

Ecology of Invasive Alien Invertebrates

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Chapter Outline

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RATES AND GLOBAL EXTENT OF FRESHWATER INVERTEBRATE INVASIONS

Under human influence, species are spreading faster and farther into new regions than at any other time in Earth's history. This process of spread and establishment is termed *biological invasion*, and species introduced beyond their native (historical) range are referred to as *alien species* (or *nonnative*, *nonindigenous*, or *exotic*). Those that spread and establish rapidly, or that become pests, are often described as “invasive.” Freshwater ecosystems worldwide are highly vulnerable to being invaded and transformed by alien invertebrates. Large aquatic ecosystems are known to contain scores of alien species, especially crustaceans and molluscs (Table 5.1). The true numbers of alien species, even in these relatively well-studied systems, are probably grossly underestimated, resulting from (1) irregular monitoring, (2) incomplete faunal inventories, (3) poor knowledge of the historical biogeography of many of the species present, and (4) insufficient taxonomic expertise for recognizing alien invertebrates. Consequently, virtually all freshwater ecosystems contain cryptogenic species (taxa that cannot be classified with certainty as either alien or native) and pseudoindigenous species (alien species mistaken as natives) (Carlton, 2009). These are typically small-bodied taxa (e.g., bryozoans, annelids, nematodes, rotifers, gastrotrichs) that are often misidentified despite being common and widespread. The inverse correlation between an organism's body size and its likelihood

of being recognized as alien is termed the *small's rule* (Carlton, 2003). This problem, along with a number of other factors (e.g., highly selective transport by humans, both intentionally and inadvertently), has contributed to an unbalanced representation of taxa among alien invertebrates in freshwater systems (Panov et al., 2004; Karatayev et al., 2009). Aquatic insects, for example, are rarely on alien species lists despite dominating benthic fauna in lakes and rivers (Table 5.1). Most winged insects are likely to have colonized their current ranges from glacial refugia much earlier (beyond the detection of biologists) than other taxa. The few unequivocal cases of alien aquatic insects are from invaded habitats very remote from their historic range and clearly beyond their natural dispersal abilities (e.g., Van de Meutter et al., 2010).

Many species believed to have natural cosmopolitan distributions are likely alien in origin (Carlton, 2009). Several of these species have globally disjunct distributions, in which records of occurrence include isolated populations apparently far removed from a more extensive and contiguous historical range. Genetic analyses are beginning to reveal cryptic invasions in freshwater systems worldwide (e.g., Walthert et al., 2006; Folino-Rorem et al., 2009). In contrast, some invasions have involved conspicuous, even spectacular, range extensions. The freshwater jellyfish *Craspedacusta sowerbyi* Lankester, 1880, native to the Yangtze River valley, is established on every continent except Antarctica, and it continues to be discovered in lakes and ponds across the world. Global introductions of the Asian clam *Corbicula fluminea* (Müller,

TABLE 5.1 Number of Alien Macroinvertebrate Taxa Recorded as Established in Large Freshwater Ecosystems

System	Molluscs	Crustaceans	Annelids	Insects	Other	Reference
Laurentian Great Lakes	18	21	6	2	23	Mills et al., 1993; Ricciardi, 2006; Ricciardi, unpublished data
Lake Champlain	11	5	0	0	2	Marsden and Hauser 2009
Hudson River	19	6	1	0	2	Mills et al., 1997
Mississippi River	8	6	0	0	1	Rasmussen 1998; Grigorovich et al., 2008; Wood et al., 2011
Columbia River	3	4	7	0	3	Sytsma et al., 2004
Rhine River	10	23	6	1	6	Leuven et al., 2009
Thames River	8	15	3	2	13	Jackson and Grey 2013
Ebro River (Spain)	7	11	1	0	5	Oscoz et al., 2010
Lake Balaton (Hungary)	3	10	0	0	1	Muskó et al., 2007; Muskó et al. 2008; Gábor 2009

