table 2 Numbers of alien species recorded as established in the fresh waters of North America and Europe (Gherardi *et al.*, 2009; USGS, 2008). For poorly studied taxa, the number of actual introductions may be substantially larger than the number recorded here

	North America			Europe		
Taxon	Transplants within North America	Introductions from outside North America	Total	Transplants within Europe	Introductions from outside Europe	Total
Plants	20	114	136*	ND	ND	ND
Molluscs	19	31	50	14	32	46
Crustaceans	25	29	54	45†	104†	149†
Other invertebrates	7	18	25	19	65	84
Fishes	314	116	430	58‡	95‡	153‡
Amphibians	17	8	25			
Reptiles	15	6	21			
Mammals	2	1	3			
Total	419	323	744	136	296	432

*Greater than the sum of the previous two columns because of two species of unknown origin.
†All arthropods.
‡All chordates.

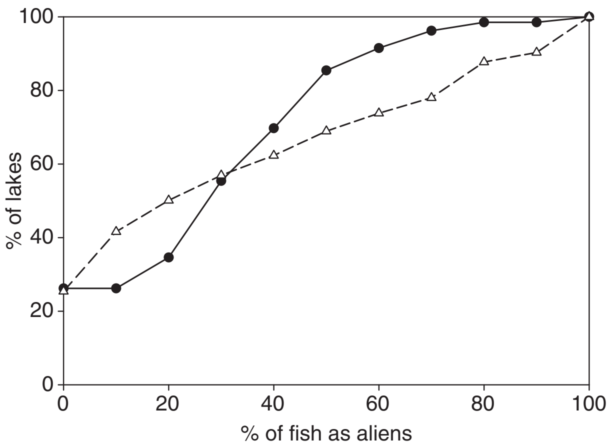

Fig. 1 Cumulative distribution of proportion of lakes in the northeastern United States with a given percentage of alien fish species (closed circles) or individuals (open triangles). From data of Whittier & Kincaid (1999).

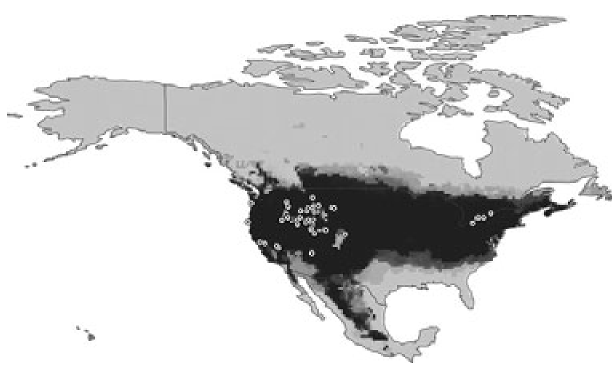

Fig. 2 Potential range of the alien freshwater snail *Potamopyrgus antipodarum* in North America based on its existing range in North America (circles). Darker shades show areas where more models predict occurrence (Loo *et al.*, 2007).

sampled the entire freshwater biota, and all published inventories must underestimate the actual number of alien species. For instance, no invasion ecologists have sampled for freshwater gastrotrichs, nor would they be likely to recognise an alien gastrotrich if they saw one. However, it seems likely that the same groups that have been overlooked by invasion ecologists have been overlooked by taxonomists. The mismatch shown in Fig. 3 would require that a taxonomic group have very different detection probabilities by taxonomists and invasion ecologists, which seems unlikely. Second, the pathways that transport alien species (described below) all are highly selective (cf. Hulme *et al.*, 2008), which partially explains Fig. 3. For instance, humans have deliberately stocked many fishes but few chironomids, which (along with releases from aquaria, aquaculture, and bait buckets) accounts for the overrepresentation of vertebrates among alien species. Third, because different taxonomic groups are differentially susceptible to the barriers that set up differences between the biotas of different basins or continents in the first place, they should respond differentially to the breaching of those

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Table 3 Characteristics of some important classes of alien species in fresh waters

Group	Major impacts	Major vectors	Examples
Herbivorous molluscs	Reduction of biomass and production of edible primary producers, with consequent effects on composition and abundance of all biota, water chemistry, water clarity	Usually inadvertently introduced by ballast water, releases from aquaria and water gardens, and contamination	*Dreissena* spp., *Corbicula* spp., *Limnoperna fortunei*, *Potamocorbula amurensis* among the bivalves; *Potamopyrgus antipodarum*, *Pomacea canaliculata* among the snails
Fishes (and other vertebrates)	Loss of large, active prey, including native fish	Often deliberately stocked; releases from aquaria and bait buckets	Various salmonids, centrarchids, and cichlids; *Cyprinus carpio* Linneaus, *Ctenopharyngodon idella*, *Hypophthalmichtys* spp., *Lates niloticus*, *Gambusia affinis* (Baird & Girard), *Petromyzon marinus*, silurid and ictalurid catfishes, *Rana catesbeiana* Shaw
Aquatic plants	''Ecosystem engineering'' effects on current, air-water-sediment exchanges and the amount of surfaces for chemical reactions and biotic attachment; changes in the amount and quality of primary production and detritus; effects ramify through ecosystem	Horticulture, releases from aquaria and water gardens, contamination	*Alternanthera philoxeroides* (Mart.) Griseb., *Azolla* spp., *Egeria densa* Planch., *Eichhornia crassipes*, *Elodea* spp., *Hydrilla verticillata* (L.f.) Royle, *Lythrum salicaria*, *Myriophyllum spicatum*, *Phragmites australis*, *Pistia stratiotes* Linneaus, *Nasturtium officinale*, *Salvinia* spp., *Tamarix* spp., *Trapa natans*, *Typha* spp.
Decapods	Loss of macrophytes, snails, and other benthic animals, with consequent effects on other parts of the food web	Deliberate stocking, bait bucket releases, ballast water (*Eriocheir* only)	*Orconectes rusticus*, *O. limosus* (Rafinesque), *O. virilis* (Hagen), *Procambarus clarkii* (Girard), *Pacifastacus leniusculus* (Dana), *Eriocheir sinensis*
Diseases	Loss of affected species, with consequent effects on ecosystem	Ballast water, contamination of stock	Chytridiomycosis, *Aphanomyces astaci* (crayfish plague), *Myxobolus cerebralis* (whirling disease), viral hemorrhagic septicaemia, various diseases of humans

barriers. Generally, species that disperse poorly on their own but are readily moved by humans would be expected to respond most dramatically, which is consistent with the observed dominance of fishes and molluscs among invaders.

The non-random selection of invaders must apply to ecological traits as well as taxonomic composition, although this has not been well documented (but see Olden, Poff & Bestgen, 2006b; Statzner, Bonada & Dolédec, 2008). For instance, 45% of the alien freshwater fish species in the Hudson River basin are substantially piscivorous, compared with just 14% of the natives, so species introductions have greatly increased the number and distribution of piscivorous fish in the basin (Mills *et al.*, 1996a), which may have had large ecological effects (see below). Consequently, the highly selective transport of alien species by humans changes the taxonomic and ecological character of the local and regional freshwater biota, as well as its size.

