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Facilitation and Synergistic Interactions between Introduced Aquatic Species

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Interactions between introduced species have long been ignored or presumed to be competitive and mutually detrimental. However, in recent years studies have suggested that the establishment and persistence of introduced species are commonly facilitated by other introductions; the best examples are plant invasions that have been aided by animal pollinators and seed dispersers (Simberloff and Von Holle 1999; Richardson et al. 2000). Terrestrial studies also reveal that multiple introductions can produce synergistic impacts (in which the joint effect of two or more invasions is greater than the sum of their individual effects), which might accumulate over time, a phenomenon called invasional meltdown (Richardson, Cowling, and Lamont 1996; Simberloff and Von Holle 1999).

By contrast, aquatic invasions are often treated as isolated events whose impacts are independent of one another. Judging from the scientific literature and invasive species conferences, it seems aquatic ecologists and fishery managers have overlooked the potential importance of facilitation between invaders, possibly because the consequences of such interactions are less conspicuous in aquatic systems. This chapter examines evidence that aquatic invasions may produce synergistic impacts that pose a formidable challenge to conservation and resource management. Herein, *invasion* is defined as the establishment of a reproducing population by an introduced species, and *facilitation* is defined as an interaction in which one species has a positive effect on the persistence or population growth of another species.

Case Studies

Facilitation of Introduced Species by Zebra Mussels in the Great Lakes

The effects of several invaders of the North American Great Lakes have been altered by the introduction of the Eurasian zebra mussel (*Dreissena polymorpha*) in the mid-1980s. *Dreissena* provides other benthic invertebrates with nourishment (in the form of fecal deposits) and shelter (interstitial spaces between clumped mussel shells), causing local enhancement of benthic invertebrate abundance and diversity (Ricciardi, Whoriskey, and Rasmussen 1997; Ricciardi 2003). Among the invertebrates responding positively to zebra mussel colonization is a Eurasian amphipod crustacean (*Echinogammarus ischnus*), which is replacing a North American amphipod in the Great Lakes–St. Lawrence River system (Van Overdijk et al. 2003; A. Ricciardi, unpublished data, 1998). By colonizing silty sediments in western Lake Erie, *Dreissena* facilitated the expansion of *Echinogammarus* into habitats that would otherwise be unsuitable (Bially and MacIsaac 2000). Field experiments demonstrate that the presence of *Dreissena* can cause a 20-fold increase in *Echinogammarus* biomass (Stewart, Miner, and Lowe 1998). This produces an abundant prey resource for the round goby (*Neogobius melanostomus*), a Eurasian fish that feeds primarily on amphipods during its juvenile stage and on zebra mussels during its adult life (Shorygin 1952; Diggins et al. 2002). Shortly after the round goby invaded the St. Clair River, populations of native logperch (*Percina caprodes*) and mottled sculpin (*Cottus bairdi*) declined (Jude, Janssen, and Crawford 1995). Mottled sculpin are nearly extirpated from a harbor in southern Lake Michigan by competition with the round goby for shelter and spawning sites (Janssen and Jude 2001). The goby's ability to consume zebra mussels gives it a competitive advantage over sculpin and logperch. Moreover, its feeding activities reduce benthic invertebrate (non-mussel) biomass, thereby affecting the food resources of other benthic fishes (Kuhns and Berg 1999).

Dreissena is involved in at least two mutualistic interactions in the Great Lakes. The first case, demonstrated experimentally, is the European faucet snail (*Bithynia tentaculata*), whose abundance is several times higher in dreissenid mussel patches (Ricciardi, Whoriskey, and Rasmussen 1997). Mussel shells provide the snail with grazing area and protection from large predators (Ricciardi, Whoriskey, and Rasmussen 1997; Stewart, Miner, and Lowe 1999) and might also release it from competition with larger native snails, such as pleurocerids, which tend to be excluded from dense mussel patches (Ricciardi, Whoriskey, and Rasmussen 1997; Haynes, Stewart, and Cook 1999). In exchange, *Bithynia*'s grazing activities prevent mussels from becoming excessively fouled by sponges and other attached organisms (A. Ricciardi, unpublished data), which can reduce mussel recruitment and survival (Ricciardi et al. 1995; Lauer et al. 1999).