1774) and its congeners began more than 100 years ago and continue today. Within the past 25 years, more than a dozen invertebrate species from the Black and Caspian sea basins have invaded the North American Great Lakes (Ricciardi, 2006); these include the zebra mussel *Dreissena polymorpha* (Pallas, 1771) and the quagga mussel *Dreissena rostriformis bugensis* (Andrusov, 1897), which have since spread farther across the Rocky Mountains into the western United States (Stokestad, 2007). Numerous gastropods have become invasive globally, including Chinese mystery snails (*Bellamya/Cipangopaludina* spp.), Central American apple snails (*Pomacea* spp.), the New Zealand mud snail *Potamopyrgus antipodarum* (Grey, 1853), and a variety of pulmonate snails (e.g., *Physella* spp.). Intercontinental transfers of crustaceans are even more frequent. Alien crustaceans, including cladocerans, copepods, amphipods, mysids, and crayfish, are found in most large freshwater lakes and rivers worldwide (Table 5.1). Some crustaceans that were previously confined to coastal environments, such as the copepod *Eurytemora affinis* (Poppe, 1880), are now being discovered more frequently in freshwater lakes and rivers, suggesting a recent adaptation to low-salinity waters (Lee and Bell, 1999).

Alien invertebrates are being discovered at increasing rates in large freshwater systems (Figure 5.1). Multiple factors may contribute to this apparent pattern, the most plausible being increased opportunities for introduction through human activities. In the Great Lakes, the composition of alien species discovered during the past century correlates with changes in shipping and other vectors. Thus, species known to be moved by particular vectors become more prevalent when that vector is most active (Ricciardi, 2006). Rates of invasion by freshwater invertebrates appear to be orders of magnitude

greater now than before human influence (Ricciardi, 2006). Molecular evidence has revealed that the modern rate of invasion of North American lakes by European cladocerans is ~50,000 times greater than the prehistoric rate (Hebert and Cristescu, 2002).

HUMAN VECTORS OF DISPERSAL

Invertebrates are being dispersed worldwide primarily by vectors associated with both shipping and live trade in aquatic organisms. Carlton (1993) identified more than 20 distinct human-mediated mechanisms of dispersal of the zebra mussel involving canals, shipping activities (ballast water, hull fouling, movement of navigational buoys, and boatyard equipment), and fishing activities, including the transport and release of live bait. On a global scale, molluscs and crustaceans are distributed through the commercial importation of aquatic organisms for the aquarium trade or for human consumption (Padilla and Williams, 2004; Keller and Lodge, 2007). For example, the red swamp crayfish *Procambarus clarkii* (Girard, 1852), native to the southeastern United States, has been introduced to two dozen countries in South America, Africa, Asia, and Europe, often deliberately for use in aquaculture and the aquarium trade, and as an agent to control pest snails (Gherardi, 2011). The importation of water plants for ornamental gardens likely contributed to the inadvertent introduction of the Asian bryozoan *Lophopodella carteri* (Hyatt, 1866) into North America during the 1930s (Ricciardi and Reising, 1994). Shipping is assumed to be responsible for hundreds of freshwater invertebrate invasions worldwide (e.g., Ricciardi, 2006; Leuven et al., 2009; Jackson and Grey, 2013) including, for example, the occurrence in the Panama Canal of sponges