Alien species are moving between the world's fresh waters by known vectors

Early inferential studies of the likely vectors by which alien species were transported (e.g., Mills *et al.*, 1993, 1996a) have been supplemented recently by direct studies of the species moved by different vectors (e.g., Padilla & Williams, 2004; Duggan *et al.*, 2005; Gertzen, Familiar & Leung, 2008). Consequently, we can identify the major vectors that transport alien species between the world's fresh waters, as well as the kinds of species that are most likely to be transported by each vector (Table 4). Direct studies of vectors have

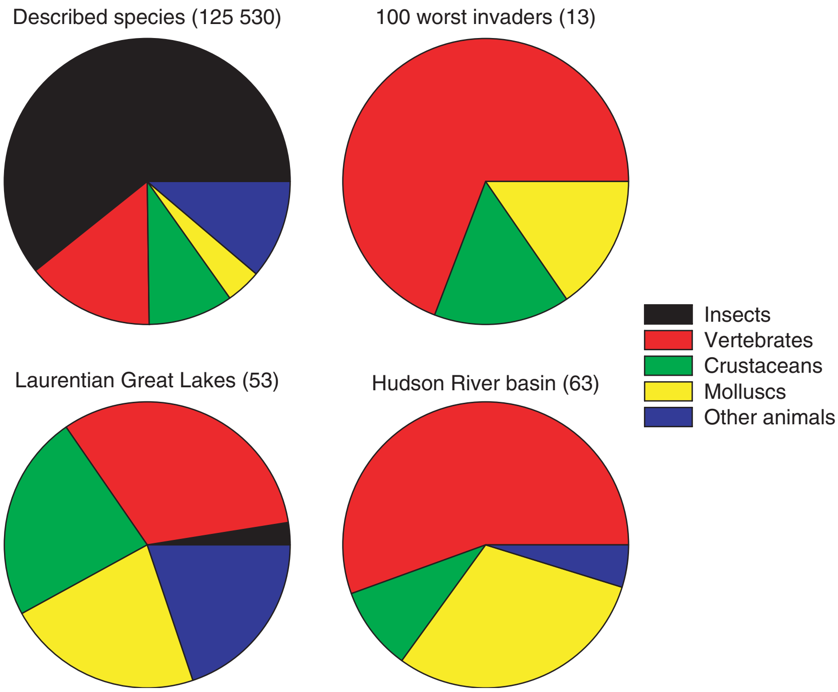

Fig. 3 Comparison of the taxonomic composition of described animal species in fresh water (Balian *et al.*, 2008) with that of freshwater animal species included among the world's 100 worst invaders (Lowe, Browne & Boudjelas, 2008), and that of known alien animal species in the Laurentian Great Lakes (Ricciardi, 2006) and the freshwater parts of the Hudson River basin (Mills *et al.*, 1996a). The total number of species in each group is given in parentheses.

Table 4 Major vectors thought to transport freshwater alien species. Modified from Mills *et al.* (1993, 1997)

Vector	Typical scale	Taxa typically transported
Stocking	Local to intercontinental	Sport fishes, forage animals (e.g., crayfishes, *Mysis*, small fishes), ornamental plants
Aquarium releases	Local to intercontinental	Ornamental fishes, invertebrates, and plants
Garden escapes	Local to intercontinental	Ornamental fishes, invertebrates, and plants
Bait bucket escapes	Local or interbasin	Bait fishes or crayfishes
Stocking contaminants	Local to intercontinental	Contaminants of stocks of sport, forage, or bait species, or of horticultural or aquarium stock
Escapes from commercial aquaculture	Local to intercontinental	Fish or large crustaceans grown in outdoor facilities
Ballast water	Local to intercontinental	Nekton, plankton, or species with free-living larvae or resting stages
Canals	Interbasin	All species, but especially motile or fouling species

great potential for improving procedures and policies to prevent the spread of alien species.

Alien species are capable of deep and far-reaching ecological effects

I will divide the ecologically important invaders of fresh waters into five broad classes, which differ in their origins and their effects. This classification is admittedly Procrustean and overlooks or misclassifies some important invaders, but I think that it is useful in organising a large body of information about hundreds of alien species, each with its own dispersal vectors, biology, and idiosyncratic effects.

Primary consumers, especially molluscs

One of the most important classes of freshwater invaders includes molluscs that suspension-feed on phytoplankton and seston, graze on periphyton, or browse on vascular plants. These species can develop massive populations in all kinds of fresh waters, consuming so much primary production that they substantially affect the amount and composition of primary producers. Interactions radiating out from the primary producers can affect nearly every part of the ecosystem.

Possibly the best-known of these species is the zebra mussel (*Dreissena polymorpha* [Pallas]), a native of the

Ponto-Caspian region that has been introduced widely into lakes and rivers in western Europe and North America. Populations of zebra mussels often are so large that they dominate heterotrophic biomass and clear large volumes of water. For instance, the population of zebra mussels that appeared in the Hudson River in 1991 usually has constituted >50% of all heterotrophic biomass in the river and had a growing-season clearance rate equal to 25–100% of the river's volume each day (Strayer *et al*., 1999). As a result, phytoplankton biomass in the river fell by ~80%, the pelagic part of the food web withered, and the littoral part of the food web flourished in response to increased water clarity (Fig. 4). Similar changes have been documented in other ecosystems invaded by zebra mussels (Strayer, 2009). Other suspension-feeding alien bivalves that have had large effects on freshwater ecosystems similar to those described for the zebra mussel include the quagga mussel (*Dreissena bugensis* Andrusov) from southeastern Europe, now spread widely through western Europe and North America (Mills *et al*., 1996b; Vanderploeg *et al*., 2002; Orlova *et al*., 2005); *Corbicula fluminea* (Muller) and possibly other species in this genus from east Asia, now widely distributed in North America, western Europe, and the Plata River system of South America

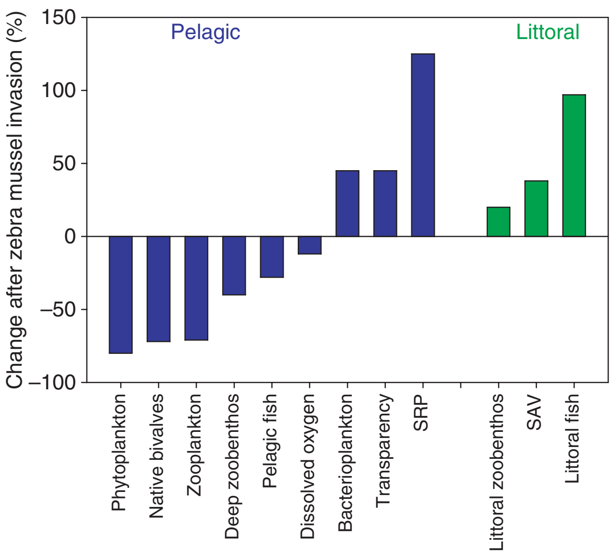

Fig. 4 Summary of the effects of the zebra mussel on the Hudson River ecosystem, showing a withering of the pelagic food web and a flourishing of the littoral food web. Based on Strayer *et al.* (1999, 2004), Caraco *et al.* (2000), and Strayer & Smith (2001).