A second mutualistic interaction observed in Lake St. Clair and Saginaw Bay (Lake

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Huron) is supported by correlation. In both of these ecosystems, zebra mussel filtration has increased water clarity, thus stimulating prolific growth of exotic weeds such as Eurasian milfoil (*Myriophyllum spicatum*) and curly pondweed (*Potamogeton crispus*) (Skubinna, Coon, and Batterson 1995; MacIsaac 1996). The weeds act as substrates for settling mussel larvae (possibly alleviating intraspecific competition with adult mussels) and also facilitate the dispersal of attached mussels via rafting on fragmented vegetation (Horvath and Lamberti 1997). As a result of the system-wide changes produced by *Dreissena,* the fish community in Lake St. Clair shifted from dominance by commercially important walleye (*Stizostedion vitreum*) to bass (*Micropterus* spp.) and pike (*Esox lucius*) (MacIsaac 1996). Similar cascading impacts have been observed in the Potomac River after invasion by the Asiatic clam (*Corbicula fluminea*), whose intense filtration activity caused increased water clarity and prolific growth of the exotic weeds *Hydrilla verticillata* and *Myriophyllum spicatum.* Habitat provided by weed beds resulted in increased populations of introduced largemouth bass (*Micropterus salmoides*) (Phelps 1994; Serafy, Harrell, and Hurley 1994).

Through their filtration activities in the lower Great Lakes, zebra and quagga mussels probably stimulated the proliferation of botulism bacteria, which thrives in decaying vegetation and possibly accumulations of mussel feces. Outbreaks of Type E botulism have occurred in Lake Erie each summer since 1999 and are responsible for bird and fish die-offs. Carcasses of tens of thousands of waterfowl, particularly fish-eating and scavenging birds such as common loons (*Gavia immer*), red-breasted mergansers (*Mergus serrator*), and ring-billed gulls (*Larus delawarensis*), have been found on the shores of Lake Erie and, more recently, Lake Ontario. There have also been large die-offs of freshwater drum (*Aplodinotus grunniens*), a native fish that feeds on other fishes and mollusks, including dreissenid mussels (Morrison, Lynch, and Dabrowski 1997). The botulin toxin has been found in dreissenid mussels as well as their principal predator, the round goby, which is commonly found in the stomachs of affected birds. Therefore, it is hypothesized that the round goby is transferring toxin from the dreissenid mussels to higher trophic levels (Campbell et al. 2002; McLaughlin 2002; W. Stone, pers. comm., 2002).

Facilitation of Exotic Planktivorous Fishes by the Sea Lamprey in the Great Lakes

Synergistic impacts also resulted from the indirect facilitation of exotic planktivores by the sea lamprey (*Petromyzon marinus*) in the Great Lakes. It is not known when the sea lamprey became established in the basin, but the species was recorded in Lake Ontario as early as the 1830s. It may have entered the lake through the Erie Canal, which opened a passage to the Atlantic Ocean in 1819, and subsequently gained access to the upper Great Lakes by passing Niagara Falls through the Welland Canal (Coon 1999). The sea lamprey invaded Lake Erie by 1921 and had spread to Lake Huron, Lake Michigan, and Lake Superior by 1947 (Lawrie 1970).

Sea lampreys are voracious external parasites of other fish, to which they attach using a rasping suctorial mouth that causes bloody lesions in their victims. Host fish often die from multiple attacks. In each of the upper Great Lakes, invasion by the lamprey was immediately followed by a sharp decline in the resident lake trout (*Salvelinus namaycush*) population, which was already weakened by intense fishing (Lawrie 1970). Consequently, lake trout were extirpated from Lake Michigan and nearly eliminated from lakes Huron and Superior. Stocks of lake whitefish and deepwater ciscoes (*Coregonus* spp.) also collapsed, coincident with the order of establishment of the sea lamprey in each lake (Christie 1974). In combination with overfishing, the sea lamprey contributed to the extinctions of three endemic fishes—the deepwater cisco (*Coregonus johannae*), the shortnose cisco (*Coregonus reighardi*), and the blackfin cisco (*Coregonus nigrippinus*)—as well as the extirpation of populations of shortjaw cisco (*Coregonus zenithicus*) from the Great Lakes (Coon 1999).