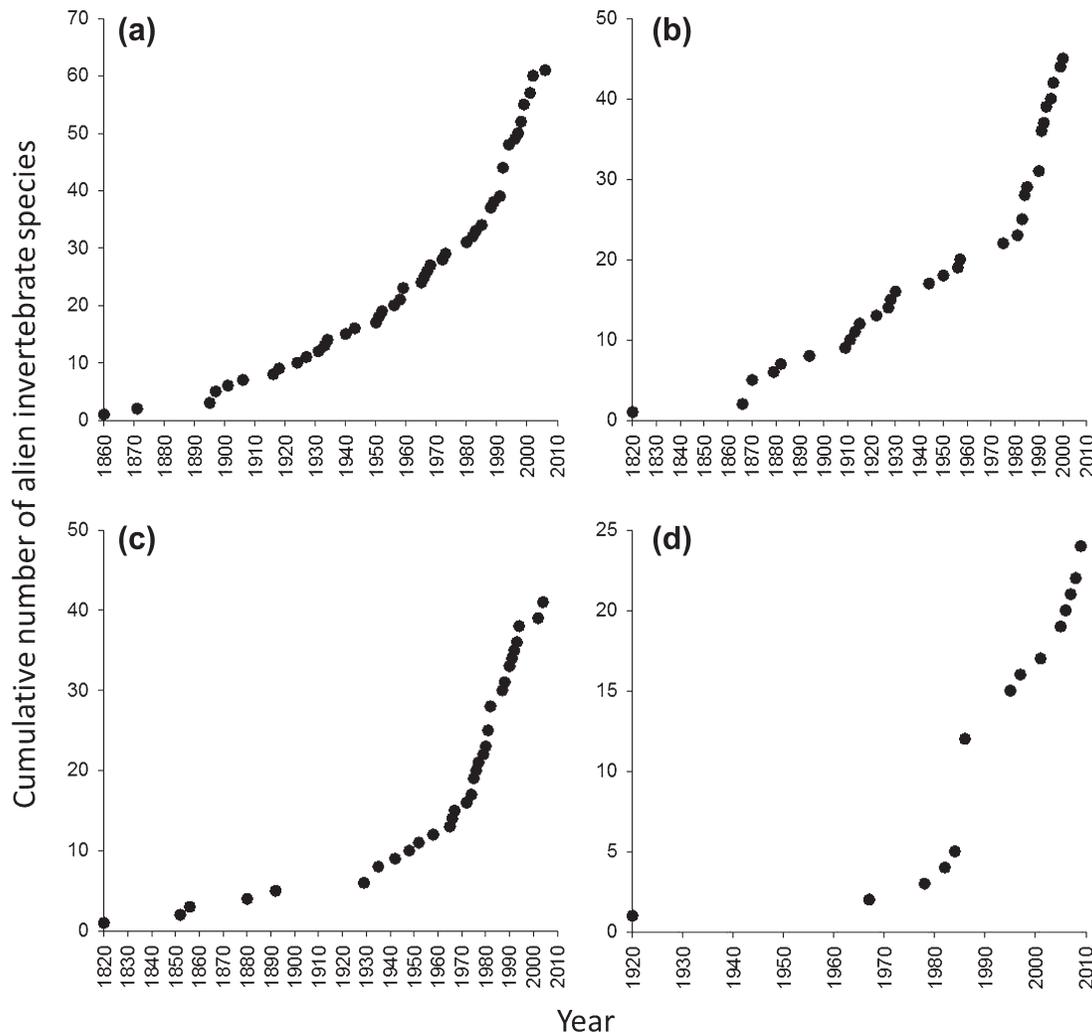


FIGURE 5.1 Accumulation of alien invertebrate species recorded as established in (a) the Laurentian Great Lakes, (b) the Rhine River, (c) the Thames River, and (d) the Ebro River, as a function of year of discovery. Sources: Ricciardi, 2006; Leuven et al., 2009; Jackson and Grey, 2013; Osoez et al., 2010.

Eunapius carteri (Bowerbank, 1863) and *Trochospongilla leidii* (Bowerbank, 1863), the former previously unrecorded in the western hemisphere and the latter found previously only in the United States (Jones and Rützler, 1975; Poirrier, 1990). Resting eggs of cladocerans, copepods, rotifers, and bryozoans occur commonly in the bottom sediments of the ballast tanks of ships originating from freshwater and estuarine ports, in numbers that reach tens of millions of eggs per ship (Bailey et al., 2005; Duggan et al., 2005; Kipp et al., 2010). The number of freshwater bryozoan taxa found as statoblasts in the ballast sediments of 33 ships visiting the Great Lakes during a 2-year period accounted for more than 10% of all described species (Kipp et al., 2010). Indeed, the intercontinental movement of statoblasts by ships is assumed to be responsible for introducing an Asian bryozoan, *Asajirella gelatinosa* (Oka, 1891), into the Panama Canal region (Wood and Okamura, 1998).