(e.g., Cohen *et al*., 1984; Hakenkamp & Palmer, 1999; Sousa, Antunes & Guilhermino, 2008); *Potamocorbula amurensis* (Schrenck), also originally from east Asia but now in brackish waters in California (e.g., Alpine & Cloern, 1992; Kimmerer, 2002); and *Limnoperna fortunei* (Dunker), an Asian mytilid that is ecologically similar to the dreissenid mussels and which has developed large populations in the Plata system of South America (e.g., Ricciardi, 1998; Darrigran & Damborenea, 2005; Boltovskoy *et al*., 2006). All of these species are poised to spread around the world with careless global trade.

Other alien molluscs have had large effects on freshwater ecosystems through their consumption of benthic primary producers. The New Zealand mud snail (*Potamopyrgus antipodarum* [Gray]), which has invaded large areas of Australia, Europe, and North America (Loo, MacNally & Lake, 2007), can reach very high densities (>10 000/m^2) in lakes and hydrologically stable streams. At such sites, this periphyton feeder can consume almost all algal production and dominate nutrient cycling (Hall, Tank & Dybdahl, 2003). These basal impacts must propagate to other parts of the ecosystem, but have not yet been fully investigated (but see Kerans *et al*., 2005; Riley, Dybdahl & Hall, 2008). Other snails that feed on periphyton have been introduced widely outside of their native ranges (e.g., *Physa acuta* Draparnaud, *Bellamya* [=*Cipangopaludina*] spp., *Melanoides tuberculatus* [Müller]), and may affect ecosystem functioning at least occasionally.

Herbivorous molluscs also have had large impacts on ecosystems into which they were introduced. The South American golden apple snail (*Pomacea canaliculata* [Lamarck]) has spread widely through southeastern Asia as an escape from aquaculture (Hayes *et al*., 2008). It reaches high population densities, and feeds voraciously on a wide range of aquatic plants (Carlsson, Brönmark & Hansson, 2004). Golden apple snails nearly eliminate macrophytes from the wetlands that they invade, causing concentrations of nutrients and phytoplankton to increase enormously. Again, impacts on other parts of the ecosystem, including economically valuable fisheries, seem likely to occur but have not yet been well documented. The effects of herbivorous molluscs like the golden apple snail thus cause a regime shift similar to that of severe eutrophication in shallow lakes (Carlsson *et al*., 2004).

In general, all of these molluscs graze down some primary producers severely. Their activities favour primary producers (if any) that can live in a given habitat but avoid being eaten (e.g., macrophytes or toxic cyanobacteria in the case of zebra mussels – Vanderploeg *et al*., 2001; phytoplankton in the case of the golden apple snail – Carlsson *et al*., 2004). The shift in the amount and quality of primary production usually raises concentrations of dissolved nutrients, and may produce large effects that ramify through the entire food web. The size and breadth of these effects arising from even a single mollusc species (Fig. 4) may rival or exceed those produced by any human stress on freshwater ecosystems.

Fishes

Many species of fishes have been deliberately introduced around in world to provide food or sport. In addition to these deliberate introductions, a large number of fish species have been spread beyond their native range by releases from aquaria, bait buckets, and water gardens, as contaminants of fish intended for stocking, or in ballast water. Some of these fishes have had large ecological effects.

Especially in mountainous, glaciated terrain, many lakes, ponds, and small streams were naturally fishless (e.g. Knapp, Matthews & Sarnelle, 2001; Hesthagen & Sandlund, 2004; Schilling *et al*., 2008). The widespread introduction of fishes into these habitats brought large, active predators into highly vulnerable communities for the first time. As often is the case when a new functional group is introduced into an island community, the establishment of fishes into these formerly fishless habitats has had large effects on the behaviour, distribution, and abundance of native species, as well as ecosystem functioning (Simon & Townsend, 2003). The most obvious effects of fish introductions to formerly fishless sites include the near-disappearance of large, active prey species (Fig. 5) and behavioural changes in remaining prey species to avoid daytime use of microhabitats frequented by fish (reviewed by Simon & Townsend, 2003). Less direct changes to the community and ecosystem must be common and sometimes strong as well, as a result of nutrient excretion by fish and cascading effects from the loss of the most vulnerable prey species (Simon & Townsend, 2003).

Humans also often introduce fishes into fresh waters that already contain fish, either accidentally or in a deliberate attempt to improve the fish community. Again, the most obvious impacts have been losses of favoured prey species, especially in cases where the alien has no native trophic analogue in the system. Perhaps the most dramatic example is the global extinction of ~200 species of cichlids from Lake Victoria following the invasion of the Nile perch (*Lates niloticus* [Linneaus]) (Lowe-McConnell, 1993), but many other examples exist, including the decline in lake trout (*Salvelinus namaycush* [Walbaum]) from

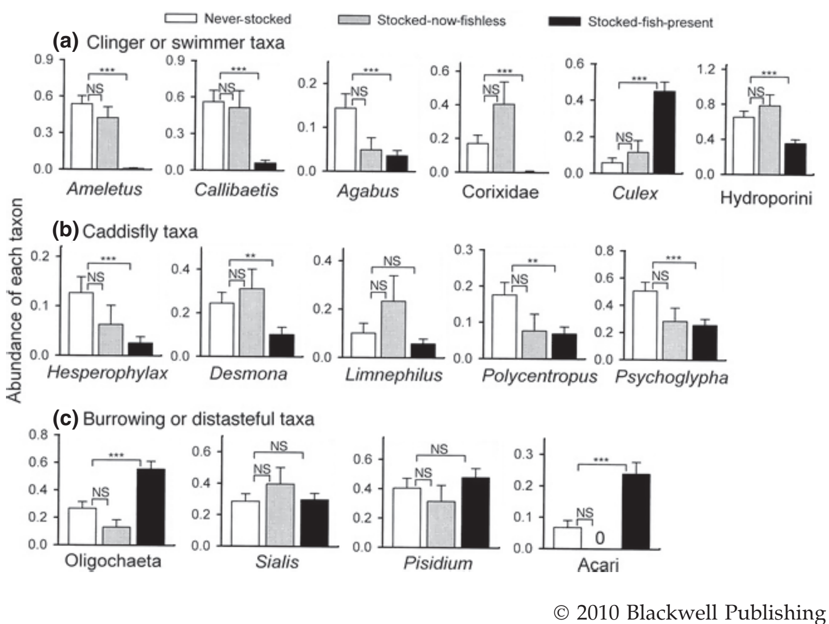

Fig. 5 Abundance (number per 15 standard sweeps, log_{10}-transformed) of various kinds of benthic macroinvertebrates in lakes of the Sierra Nevada that never contained fish, that had been stocked but are now fishless, and that were stocked and still contain fish. Bars show means +1SE, NS = not significant ($P > 0.05$), $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, according to a pairwise Wilcoxon rank-sum test. From Knapp *et al*. (2001).

the upper Great Lakes after the arrival of the sea lamprey (*Petromyzon marinus* Linneaus), the near-disappearance of galaxioids from Southern Hemisphere streams after salmonids were introduced (McDowall, 2006), and the decline or disappearance of cyprinids from American lakes after any of several large piscivores were introduced (Whittier, Halliwell & Paulsen, 1997; Findlay, Bert & Zheng, 2000).