The near total extinction of lake trout, the dominant piscivore, from the upper Great Lakes facilitated the explosive proliferation of two invasive planktivores, alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*). The alewife, like the sea lamprey, probably penetrated the Great Lakes from the Atlantic drainage via shipping canals, whereas rainbow smelt was intentionally stocked in a Michigan lake that became the source for populations in the upper Great Lakes (Smith 1970; Christie 1974). Before lake trout populations collapsed, alewife did not appear in Lake Michigan and were sparse in Lake Huron. In Lake Superior, alewife became common only after lake trout abundance diminished to its lowest level in the early 1960s (Smith 1970). After sea lamprey were controlled by lampricides in the mid-1960s, lake trout began to increase, and alewife subsequently declined (Smith 1970). Alewife populations were further reduced by stocking of nonindigenous strains of lake trout and Pacific salmonids in the 1960s (Stewart, Kitchell, and Crowder 1981). Similarly, rainbow smelt reached peak abundances in Lake Michigan, Lake Huron, and Lake Superior soon after lake trout populations crashed (Christie 1974).

Alewife undergo boom-and-bust cycles, in which die-offs litter beaches and clog water intakes (Kitchell and Crowder 1986). Population explosions of alewife and smelt triggered changes in the composition and abundance of zooplankton in the upper Great Lakes. Size-selective predation by alewife suppressed populations of large-bodied cladocerans and copepods in Lake Michigan (Wells 1970). Moreover, alewife and smelt consumed the pelagic eggs and larvae of several native planktivores, including important forage fishes such as emerald shiner (*Notropis atherinoides*) and lake herring (*Coregonus artedii*), all of which abruptly declined (Christie 1974; Crowder 1980; Stewart, Kitchell, and Crowder 1981). Commercial yields of lake herring crashed in lakes Superior, Michigan, Huron, and Ontario (Christie 1974). Thus, a combination of competition and predation by these exotic planktivores, facilitated by the sea lamprey, reduced native planktivores and overall fishery productivity (Smith 1970; Stewart, Kitchell, and Crowder 1981).

Facilitation of a Japanese Seaweed by Exotic Invertebrates on the Atlantic Coast of North America

Another instructive example of unanticipated synergy involves a recent series of invasions along the Atlantic coast of Nova Scotia, Canada. Species interactions within the rocky subtidal community were studied for several years before and after the establishment of a Japanese green alga (*Codium fragile* ssp. *tomentosoides*) and a European epiphytic bryozoan (*Membranipora mebranacea*) in the early 1990s. Before these invasions, the structure and stability of the community were regulated by sea urchin grazing. In the absence of intense grazing, the subtidal zone normally is dominated by kelp beds (*Laminaria longicruris*), which limit the abundance of understory alga species (Johnson and Mann 1988). Periodic formation of dense feeding aggregations of sea urchins (*Strongylocentrotus droebachiensis*) defoliated kelp beds, leaving open barrens dominated by thin crusts of coralline algae (Scheibling, Hennigar, and Balch 1999).

Recurrent outbreaks of disease caused by the amoeba *Paramoeba invadens* resulted in mass mortalities of sea urchins in the early 1980s, 1993, and 1995 (Scheibling and Hennigar 1997). After each outbreak, the elimination of sea urchins was accompanied by increases in kelp cover and biomass, reaching levels comparable to those of mature kelp beds within a few years (Miller 1985; Scheibling 1986). Thus, a cyclical shift of community states was driven by the population dynamics of sea urchins, which responded to the population dynamics of the amoeba. *Paramoeba invadens* is thought to be a nonindigenous species periodically introduced to the coastal waters of Nova Scotia by the movement of warm water masses, which are also responsible for the high temperatures that stimulate its growth. This hypothesis is favored by experiments demonstrating the inability of *Paramoeba* to survive in laboratory culture below 2°C (the winter minimum temperature along the northwest Atlantic is 0°C to –2°C) (Jellett and Scheibling 1988). Outbreaks occur in late summer during unusually warm years (Scheibling and Hennigar 1997), consistent with laboratory findings that show strong temperature dependence of the amoeba's growth rate (Jellett and Scheibling 1988). Furthermore, *Paramoeba* is waterborne and can be cultured on marine bacteria, indicating that it is not an obligate parasite of urchins (Jones and Scheibling 1985), yet it has been found only in diseased urchin tissues and not in healthy urchins or in the natural environment (Jellett et al. 1989).