The development of canals and navigational waterways can promote intracontinental invasions, as in the case of the spread of Ponto-Caspian animals across Europe (bij de Vaate et al., 2002). Several alien invertebrate species have dispersed through European waterways at mean rates of 40–130 km/yr (Leuven et al., 2009). Recreational boating is responsible for the overland dispersal of invertebrates attached to the boat hull or in bilge water (Johnson et al., 2001; Havel, 2012). The long-distance dispersal of dreissenid mussels has been aided by their attachment to barge traffic (Keevin et al., 1992) and to vessels trailered over land (Stokestad, 2007). For asexually reproducing organisms in particular, any form of transport of small amounts of water could potentially facilitate invasions over distances of thousands of kilometers. The interbasin movement of fishing gear [e.g., nets (Jacobs and MacIsaac, 2007)] almost certainly contributes to the spread of some

invertebrate species. An interesting case involves a North American triclad flatworm (*Phagocata woodworthi* Hyman, 1937) that was introduced to Loch Ness, Scotland, at some point before 1977 (Reynoldson et al., 1981), conceivably on equipment transported by American monster hunters!

TRAITS CONFERRING INVASION SUCCESS

Some hypothesized general attributes of successful aquatic invertebrate invaders are listed in Table 5.2. Although these generalizations have been widely cited, few have been tested rigorously. In a statistical comparison of European stream invertebrates, Statzner et al. (2008) found that genera with invasive species tended to reproduce more frequently and achieve greater abundances where they occurred, and also had significantly more ovoviviparity, which could enable colonization by a single individual that provides parental care and thus releases more viable offspring. Trait-based comparisons of alien and native gammarid amphipods in central Europe suggest that invasive aliens often have a combination of early maturity, greater fecundity (e.g., larger brood sizes), a greater number of generations per year, and a broad tolerance to habitat stressors (Grabowski et al., 2007); however, these traits may not be universal (e.g., Devin and Beisel, 2007). For bivalves, invasive taxa can be distinguished from natives by a set of biological traits that include shorter life spans, early maturity, and rapid growth (Morton, 1997; McMahon, 2002). Potentially confounding these patterns are traits that happen to promote uptake and transport by human vectors. For example, unionids are generally poor colonizers, and many have experienced range declines, although their larval stages are dispersed by fish.

One notable exception, however, is the Chinese pond mussel *Sinanodonta (Anodonta) woodiana* (Lea, 1834), which uses of broad range of fish hosts—including, most importantly, commercially cultivated species—that have caused it to be distributed to various continents inadvertently through aquaculture activities (Douda et al., 2012). Tolerance to aerial exposure may also aid in dispersal between water bodies, such as by overland transport on recreational boats (Johnson et al., 2001; Havel, 2012).

Some studies have reported enhanced salinity tolerance among alien invertebrates, particularly crustaceans, compared with their native counterparts (Devin and Beisel, 2007; Grabowski et al., 2007). Similarly, introduced invertebrates discovered in the Great Lakes in recent decades consist predominantly of euryhaline species (Ricciardi, 2006). This pattern can be attributed to an enhanced capacity for euryhaline species to become abundant around estuarine ports and to tolerate fluctuating salinities within ballast tanks during long voyages. Many successful invaders also have resting (diapausing) stages that allow them to survive periods of unfavorable conditions, including hypoxia and temperature fluctuations, such as those typical of ballast tank environments (Panov et al., 2004). Invertebrate resting eggs may remain viable even during transport in mud attached to road vehicles and footwear (Waterkeyn et al., 2010).