Alien fishes that are not piscivores may also have large effects on their food. For example, introduced alien planktivores such as *Alosa* spp. and kokonee salmon (*Oncorhynchus nerka* [Walbaum]) can greatly alter zooplankton (Brooks & Dodson, 1965), introduced salmonids have had large direct and indirect effects on stream invertebrates (Flecker & Townsend, 1994; Simon & Townsend, 2003; Baxter *et al*., 2004), even when introduced to sites where fishes already live; and even tiny mosquitofish (*Gambusia* spp.) have reduced densities of native invertebrates and outcompeted native fishes (Pyke, 2008). Herbivorous alien species such as grass carp (*Ctenopharyngodon idella* [Valenciennes]) likewise can have strong effects on the amount and composition of aquatic vegetation (Bain, 1993; Cudmore & Mandrak, 2004; Pipalova, 2006).

As is now well appreciated, indirect effects of alien fishes can be propagated through the food web and affect many parts of the ecosystem. Thus, both alien piscivores and alien invertivores can have large effects on primary producers (Carpenter *et al*., 1987; Flecker & Townsend, 1994; Simon & Townsend, 2003) and exchanges with neighbouring ecosystems (Baxter *et al*., 2004), and bioturbation and nutrient excretion by alien fishes may alter light and nutrient availability (e.g., Vanni, 2002; Parkos, Santucci & Wahl, 2003; Simon & Townsend, 2003).

Thus, as was the case with alien molluscs, alien fishes have had large, far-reaching effects on almost all parts of freshwater ecosystems, both lentic and lotic. It is possible that these effects have been so dramatic because most fishes are able to disperse so poorly (if at all) on their own between continents and drainage basins that many sites support naturally depauperate fish faunas. Introductions of new species into such sites are therefore likely to bring in functionally distinctive species, which often have large ecological effects in insular ecosystems (Vitousek, 1990; Cox, 1999; Lockwood *et al*., 2007) such as remote lakes and drainage basins.

Aquatic plants

Countless aquatic plants (including macroalgae) have been introduced around the world, either deliberately because they were thought to be ornamental or otherwise desirable, or inadvertently as releases from aquaria or water gardens or contaminants of solid ballast or agricultural stock. Some of these plants have spread and flourished in the wild, and have had large ecological impacts. Important invaders cover all of the major guilds of aquatic plants, including riparian species (*Tamarix* spp.), emergent plants (*Phragmites australis* [Cav.] Trin. ex Steud, *Typha* spp., *Lythrum salicaria* Linneaus), submerged species (*Elodea* spp., *Myriophyllum spicatum* Linneaus), floating-leaved species (*Trapa natans* Linneaus), and floating plants (*Azolla* spp., *Salvinia molesta* Mitchell, *Eichhornia crassipes* [Mart.]). The most obvious impacts of hypersuccessful alien plants have been to outcompete or hybridise with native plants (e.g., Boylen, Eichler & Madsen, 1999; Ailstock, Norman & Bushmann, 2001; Moody & Les, 2007; but see Houlahan & Findlay, 2004), increase the amount of plant biomass and primary production (Fig. 6; Farnsworth & Ellis, 2001; Kelly & Hawes, 2005), and change the quality of that primary production. Increases in primary production

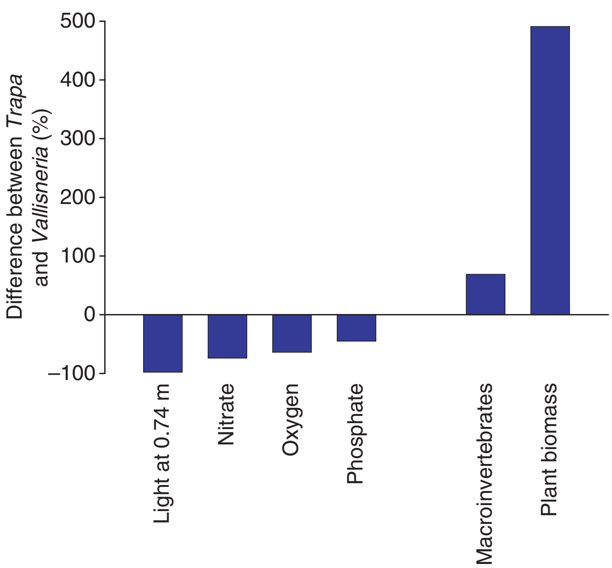

Fig. 6 Summary of differences between beds of the alien water-chestnut (*Trapa natans*) and nearby beds of the native water-celery (*Vallisneria americana)* in the freshwater tidal Hudson River, based on Caraco & Cole (2002), Strayer *et al.* (2003), and Goodwin *et al.* (2008).

alone can affect rates of many biogeochemical processes in the ecosystem. In addition, the nutrient content and physiology of the alien plant may differ greatly from that of the native plants that it replaces, causing changes in nutrient cycling (Wigand, Stevenson & Cornwell, 1997; Templer, Findlay & Wigand, 1998; Angeloni *et al.*, 2006), rates of herbivory and decomposition, and consumer growth (Going & Dudley, 2008; Moline & Poff, 2008). Some alien plants (e.g., watercress, *Nasturtium officinale* Aiton) contain potent chemicals that prevent herbivores from using the alien as effectively as native plants (Newman, Kerfoot & Hanscom, 1996).

In addition, the high biomass and often-distinctive physical structure of alien plants frequently cause strong and varied engineering effects (in the sense of Jones, Lawton & Shachak, 1994). The high surface area provided by dense beds of alien plants offers colonisation space for epiphytic algae, invertebrates, and fishes, and can greatly increase the diversity and populations of these organisms (e.g., Strayer *et al.*, 2003; Kelly & Hawes, 2005; Troutman, Rutherford & Kelso, 2007). However, alien plant species do not always support more animals than their native counterparts (Keast, 1984; Toft *et al.*, 2003; Theel, Dibble & Madsen, 2008), although community composition of the fauna usually differs. Even in cases where alien species increase animal densities, their beds can be so dense that they inhibit foraging of predatory fishes (Valley & Bremigan, 2002; Theel & Dibble, 2008), preventing them from taking advantage of the high productivity of these beds. Likewise, the invasion of alien plant species can change wildlife use of the area (e.g., Benedict & Hepp, 2000; Maddox & Wiedenmann, 2005; Rybicki & Landwehr, 2007). Dense plant beds reduce current speed and increase water depth in running waters (Wilcock *et al.*, 1999), prevent sediment resuspension (Huang, Han & Liu, 2007), trap suspended particles, and lead to greatly increased sedimentation rates (Rooth, Stevenson & Cornwell, 2003), and protect shorelines from erosion (Coops *et al.*, 1996). The dense shade produced by stands of alien plants can inhibit understory species (Angeloni *et al.*, 2006) and reduce temperature. In the case of floating or floating-leaved species, shading can cause hypoxia or anoxia in the underlying water (Thomas & Room, 1986; Caraco & Cole, 2002). Alien riparian plants like *Tamarix* spp. can colonise and stabilise floodplain soils, ultimately affecting channel morphology (e.g., Graf, 1978; Birken & Cooper, 2006). Thus, the establishment of even a single alien plant species can radically transform the entire character of an aquatic ecosystem, affecting nearly every aspect of ecosystem structure and function, and having effects that reach far beyond the boundaries of the plant bed itself.