In the 1990s, a sequence of events caused an unprecedented transformation of the subtidal ecosystem. In 1995, a mass mortality of sea urchins resulted from a *Paramoeba* outbreak during anomalous warm temperatures and large-scale mixing of ocean currents (Scheibling and Hennigar 1997). This event interrupted the transition to urchin barrens and caused kelp beds to reestablish. Warm water temperatures also stimulated prolific growth of the bryozoan *Membranipora*, which was first recorded in the Gulf of Maine in the late 1980s (Lambert, Levin, and Berman 1992) and has been present on the Atlantic coast of Nova Scotia since at least 1992 (Scheibling, Hennigar, and Balch 1999). The suppression of sea urchins by *Paramoeba* in 1995 created an abundance of substrate for *Membranipora*, which forms calcareous coatings on kelp fronds. Intense bryozoan colonization increases the brittleness of kelp fronds so that they are easily damaged by heavy wave action, which destroys the kelp canopy (Dixon, Schroeter, and Kastendiek 1981; Lambert, Levin, and Berman 1992; Scheibling, Hennigar, and Balch 1999). The loss of the kelp canopy usually is temporary because recruitment from a local spore source can regenerate a kelp bed (Scheibling, Hennigar, and Balch 1999).

After the successive outbreaks of *Paramoeba* and *Membranipora*, the Japanese alga *Codium fragile* became abundant in the shallow subtidal for the first time. *Codium* had already been present on the Nova Scotia coast since the early 1990s (Bird, Dadswell, and Grund 1993) but at low densities because of intense sea urchin grazing in barrens and because of competition in kelp beds (Scheibling 2000). Previously, *Membranipora* outbreaks resulted in temporary kelp defoliation, followed by kelp resurgence and subsequent colonization by the bryozoan. In 1995, *Codium* replaced kelp before it could resurge. *Codium*'s growth was promoted by the reduction in kelp canopy cover, which permitted increased light penetration to the bottom sediments (Scheibling 2000). Because *Membranipora* rarely colonizes *Codium* (R. E. Scheibling, pers. comm., 2000), its population probably will diminish in the absence of suitable macroalgal substrate. Thus, *Membranipora* has acted as a transient facilitator of the *Codium* invasion by releasing it from competition with *Laminaria*. An identical facilitation of *Codium* by *Membranipora* has occurred in the Gulf of Maine (Harris and Tyrrell 2001).

The emergence of *Codium* as the dominant alga has disturbing implications for Atlantic coastal fisheries. Unlike kelps that form a canopy with an understory of algae, *Codium* is a branching alga that forms a short bushy meadow almost impenetrable to large fish and invertebrates such as lobster. There appear to be no herbivores capable of limiting the growth and expansion of these meadows. In mixed-diet feeding experiments involving *Codium*, sea urchins prefer kelp, although they will feed on *Codium* in the absence of kelp (Prince and LeBlanc 1992; Scheibling and Anthony 2001). However, a single diet of *Codium* inhibits urchin gonadal development (Scheibling and Anthony 2001). Therefore, if the shift in algal dominance from kelp to *Codium* is sustained, it should have negative consequences for urchin population growth and thus for an important commercial fishery (Hatcher and Hatcher 1997). Furthermore, if reductions in kelp beds cause lower lobster yields (Wharton and Mann 1981), the *Codium*–*Membranipora* synergism will affect the Atlantic lobster fishery.

Does Facilitation Increase Rates of Invasion in Aquatic Ecosystems?