ECOLOGICAL IMPACTS

Although the impacts of invertebrate invasions are often inconspicuous and rarely studied, documented impacts are broad in scope and include native population declines, altered nutrient cycling, changes to contaminant bioaccumulation

TABLE 5.2 Hypothesized Attributes of Highly Invasive Freshwater Invertebrates

Attribute	Reference
Abundant and widely distributed in original range	Miller et al., 2007
Broad environmental tolerance	Morton 1997; Miller et al., 2007; Alonso and Castro-Díez 2008
Short generation time (early sexual maturity, short life span)	Morton 1997; McMahon 2002; Grabowski et al., 2007
High, rapid growth rate	Morton 1997; McMahon 2002; Morrison and Hay 2011
High reproductive capacity	Morton 1997; Keller et al., 2007; Grabowski et al., 2007; Alonso and Castro-Díez 2008; Statzner et al., 2008
High rate of resource consumption	Morrison and Hay 2011; Dick et al., 2013
Aggressiveness (especially among crustaceans)	Gamradt et al., 1997; Dick 2008
Possession of natural mechanisms of active and passive dispersal	Alonso and Castro-Díez 2008
Strong potential to exploit human transportation systems	Morton 1997; Alonso and Castro-Díez 2008;
Asexual/hermaphroditic modes of reproduction	Panov et al., 2004
Adaptive capacity to colonize new environments (e.g., high plasticity)	Hänfling and Kollmann 2002

pathways, indirect food web effects on plants and algae (trophic cascades), and physical habitat alteration (Ricciardi and MacIsaac, 2011). Some species have far-reaching effects through their ecosystem engineering activities. These are best exemplified by small, prolific suspension-feeding organisms, such as the dreissenid mussels (*Dreissena* spp.), the golden mussel *Limnoperna fortunei* (Dunker, 1856), Asian clams (*Corbicula* spp.), and the mud amphipod *Chelicorophium curvispinum* (Sars, 1895). *Chelicorophium* inhabits networks of mud tubes that it builds on firm surfaces, thereby altering the physical habitat of other benthic invertebrates. During the 1980s, *C. curvispinum* invaded the Rhine River and, within a few years, it established densities of hundreds of thousands per square meter and altered the rocky substrate drastically with its muddy encrustations. The habitat engineering and suspension-feeding activities of this dense population apparently caused the near extirpation of the zebra mussel and a native hydropsychid caddisfly from the lower Rhine (van den Brink et al., 1993).

Dense populations of *Corbicula* and *Dreissena* achieve filtration rates that exceed those of native bivalves by up to three orders of magnitude (Strayer et al., 1999). They can remove enormous quantities of suspended particles from the water column, causing a doubling or tripling of water clarity and promoting the expansion of weed beds (Phelps, 1994; Strayer et al., 1999; Vanderploeg et al., 2002). The influence of *C. fluminea* in the Potomac River was extensive enough to cause the appearance of submerged aquatic vegetation for the first time in 50 years, with concomitant increases in the abundances of littoral fish and waterfowl. These dramatic ecosystem changes were rapidly reversed after the clam population exceeded its carrying capacity and crashed (Phelps, 1994). Similarly, zebra mussel activities enhanced the water clarity drastically and thus stimulated luxuriant macrophyte growth in Lake St. Clair and the western basin of Lake Erie, which provoked a major shift in the fish community by displacing species sensitive to light (walleye, *Sander vitreus* (Mitchell, 1818)) and by favoring species adapted to foraging in weed beds (Vanderploeg et al., 2002).

In littoral areas, byssally attached mussels (*Dreissena* and *Limnoperna*) generally increase benthic community richness and biomass through provision of microhabitat (interstices of clumped shells), grazing surfaces (shells), and nourishment in the form of fecal/pseudofecal deposits (Ricciardi et al., 1997; Ward and Ricciardi, 2007; Burlakova et al., 2012). However, these invasive bivalves also exclude some species of invertebrates through resource competition and interference (Ricciardi et al., 1997; Lauer and McComish, 2001). Intense fouling of the exposed shells of native molluscs by dreissenids (Figure 5.2) causes negative impacts (Ricciardi et al., 1998; Van Appledorn et al., 2007; zu Ermgassen and Aldridge, 2010; Sousa et al., 2011), including severe population declines (Ricciardi et al., 1998).