The invasion of the Hudson River by the water-chestnut (*Trapa natans*) provides a good example of the strong, varied effects of a successful alien plant (Fig. 6). This plant was deliberately released into North America as an ornamental in the late 19th century, and appeared in the Hudson in the 1930s. By the 1950s, it was abundant and widespread in the river, forming large, nearly monospecific beds with biomasses of 100–1000 g DM m^{-2} (Hummel & Kiviat, 2004). These beds are *c.* 10× denser than those of the native water-celery (*Vallisneria americana* Michx.) that they replaced (Fig. 6). The combination of dense shade and high respiration in water-chestnut beds greatly reduces dissolved oxygen concentrations, leading to frequent and severe hypoxia or anoxia (Caraco & Cole, 2002; Goodwin, Caraco & Cole, 2008). Nitrate is greatly depleted in water-chestnut beds, through a combination of denitrification and plant uptake (Caraco & Cole, 2002). The invertebrate communities in water-chestnut beds are denser and have a different species composition than those of *Vallisneria* (Strayer *et al.*, 2003). It is difficult to study fish use of water-chestnut beds (the dense canopy defeats most conventional sampling gear), but there at least strong hints (reviewed by Strayer, 2006) that it has altered littoral fish communities. In addition to these ecological effects, water-chestnut is regarded as a serious nuisance in the Hudson because its dense stands prevent recreational use of hundreds of hectares of shallow-water habitat and block access to the river channel from the shore.

Unlike other alien species in fresh waters, there have been many successful programs to control or locally eradicate alien plants using mechanical removal, herbicides, or biological control (McFadyen, 1998; Cuda *et al.*, 2008).

Decapod omnivores

More than 20 species of freshwater decapods (chiefly crayfish) have been introduced around the world for human food, fish forage, and bait (Hobbs, Jass &

Huner, 1989). Decapods are adaptable omnivores that feed on algae, macrophytes, benthic invertebrates, fishes, and fish eggs. Alien crayfish species often reach high densities (>1 m^{-2}, Bobeldyk & Lamberti, 2008), and so may have strong direct and indirect ecological impacts on several parts of the food web (Hobbs *et al.*, 1989; Lodge *et al.*, 2000; Gherardi, 2007b).

The rusty crayfish (*Orconectes rusticus* [Girard]) is one of the best-studied of the alien freshwater decapods. Native to parts of the American Midwest, it has spread widely to lakes and streams elsewhere in North America through bait-bucket releases and intentional stocking (Olden *et al.*, 2006a,b). It is aggressive, and displaces or kills native crayfish (Klocker & Strayer, 2004; Olden *et al.*, 2006a,b; and references therein). Because they are active, omnivorous, and often abundant, rusty crayfish and other crayfish species have strong and wide-ranging effects. Rusty crayfish can greatly reduce macrophyte biomass and species richness (Fig. 7, Lodge & Lorman, 1987; Lodge *et al.*, 1994; Wilson *et al.*, 2004; Rosenthal *et al.*, 2006), which must in turn affect the animals that live among macrophytes (Wilson *et al.*, 2004). They also decimate populations of snails (Lodge *et al.*, 1994; Wilson *et al.*, 2004) and possibly other molluscs (Klocker & Strayer, 2004), and change the abundance and community composition of other benthic macroinvertebrates (McCarthy *et al.*, 2006). In addition to indirect effects on fish arising from their destruction of macrophytes, crayfish may be important predators of fish eggs (Dorn & Wojdak, 2004). Possibly as a result of diminished grazing by macroinvertebrates, periphyton biomass increases in at least some invaded sites (Bobeldyk & Lamberti, 2008). Crayfish also may increase rates of litter breakdown (Bobeldyk & Lamberti, 2008). Crayfish have been shown to increase rates of sediment suspension and transport (e.g., Statzner *et al.*, 2000). Thus, alien crayfish are capable of large effects on several parts of freshwater ecosystems in streams and lake littoral zones. Indirect effects arising from macrophyte destruction must be especially important, but have not yet been fully investigated.

The Chinese mitten crab (*Eriocheir sinensis* Milne-Edwards) is another widely introduced decapod with strong ecological impacts. This catadromous species can migrate inland for several hundred km into rivers, creeks, and lakes. In addition to producing effects on the food web broadly similar to those produced by crayfishes (Rudnick & Resh, 2005), mitten crabs produce extensive burrow systems in some sites, which may cause erosion of muddy creek banks (Rudnick, Chan & Resh, 2005).

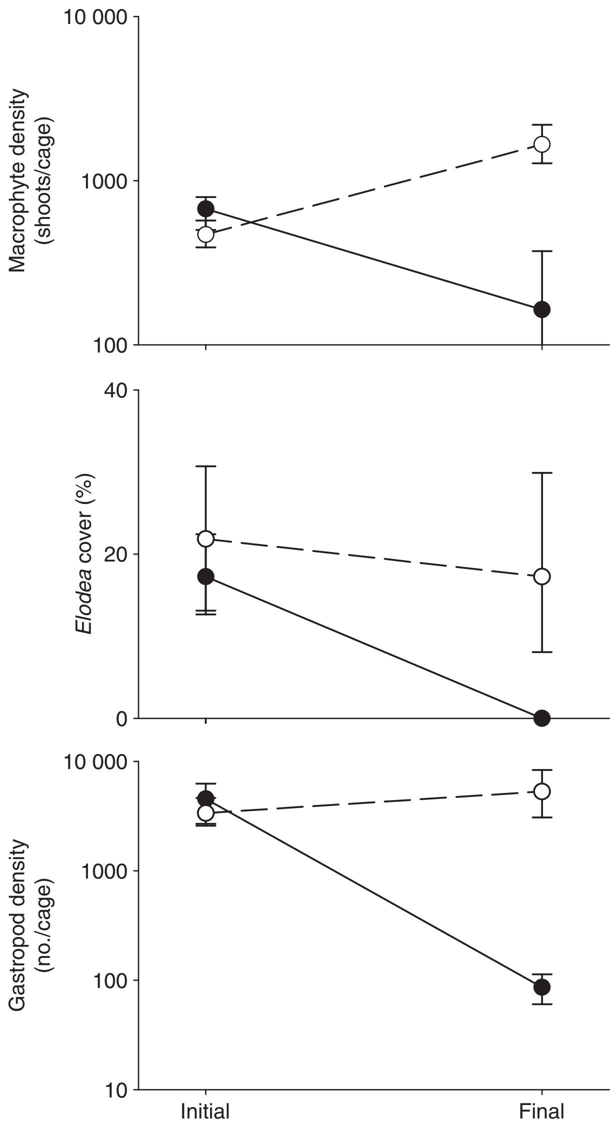

Fig. 7 Response of macrophytes and gastropods in experimental enclosures containing the rusty crayfish (*Orconectes rusticus*) (black circles, solid lines) versus exclosures (open circles, dashed lines) run for 11 weeks over the summer in Plum Lake, Wisconsin. Graphs show means ±1SE; note that some y-axes are logarithmic. From data of Lodge *et al.* (1994).