The invasional meltdown model predicts that ecosystems subjected to a chronically high frequency of species introductions will become progressively unstable and easier to invade, as each introduced species has the potential to facilitate subsequent invaders

(Simberloff and Von Holle 1999). Indeed, observed rates of invasion are increasing in several aquatic ecosystems, including the Great Lakes, San Francisco Bay, the Baltic Sea, and the Mediterranean Sea (Ribera and Boudouresque 1995; Cohen and Carlton 1998; Leppäkoski and Olenin 2000; Ricciardi 2001). These emergent patterns are thought to reflect temporal variation in dispersal opportunity, sampling bias (search effort), and changes in the resistance of the recipient environment to invasion (Ruiz et al. 2000; MacIsaac, Grigorovich, and Ricciardi 2001).

There are sparse data available to test the effect of facilitation on invasion rates. Facilitation may have lowered environmental resistance to invasion in the Great Lakes, where documented cases of facilitation among introduced species are more common than competition and amensalism (Ricciardi 2001). Moreover, several predator–prey and parasite–host interactions in the Great Lakes are strongly asymmetric in benefiting one invading species at a negligible cost to another, thus acting more as a commensal relationship (Ricciardi 2001). Virtual commensalisms of this kind are common among coevolved relationships.

In the Baltic Sea, nonindigenous species dominate the biomass at all trophic levels and form food web links involving coevolved species and species that share no coevolutionary history (Leppäkoski and Olenin 2000). In the Vistula River delta, the North American crab (*Rhithropanopeus harrisi*) feeds primarily (as juveniles) on *Cordylophora* and (as adults) on *Dreissena polymorpha* (Leppäkoski 1984). *Cordylophora* uses *Dreissena* shells as attachment substrate, and *Dreissena* larvae are its principal food source. Patches of *Dreissena* and of the North American barnacle (*Balanus improvisus*) provide habitat for several Ponto-Caspian amphipod species (Köhn and Waterstraat 1990; Olenin and Leppäkoski 1999). *Balanus* itself uses zebra mussel shells as attachment surfaces (Olenin and Leppäkoski 1999) and probably benefits from direct exposure to mussel filtration currents as it does in its commensal relationship with *Mytilus* (Laihonen and Furman 1986). However, none of these species needed any previous invasion to become established.

In fact, overall there are only a few documented cases in which the presence of an aquatic invader led to the establishment of another invader. There is little evidence linking increased invasion rates to facilitation in aquatic ecosystems, which supports the view that aquatic invasions are governed more by dispersal opportunity and physical habitat conditions than by the composition of the recipient community (Moyle and Light 1996; MacIsaac, Grigorovich, and Ricciardi 2001). However, it is clear that facilitation can enhance the abundance, persistence, and local spread of aquatic invaders. Additional examples include *Alepes djeddaba,* a carangid fish native to the Indian Ocean, which increased in abundance in the Mediterranean Sea after the appearance of swarms of the scyphomedusan jellyfish *Rhopilema nomadica,* a Red Sea migrant introduced in the 1970s; juvenile *Alepes* shelter among the jellyfish tentacles (Galil 2000). The spread and population growth of the Chinese macrofouling mussel *Limnoperna fortunei* in the Parana–Rio de la Plata system were enhanced by the previous invasion of

the Asiatic clam (*Corbicula fluminea*), which provided hard substratum for colonization by *Limnoperna* in vast stretches of the silty river bottom (Darrigran and de Drago 2000; D. Boltovskoy, pers. comm., 2000). The variety of examples in the scientific literature demonstrates the ubiquity of this phenomenon.

Are Coadapted Invaders More Likely to Cause Invasional Meltdown?

Invasional meltdown is hypothesized to occur through one of two processes: frequent disturbance through species introductions progressively lowers community resistance to invasion, and increased introductions lead to a higher frequency of potential facilitations and synergies. Evidence for the first process is in computer simulations showing that frequent and simultaneous species introductions increase invasion success (Lockwood et al. 1997). The second process is favored by an influx of coadapted propagules. Certain coadapted species combinations ("invasion cartels") might act as mutual attractors that promote the assembly of foreign food webs in new ecosystems. Highly active invasion corridors may introduce numerous species from the same endemic region or from a region each has invaded previously. Consequently, invasion corridors tend to reunite groups of coadapted species, either in simultaneous introductions (e.g., a host arriving with its parasites) or in successive introductions, thereby assembling contiguous links of a nonindigenous food web.