FIGURE 5.2 Dreissenid mussels fouling a unionid bivalve (*Lampsilis radiata*) from the St. Lawrence River.



FIGURE 5.3 The killer shrimp *Dikerogammarus villosus*. Photo courtesy of J.T.A. Dick.

Introduced predatory invertebrates have caused conspicuous biodiversity loss in benthic and pelagic communities. The amphipod *Dikerogammarus villosus*, known as the “killer shrimp” (Figure 5.3), is a voracious predator of benthic invertebrates. It is rapidly eliminating native and alien gammarid populations from parts of western Europe (Dick et al., 2002), and these species displacements may have consequences for ecosystem functioning (MacNeil et al., 2011). The introduction of the Eurasian spiny water flea *Bythotrephes longimanus* Leydig, 1860, into Canadian Shield lakes has apparently resulted in rapid and persistent declines in native zooplankton richness (Boudreau and Yan, 2003). A similar predator, the fishhook water flea *Cercopagis pengoi* (Ostroumov, 1891), has invaded the Baltic Sea and the lower Great Lakes. *Cercopagis* feeds readily on small-body cladocerans; its population expansion during a 3-year period in Lake Ontario coincided with sharp declines in the abundance of dominant members of the zooplankton community, including two daphniid species that have been observed to be preyed upon by *C. pengoi* in lab experiments. One of these

species declined despite exhibiting high fecundity during all 3 years (Laxson et al., 2003). After the appearance of *C. pengoi* in the Baltic Sea, densities of small-body cladocerans and copepods declined, particularly above the thermocline (Kotta et al., 2006). Where it occurs in dense patches, the *C. pengoi* population is estimated to consume tens of thousands of copepods per cubic meter per day, which implicates it as the cause of a drastic decline in copepod abundances in the Gulf of Finland (Lehtiniemi and Gorokhova, 2008).

Another group of crustacean predators, mysid shrimp were stocked as a supplementary food source for sportfish in many North American and European lakes during the latter half of the previous century. Through vertical migration in the water column, mysids escape predation from planktivorous fish, including those species whose diets they were meant to supplement. The mysids themselves exert strong predation pressure on large zooplankton, often causing severe (>60%) reductions in cladoceran density and biomass within one to two decades after their introduction (Ricciardi et al., 2012). These reductions may lead to declines in the growth, abundance, and productivity of pelagic fishes. Mysid invasions can also alter the cycling of heavy metals and other contaminants. Vertical migrations of mysids increase the transfer of heavy metals between benthic and pelagic communities; and by lengthening the food chain, introduced mysids may increase the biomagnification of polychlorinated biphenyls and mercury contaminants in fish (Rasmussen et al., 1990; Cabana et al., 1994). The potential for mysids to generate cascading effects in food webs is exemplified by the well-documented introduction of the opossum shrimp *Mysis diluviana* Audzinyte and Väinölä, 2005 (formerly *Mysis relicta*) into Flathead Lake, Montana, as a prey item for another introduced species, kokanee salmon *Oncorhynchus nerka* (Walbaum, 1792). The opossum shrimp not only avoided predation by the diurnally feeding salmon, but also outcompeted it for dwindling food resources and thus caused the salmon population to crash. The loss of salmon was followed closely by declines in local populations of grizzly bears and bald eagles, which depended on salmon spawners as a food source (Spencer et al., 1991).

CAN THE IMPACTS OF ALIEN INVERTEBRATES BE PREDICTED?