Diseases

Alien diseases have not been as well-studied as other freshwater invaders, but several examples show that may have strong ecological effects. Perhaps the best-known is amphibian chytridiomycosis, which now appears to be responsible for breathtakingly dramatic declines of amphibians around the world (Lips *et al*., 2006, 2008): ''the most spectacular loss of vertebrate biodiversity due to disease in recorded history'' (Skerratt *et al*., 2007). Amphibians play important roles in small-stream and pond ecosystems, so the near-disappearance of once-abundant amphibians probably has important, varied ecological consequences (Whiles *et al*., 2006). Crayfish plague (*Aphanomyces astaci* Schikora) is a fungus that was introduced from North America into Europe in the 19th century (Edgerton *et al*., 2004). Crayfish native to Europe are highly susceptible to this disease, so many European populations have declined or disappeared. Because crayfish play such important roles in freshwater ecosystems (see above), these losses probably have led to other ecological changes (Matthews & Reynolds, 1992). Other diseases that may be ecologically important in fresh waters include whirling disease (*Myxobolus cerebralis* Hofer), probably originally from Europe, but now widespread around the world, and capable of killing large numbers of salmonids in hatcheries and possibly affecting wild populations (Bartholomew & Reno, 2002; Kerans & Zale, 2002); viral hemorrhagic septicaemia (VHS), which has appeared in several sites in eastern North America, presumably as a result of ballast water releases, and has caused large fish kills involving several species (Groocockl *et al*., 2007; Lumsden *et al*., 2007); an enigmatic infectious pathogen that was carried by the alien fish *Pseudorasbora parva* (Temminck & Schlegel) into Europe, where it now endangers the native *Leucaspius delineatus* (Heckel) and other cyprinids (Gozlan *et al*., 2005); and the Asian tapeworm *Bothriocephalus acheilognathi* Yamaguti, which has been widely introduced throughout the world with cultured fish, and which may harm many fish species, including endangered cyprinids in the American Southwest (Henja, 2009). Finally, several important human diseases associated with fresh waters have been moved outside their native ranges by humans (e.g., introduction of malaria, schistosomiasis, onchocerciasis, and lymphatic filariasis into the New World – Cox, 2002; Lammie *et al*., 2007) and have affected not only human populations, but human impacts on fresh waters.

Diseases constitute a much more heterogeneous group than the other classes of aliens just discussed: vectors carrying diseases are highly varied (e.g., ballast water for VHS, contaminated stock for crayfish plague and whirling disease, infected humans for our diseases), and the ecological effects of diseases depend entirely on which species are affected. Nevertheless, like the other classes of invaders, diseases have the potential to have strong effects on many aspects of freshwater ecosystems. Because non-human diseases have received so little attention, the effects of alien diseases on freshwater ecosystems probably have been underestimated.

Other aliens in fresh waters

There is not space to list all of the alien species in fresh water or describe their ecological effects in detail, but I will mention briefly some of the important freshwater invaders that do not fit neatly into my rough classification. Several predatory zooplankton (*Mysis*, *Cercopagis*, *Bythotrephes*) have been widely introduced and have strong effects on zooplankton that ramify to other parts of the ecosystem (e.g., Spencer, McClelland & Stanford, 1991; Yan & Pawson, 1997; Strecker & Arnott, 2008). Likewise, benthic amphipods (e.g., *Dikerogammarus*, *Gammarus tigrinus* Sexton, *Echinogammarus ischnus* [Stebbing], *Corophium curvispinum* Sars, *Gammarus pulex* [Linneaus]) have been widely established in Europe and North America outside of their native ranges, where they may affect at least macroinvertebrates and fish (e.g., Kinzler & Maier, 2003; Kelly & Dick, 2005; Berezina, 2007). Fur-bearing aquatic mammals such as beavers, muskrat, mink, and nutria, and ornamental waterfowl such as the mute swan (*Cygnus olor* [Gmelin], alien to North America) and the Canada goose (*Branta canadensis* [Linneaus], alien to Europe and New Zealand) have established many populations beyond their native range, and surely have affected many aspects of freshwater ecosystems.

Multiple stressors: interactions between alien species and other stressors

The same ecosystems that are being invaded by alien species are also subjected to other anthropogenic stresses, which interact with species invasions. In a broad sense, there are two classes of interactions between species invasions and other stressors: (i) the existence or intensity of other stressors may make it easier or harder for alien species to invade and establish themselves; or (ii) alien species and other stressors may jointly determine ecological conditions in fresh waters and the ecosystem services that they provide. Neither class of interaction has been fully worked out, so the following account is exemplary rather than exhaustive.

Effects of other stressors on species invasions

Some common stresses on freshwater ecosystems may make it easier for alien species to establish themselves. Plant ecologists (e.g., Davis, Grime & Thompson, 2000; Zedler & Kercher, 2004) have suggested that disturbance and nutrient enrichment facilitate invasions of alien plants, because they free up resources that can be used by new invaders. Increased disturbance and nutrient loads both are very common in fresh waters, and may substantially enhance establishment of alien freshwater plants. There are other examples in which stressors may lead to increases in resource availability and thereby facilitate species invasions. For instance, food web disruptions (e.g., overfishing) and disturbance may facilitate invasions of alien animals by making resources available to them.

Although climate change may make local conditions either better or worse for specific alien species, it generally will affect the vectors that transport alien species, and may increase disturbance intensity in many fresh waters, making them easier to invade (Rahel & Olden, 2008). The number, identity, and effects of alien species thus are likely to change as climate changes.

Humans may deliberately introduce alien species to ameliorate the negative effects caused by other stressors. Alien fishes often have been introduced to supplement or replace fisheries lost from overfishing, habitat degradation, or other causes. Familiar examples include Pacific salmonids in the Laurentian Great Lakes and brown trout brought into many North American streams after land-use change made them too warm to support the native brook trout. Likewise, alien species sometimes are used to provide specific functions in ecological restoration (D'Antonio & Meyerson, 2002; Strayer *et al.*, 2005). For instance, the grass carp has been widely introduced into North America waters to control weed problems that may have originated from excessive nutrient loading or the introduction of alien plants.

Other interactions between species invasions and other stressors are less well understood, including the apparent positive association between impoundments and alien species (Johnson, Olden & Vander Zanden, 2008), which again may greatly increase species invasions around the world. Whatever the mechanisms, several widespread human impacts on fresh waters probably increase invasions of alien species.

Effects of species invasions and other stressors on freshwater ecosystems

Many examples show that alien species may interact strongly with other stressors, modulating their effects and making them harder to manage. Alien species affect water quality. The establishment of zebra mussels in the Seneca River, New York, caused dissolved oxygen concentrations to fall so much that the river was no longer suitable for sewage disposal, forcing the city of Syracuse to change its long-term plans for sewage management (Effler *et al.*, 2004). The decreases in phytoplankton and increases in water clarity and dissolved nutrients often caused by alien suspension-feeders (Fig. 4) have obvious links to eutrophication (Caraco, Cole & Strayer, 2006). In fact, nearly all of the important classes of invaders discussed above have been shown to have strong effects on such key aspects of water quality as transparency, nuisance algal blooms, nutrient concentrations, and dissolved oxygen.