Over the past two decades, the Great Lakes have been invaded predominantly by species native to the Black and Caspian seas, that is, Ponto-Caspian species (Ricciardi and MacIsaac 2000; Ricciardi 2001). This influx is attributable largely to shipping traffic linking the Great Lakes to western European ports, which have become increasingly invaded by Ponto-Caspian species (MacIsaac, Grigorovich, and Ricciardi 2001). Even though they still make up only a minor proportion (about 11 percent) of all introduced biota, Ponto-Caspian species dominate facilitations in the Great Lakes, and their food webs are being reassembled in the region (Ricciardi 2001). For example, the introductions of dreissenid mussels, amphipod *Echinogammarus ischnus,* and the round goby (*Neogobius melanostomus*) reassembled a tripartite cartel of Ponto-Caspian species in the Great Lakes. In fact, the number of coadapted foreign (predominantly Eurasian) food web links in the Great Lakes has increased exponentially over the past century (Figure 7.1). As discussed previously, the *Dreissena*–round goby interaction is apparently responsible for outbreaks of avian botulism in Lake Erie and Lake Ontario. In western Europe, sequential invasions by Ponto-Caspian species completed the parasitic life cycle of the trematode *Bucephalus polymorphus.* The introductions of the zebra mussel (*Dreissena polymorpha,* the trematode's first intermediate host) and the pike perch (*Stizostedion lucioperca,* its definitive host) allowed *B. polymorphus* to spread into inland waters and cause high mortality in local populations of cyprinid fishes, which act as secondary intermediate hosts (Combes and Le Brun 1990).
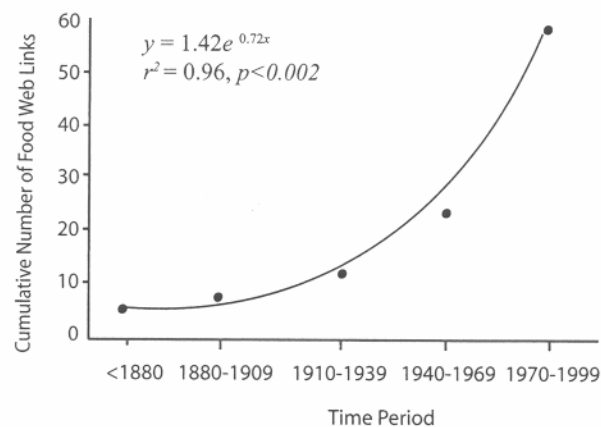
$y = 1.42e^{0.72x}$
$r^2 = 0.96, p < 0.002$

Figure 7.1. Increasing rate of establishment of coadapted foreign links in Great Lakes food webs. Each data point represents the cumulative number of links established at each 30-year interval. Model fitted by least-squares regression. Data are from Ricciardi (2001) and Mills et al. (1993).

If coadaptation reduces the intensity of predation and parasitism (Levin et al. 1982), then positive interactions probably dominate invasion cartels, and successive introductions of coadapted species might produce a higher rate of invasion than would introductions of unacquainted species. This is an alternative to the enemy release hypothesis, which relates the success of an invader to the absence of its natural predators and parasites in the invaded region (Wolfe 2002). Introduced predators and parasites may increase the invasion success of their natural hosts by differentially affecting the host's competitors: naive resident hosts that have not had selection pressure to adapt to their new enemies. While its natural host is present, the parasite is not limited by rapid declines of resident hosts. In this way, a fungal parasite (*Aphanomyces astaci*) transported with shipments of the American crayfish (*Pacifastacus leniusculus*) caused a large-scale plague that wiped out many native crayfish populations in Europe in the 1930s, including commercially important stocks (Reynolds 1988). Although the *Aphanomyces–Pacifastacus* relationship normally would be considered an exploitive interaction, in this case it is virtually mutualistic because the pathogen eliminated the crayfish's competitors. A similar, terrestrial example is the ongoing replacement of the red squirrel (*Sciurus vulgaris*) in the United Kingdom by the North American gray squirrel (*S. carolinensis*), which is promoted by the vulnerability of the native species to a viral disease introduced by the invading species (Tompkins, White, and Boots 2003). In Australia, introduced parasites are thought to have likewise aided the success of their introduced host fishes by reducing native fish populations (Dove 1998).