A more predictive understanding of the impacts of invertebrate invasions is needed for prioritizing management interventions (Ricciardi, 2003) and for interpreting water quality assessments accurately that are based on benthic invertebrate community composition and relative abundance (MacNeil and Briffa, 2009). Unfortunately, only a few generalizations can be made. Invertebrate taxa that cause the greatest ecological impacts tend to be functionally unique in the invaded environment (Ricciardi and Atkinson, 2004), such that they use critical resources differently than native species (e.g., by displaying a unique form or a greater rate

of consumption) (Carlsson et al., 2004; Dick et al., 2013). They are typically predators or grazers that are unregulated by higher consumers because of their trophic position, recruitment rate, or antipredatory defenses. They generally have a greater fecundity and abundance than related native species (Keller et al., 2007; Gherardi, 2011), and—in the case of crustaceans—are more aggressive (Gamradt et al., 1997; Dick, 2008).

An invader's impacts can vary along environmental (e.g., temperature, oxygen, conductivity) gradients, such that they differ at various sites within a single heterogeneous aquatic system. Consequently, the invader may extirpate a native species at one site but coexist with it elsewhere (Jokela and Ricciardi, 2008; Kestrup and Ricciardi, 2009). For example, the impetus for introducing the opossum shrimp *M. diluviana* into lakes beyond its native range in North America was derived largely from the positive response of kokanee salmon to the mysid when it was introduced to Kootenay Lake, British Columbia. The hydrology of the lake was such that it provided upwelling currents that flushed out the mysid to make it available to salmon during daylight hours; thus, it was an inappropriate model to predict the outcome of such introductions in most deep lakes in which mysids can migrate to profundal areas (Martin and Northcote, 1991). The composition of the invaded community also influences impact. The effects of even highly invasive species may be modified by the presence of predators, pathogens, or competitively dominant species (Kuhns and Berg, 1999; Ward and Ricciardi, 2010; Kestrup et al., 2011).

The context dependency of impact presents the largest impediment to risk assessment. However, ecologically damaging invaders often have a history of strong impacts in other invaded regions (e.g., Ricciardi et al., 2012). This history, if documented sufficiently, can be used to generate predictive models for those species, taking into consideration key environmental variables that have been identified as modulators of the invader's impact (Ricciardi, 2003; Ward and Ricciardi, 2007).

An intuitive, but largely untested, hypothesis is that introduced invertebrates that cause strong ecological impacts also cause strong socioeconomic impacts (e.g., on outdoor recreation, fisheries, water supply systems). Species that are otherwise rather innocuous to ecological communities may still pose health risks to humans and domestic animals, if they are vectors of disease. Even commercially valuable invertebrate species can cause unforeseen economic damage (Gherardi, 2011).

MANAGEMENT OF INVASIVE AQUATIC INVERTEBRATES

Although the costs of prevention may be far outweighed by chronic costs of impacts, management has, traditionally, been reactive to invasion threats, usually responding after

a problematic species has become well established. Consequently, successful eradication attempts are extremely rare. Efforts to contain, reduce, or remove alien invertebrate populations have used biological, chemical, and mechanical controls (e.g., Pointier and David, 2004; Wittmann et al., 2012). The benefits of these efforts are often limited by the lack of early detection and the difficulties of managing an expanding population. Targeted harvesting and the cultivation of native fish predators can aid in reducing populations of particularly harmful invaders (Robinson and Wellborn, 1988; Hein et al., 2007; Aquiloni et al., 2010).

Highly invaded systems contain greater numbers of ecologically and economically damaging species (Ricciardi and Kipp, 2008), an observation that justifies management efforts to reduce invasion rates even where numerous invasions have already occurred. Given the apparently increasing accumulation of alien species in large lakes and rivers (Figure 5.1), recent efforts to manage invertebrate invasions have focused on controlling major vectors, particularly ballast water transport. Substantive progress has been made in developing control strategies for ballast water-mediated introductions (e.g., Bailey et al., 2006); however, the invasion risk posed by resistant diapausing stages in ballast tanks remains a management challenge. Attention must also turn to fostering policies for largely unregulated vectors, such as those associated with live trade (e.g., for food markets, ornamental/pet trade, use as fishing bait) (Keller and Lodge, 2007). Lastly, public outreach, including education campaigns that target anglers, boaters, and pet owners, may aid in limiting the spread of alien invertebrates.

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