Alien species affect conservation of imperiled species. The long-term losses of North American unionid mussel populations from pollution, land-use change, and altered hydrology became much worse with the arrival of alien bivalves (*Dreissena* and *Corbicula*), which have caused rapid catastrophic losses of many populations of unionids (Ricciardi, Neves & Rasmussen, 1998). Likewise, the introduction of mosquitofish around the world imperiled or extinguished many populations of rare fishes (Pyke, 2008), and the arrival of Nile perch in Lake Victoria may have led to the extinction of *c.* 200 endemic fish species (Lowe-McConnell, 1993). Perhaps the most troubling example is the recent spread of amphibian chydridiomycosis, which is devastating amphibian populations around the world. In each of these cases, the arrival of the alien made a challenging conservation problem much more difficult or even impossible, and greatly restricted the range of possible conservation options.

Alien species often affect fisheries. The loss of lake trout from the Laurentian Great Lakes following the arrival of the sea lamprey provides a spectacular example; there are many similar examples from around the world (e.g., Kolding *et al*., 2008). More recently, the poorly controlled movement of fish parasites and diseases such as VHS and Asian fish tapeworm threatens valuable fish stocks around the world. The impacts of alien species on valuable fish populations are difficult to undo or manage through traditional tools such as gear- or harvest regulations, or habitat improvement.

Restoration of habitats can be difficult or impossible once alien species establish themselves (D'Antonio & Meyerson, 2002; Ewel & Putz, 2004). For instance, attempts to restore the hundreds of hectares of lost and ecologically valuable shallow-water habitats in the Hudson River would probably result in beds of the alien *Trapa natans* rather than the native vegetation (Strayer *et al*., 2005), with far-reaching consequences for ecosystem function (Fig. 6). As for conservation, the presence of alien species can greatly limit the range of options in ecological restoration.

Alien species even affect toxicology; the establishment of the alien bivalve *Potamocorbula amurensis* in San Francisco Bay reconfigured the food web to allow much more efficient transfer of selenium into the waterfowl (Stewart *et al*., 2004), showing a strong interaction between alien species and toxification as stresses.

These few examples show that alien species interact with nutrient loading, hydrologic change, habitat destruction or restoration, fisheries harvests, and toxification, and have the potential to influence many management plans. Interactions between alien species and other stressors are common, strong, and bi-directional, so that management of alien species is inextricably linked to management other freshwater stressors. In many cases, it probably will make sense to manage alien species and other stressors as a group of closely linked problems, rather than as separate problems.

Prospects for the future: freshwater ecosystems in the Homogocene

Invasion rates are likely to continue to be high

Three lines of evidence suggest that freshwater ecosystems around the world will continue to be flooded with new invaders in the coming decades. First, empirical studies of alien species typically show that establishment rates of new invaders are steady or rising (OTA 1993; Mills *et al*., 1996a; Ricciardi, 2006; Gherardi *et al*., 2009). Models predicting the number of species invasions from measures of economic activity also suggest that high invasion rates will continue into the near future (e.g., Levine & D'Antonio, 2003; Taylor & Irwin, 2004; Westphal *et al*., 2008).

Second, propagule pressure seems to be a primary determinant of invasion rates, and propagule pressure from many important vectors (Table 4) is still high. Large volumes of untreated ballast water and sediments still are moving around the world (e.g., Ricciardi, 2006; Donohue, 2007), the pet and horticulture trade still deals in many alien species (e.g., Maki & Galatowitsch, 2004; Keller & Lodge, 2007; Gertzen *et al*., 2008), unauthorised stocking of ''desirable'' species is still common (Rahel, 2002), canals remain open, large cross-basin water diversions are planned, and so on. It is true that intentional stocking of fishes has begun to proceed more cautiously, at least in some countries, so the species composition and ecological traits of alien species that appear in fresh waters in the 21st century may differ from what we saw in the 20th century, with relatively more plants and invertebrates, and fewer large, predatory fishes.

Third, ecosystem disturbance appears to favour the establishment of alien species, and it seems likely that freshwater ecosystems will continue to be highly disturbed as human demands for water for domestic use, irrigation, and industrial use; hydroelectricity; navigational routes; and protein from freshwater fisheries rise (Gleick, 2003). Furthermore, humans probably will respond to water shortages, flooding, and other problems associated with climate change by building large engineering projects that further disturb freshwater ecosystems and encourage alien species.

Range-filling by established aliens creates an ''invasion debt''

Even if we were to stop all long-range transport of alien species today, the numbers of alien species in individual bodies of water would continue to increase for a long time as established invaders filled in their ranges by dispersing into suitable sites within their new range. For instance, the zebra mussel (*Dreissena* *polymorpha*) has been established in North America for >20 years (Carlton, 2009), but has established populations in <8% of suitable lakes in the Great Lakes region (Fig. 8; see also Karatayev *et al.*, 2003), and presumably even fewer bodies of water further from the site of its initial introduction. In North America, problematic invaders such as the zebra mussel, the quagga mussel, the New Zealand mudsnail, Eurasian water-milfoil, the water-chestnut, the bighead, silver, and grass carps, the round goby, and dozens of others still occupy only a small fraction of suitable sites on the continent (e.g., Fig. 2), and similar situations exist around the world. Thus, we can look forward to greatly increased numbers of aliens, and impacts from these species, as established species fill in their new ranges. The rate of range-filling will depend on the dispersal capabilities and ecological requirements of each alien species, as well as the geographical characteristics of the new range, but may take decades to millennia to proceed to completion. While educational campaigns and local regulations may slow the spread of these invaders, they may not prevent these species from ultimately reaching many more bodies of water. In the same sense that Tilman *et al.* (1994) and others have written about ''extinction debt'', we can think of long-range transport of alien species as incurring an ''invasion debt'' (Fig. 8) that will not be redeemed until these species have established themselves in all suitable bodies of water within their new ranges.

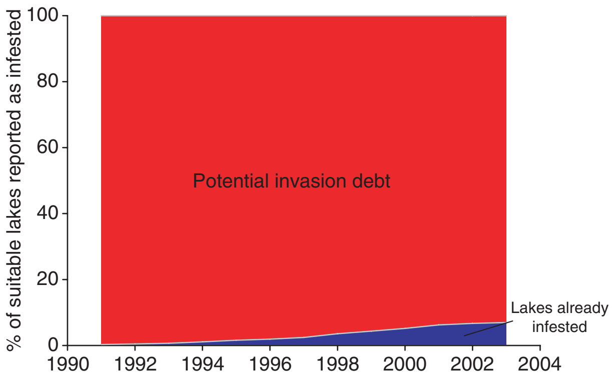

Fig. 8 Percentage of inland lakes in the Great Lakes region with habitat suitable for zebra mussels that actually were infested by the zebra mussel, 1991–2003, from Johnson, Bossenbroek & Kraft (2006). ''Potential invasion debt'' is the amount of potentially suitable habitat in an invaded region that has not yet been invaded by an alien species. Although the number of lakes suitable for zebra mussels is assumed here to be constant over time, it is actually likely to fluctuate as ecological conditions in the lakes change through time.