Recently, Fukami, Simberloff, and Drake (n.d.) found theoretical and experimental evidence that an invading prey species often serves as an additional resource to an invading coadapted predator, and the predator releases its prey from competition with native species. This finding is supported by several terrestrial case studies, including the introduction of the brown tree snake (*Boiga irregularis*) and its coevolved prey to Guam, which caused the extinction of several endemic species of birds, bats, and reptiles through hyperpredation (Fritts and Rodda 1998). Similarly, native fishes have been drastically reduced by the North American predator northern pike (*Esox lucius*), introduced into lakes in Spain, where its populations are sustained by another prey resource, the American crayfish (*Procambarus clarkii*) (Elvira, Nicola, and Almodovar 1996). In western North America, the invasion of bullfrogs (*Rana catesbeiana*) is facilitated by bluegill sunfish (*Lepomis macrochirus*), which increase the survival of their tadpoles by reducing densities of predatory macroinvertebrates (Adams, Pearl, and Bury 2003). Because introduced bullfrogs exacerbate declines in native frog populations (Kats and Ferrer 2003), the sunfish–bullfrog commensalism contributes to the impoverishment of amphibian communities. A coadapted predator–prey or parasite–host cartel thus can function mutualistically to exert a synergistic impact on the recipient community.

Implications for Policy and Management

These examples demonstrate that introduced species interact in unanticipated ways to alter aquatic ecosystems, with potentially serious consequences for biodiversity and fishery management. The aforementioned case studies corroborate terrestrial studies showing that complex combinations of direct and indirect species interactions can structure entire communities and affect ecosystem function (Richardson, Cowling, and Lamont 1996; Richardson et al. 2000; Callaway and Walker 1997; Levine 1999). Facilitation can magnify the ecological impact of an introduced species across multiple trophic levels. If trophic cascades are more common in aquatic ecosystems than in terrestrial ecosystems (Strong 1992), aquatic ecosystems might be particularly susceptible to synergistic impacts of introduced species. Unanticipated synergies reduce our capacity to predict and manage invasion threats. Therefore, we need new theoretical perspectives on the community ecology of invaders, particularly for inland and coastal aquatic ecosystems, which are being disturbed by an increasing number of invasions worldwide (Ruiz et al. 1997; Cohen and Carlton 1998; Ricciardi 2001). In particular, researchers should attempt to incorporate direct and indirect facilitation into impact models.

Risk assessments of aquatic species introductions must consider the presence of potential facilitators in the recipient community and the potential impact of simultaneous or rapidly successive invasions by coadapted species. Databases that are intended to provide managers with information to aid monitoring, risk assessment, and control of invaders should list species known to facilitate the invader's establishment and impact as well as commensal and parasitic organisms known to benefit from the

invader's presence. The identification and control of keystone facilitators may help reduce further invasions. Examples of concern include components of parasite life cycles, keystone predators, and ecological engineers (*sensu* Jones, Lawton, and Shachak 1994) likely to produce major ecosystem shifts and thus change the rules of existence for other species.

If the invasional meltdown model is valid, an increased frequency of species introduction will lead to a rapid accumulation of invaders and synergistic impacts (Simberloff and Von Holle 1999), which will cause the ecosystem to become increasingly unstable and difficult to manage. This justifies efforts to reduce inoculation pressure on ecosystems and refutes any argument that strict controls on ballast water discharge (a major vector for aquatic invasions worldwide) are unwarranted if future invasions are inevitable through more subtle vectors. Even a partial reduction of inoculation pressure might slow the buildup of feedback cycles that can destabilize an ecosystem, giving resource managers more time to adjust to changing conditions or to develop better prevention strategies.

Finally, greater effort should be made to control invasion corridors that are linked to centers of endemism because these may deliver large numbers of coadapted organisms and thus assemble synergistic invasion cartels. Although invasion cartels are expected to contribute (at least initially) to an invasional meltdown, a new equilibrium community ultimately could be reached if the dominant invasion corridors do not change; any preexisting equilibrium could be disrupted by a new suite of coadapted species. Therefore, invasion cartels might undermine efforts to restore natural communities, not only by replacing native species but also by shifting the community toward an alternative stable state (Lockwood 1997).

Acknowledgments

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