The long-term effects of aliens are difficult to predict

One of the major difficulties in forecasting the future effects of alien species in freshwater ecosystems is that we don't well understand how these effects might change through time. Invasion ecologists typically have paid little attention to how the effects of an alien species might change over time, but there are good theoretical reasons and a little empirical data suggesting that the ecological effects of an alien species may either increase or decrease substantially through time (Strayer *et al.*, 2006; Gherardi, 2007a; Hawkes, 2007). Either the invader or the invaded community may evolve; the species composition of invaded community may shift towards species that are insensitive to the invader, or even use the invader as a resource and thereby suppress its population; the effects of the invader may accumulate through time; or the invader may interact with other temporally changing variables such as weather to produce net effects that change over time. All of these mechanisms are common in nature, and all are capable of substantially modifying the effects of an alien species, but none has been well-studied in the context of species invasions.

Nevertheless, there are at least a few examples of how the effects of an alien species have changed over time. In a few more or less mysterious cases, populations of invaders have collapsed or even disappeared entirely after an initial outbreak phase, perhaps as a result of attacks by enemies that adapted to the invader or colonised its populations (Simberloff & Gibbons, 2004). The irruption and near disappearance of many populations of *Elodea canadensis* Michx. in the British Isles is perhaps the most-cited example (Simpson, 1984). In another striking example, the establishment of a large population of zebra mussels in the Hudson River caused phytoplankton biomass to fall by 80% (Caraco *et al.*, 2006), and led to a catastrophic decline of all native bivalves in the first years (1992–1999) of the invasion (Fig. 4). The native bivalve populations then recovered after 2000. We do not know if this reversal is permanent, nor do we understand the mechanism behind it; the zebra mussel population did not decline and phytoplankton biomass did not recover in the second seven-year period (Strayer & Malcom, 2007). More generally, Hawkes (2007) found that the degree of herbivory and pathogens on alien plants increased significantly over time. It seems probable that examples like these will prove to be common once ecologists look for them.

Of course, if humans actively control the population of the invader, its ecological effects will decrease over time (or increase again if control is abandoned – Strayer *et al*., 2005). Other than some successful programs to control aquatic plants (e.g., McFadyen, 1998; Gassmann *et al*., 2006), though, there have been relatively few attempts to control alien species in fresh water up to this point, and many of them have been unsuccessful (but see Knapp & Matthews, 1998; Hein, Vander Zanden & Magnuson, 2007).

Clearly, if we wish to know the long-term effects of species invasions in freshwater ecosystems, we will need to learn much more about how these effects can moderate or intensify through time. Regardless of the long-term trajectory of the effects of an alien species, and even if nature or human activities are able to reduce these effects over the long term, we need to remember that the short-term, transient effects can be ecologically and economically important as well. The entire time-course of the effects of an alien species is of interest, and is hardly known at present for any species.

Alien species create no-analogue ecosystems that may be difficult to manage

Alien species pose several challenges for the future management of freshwater ecosystems. Most obviously, the alien species itself may create problems that need to be managed, either by attempting to control the alien population or by mitigating its effects (e.g., captive breeding of endangered species that are imperiled by the alien). Up to this point, successful programs to control alien species, either before or after they establish populations, have been relatively rare (but see McFadyen, 1998; Gassmann *et al*., 2006), possibly because the alien species problem has not been seen as a coherent issue whose effects are comparable in scope and size to those of the better-known stresses to freshwater ecosystems (e.g., eutrophication, hydrologic alteration, acidification). Perhaps if we had been willing to spend as much money on alien species control as we have on these other problems, we would have more success stories to report and fewer problems with alien species in fresh waters (cf. Williams & Grosholz, 2008).

Second, the arrival of alien species can greatly complicate or limit available options for management or restoration directed at other problems of freshwater ecosystems. I described several examples in the section on interactions with other stressors. Thus, one consequence of the poor controls on alien species is that even well-conceived and expensive programs to manage freshwater ecosystems and deal with the other stresses that are the subject of this special issue are put at risk or undone.

Alien species are especially problematic for managers because they are so unpredictable. The ability of freshwater ecologists to forecast loads of nutrients, sediments, acidifying substances, and so on, from land use, population density, and industrial activities has been an essential tool in devising management and policy responses. While it is true that overall numbers of invaders are predictable simply by extrapolating past rates or by using various indicators or economic activity, the specific identity of invaders or their time of arrival is not easy to predict (but see Ricciardi & Rasmussen, 1998). Because the ecological effects of invaders, interactions with other stressors, and management options depend so strongly on which species are introduced, knowing overall invasion rates does not provide much guidance to managers. Instead, freshwater managers in the Homogocene can expect to be surprised and disappointed by the arrival of invaders that undo their good work.

Finally, alien species can take us into the *terra incognita* of no-analogue ecosystems (in the sense of Williams & Jackson, 2007). Much of our ability to manage freshwater ecosystems is based on our past experience with that ecosystem or other similar ecosystems (e.g., small, deep, dimictic lakes with piscivorous fish). The past behaviour of the ecosystem, including its responses to perturbations, gives us important insights into how it might respond to management actions. However, the establishment of alien species in an ecosystem can fundamentally transform the ecosystem into a system unlike the one that we have experience with, and in some cases, unlike any ecosystem that exists anywhere in the world (a ''no-analogue'' ecosystem). Our experience may not be a reliable guide to the management of such ecosystems. The problem of no-analogue ecosystems has been discussed mostly in the context of the difficulties posed by climate change (Williams & Jackson, 2007), but is likely to become increasingly important in fresh waters as species invasions and other stresses (unnatural hydrological regimes, novel riparian zones, etc.) take us farther and farther from the kinds of freshwater ecosystems that we have experience studying and managing.

Other than the obvious advice that we should note that we are outside the domain of our past experience, apply management actions cautiously, be sure to monitor their effects, and be prepared to change our management regime if we are surprised by the response of the ecosystem, how should we proceed when alien species produce no-analogue ecosystems? One helpful approach might be to devote more attention to how the effects of an alien species depend on the characteristics of the system into which they are placed. Although it is clear that the effects of an alien species can differ greatly across ecosystems (e.g., Strayer *et al*., 1999; Strayer, Hattala & Kahnle, 2004), ecologists haven't yet tried to explain this variation with quantitative models. Such models, if successful, could be very helpful in predicting the likely effects of an invader (Gherardi, 2007a), and therefore the kinds of management responses that might be warranted in specific ecosystems. While it probably would not be practical to develop predictive models for every important invader of fresh waters, it might be possible to develop models for the major classes of invaders (e.g., suspension-feeding bivalves, crayfishes).

Ultimately, I think that the best solution to the management problems caused by alien species will be to work aggressively to cut the arrival rates of new invaders. This will involve reducing the numbers of new invaders that arrive through poorly controlled pathways such as ballast water; releases from the pet trade, aquaculture, and horticulture; bait buckets; and canals (especially those that are no longer used heavily). Research on effective technologies, outreach to various audiences (e.g., anglers, boaters, professionals in the pet and nursery trades, freshwater managers, policy-makers, and the general public), and new policies all will be essential elements of a long-term solution. Unless we can substantially reduce establishment rates of alien species, freshwater ecosystems of the future (and their managers) will continue to be jolted by the arrival of new invaders.

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Conflicts of interest

The author has declared no conflicts of interest.

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