will likely happen on a case-specific basis, it does argue that invasion control should be considered in the context of restoration—wherein the ultimate goal is not to get rid of target invaders but rather to restore natural integrity. It is also important to recognize that there also might be lags related to assessing effectiveness of control efforts caused by persistent legacies of removed invaders. Most fundamentally, however, it further reinforces the need to prevent unwanted invasions rather than to deal with them later.

Although the inability to recognize and predict lags poses serious management problems, there can be benefits of both time lags and understanding the processes that produce them. Lags imply that in many instances there might be relatively long windows of opportunity when invasive populations are small and confined. Somewhat paradoxically, however, action during this phase must occur at just the time when we often know least about the invasion. Working to understand the factors causing lags suggests that we might exploit invader vulnerabilities in order to control biological invasions better.

SEE ALSO THE FOLLOWING ARTICLES

Demography / Dispersal Ability, Animal / Dispersal Ability, Plant / Disturbance / Evolutionary Response, of Natives to Invaders / Evolution of Invasive Populations / Habitat Compatibility / Invasibility, of Communities and Ecosystems

FURTHER READING

Caley, P., R.H. Groves, and R. Barker. 2008. Estimating the invasion success of introduced plants. *Diversity and Distributions* 14: 196–203.

Crooks, J.A., and M.E. Soulé. 1999. Lag times in population explosions of invasive species: Causes and implications (103–125). In O.T. Sandlund, P.J. Schei, and A. Viken, eds. *Invasive Species and Biodiversity Management.* Dordrecht, the Netherlands: Kluwer Academic Publishers.

Crooks, J.A. 2005. Lag times and exotic species: The ecology and management of biological invasions in slow-motion. *Ecoscience* 12(3): 3116–3329.

Doak, D.L., J.A. Estes, B.S. Halpern, U. Jacob, D.R. Lindberg, J. Lovvorn, D.H. Monson, M.T. Tinker, T.M. Williams, J.T. Wooton, I. Carroll, M. Emmerson, F. Micheli, and M. Novak. 2008. Understanding and predicting ecological dynamics: Are major surprises inevitable? *Ecology* 89(4): 952–961.

Hengeveld, R. 1989. *Dynamics of Biological Invasions.* New York: Chapman and Hall.

Kowarik, I. 1995. Time lags in biological invasions with regard to the success and failure of alien species (15–38). In P. Pyšek, K. Prach, M. Rejmánek, and M. Wade, eds. *Plant Invasions: General Aspects and Special Problems.* Amsterdam: SPB Academic Publishing.

Liebhold, A., and J. Bascompte. 2003. The Allee effect, stochastic dynamics and the eradication of alien species. *Ecology Letters* 6: 133–140.

Pyšek, P., and V. Jarošík. 2005. Residence time determines the distribution of alien plants (77–96). In S. Inderjit, ed. *Invasive Plants: Ecological and Agricultural Aspects.* Basel: Birkhauser Verlag.

Sakai, A.K., F.W. Allendorf, J.S. Holt, D.M. Lodge, J. Molofsky, K.A. With, S. Baughman, R.J. Cabin, J.E. Cohen, N.C. Ellstrand, D.E. McCauley, P. O'Neil, I.M. Parker, J.N. Thompson, and S.G. Weller. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* 32: 305–332.

Strayer, D.L., C.T. Eviner, J.M. Jeschke, and M.L. Pace. 2006. Understanding the long-term effects of species invasions. *Trends in Ecology and Evolution* 21: 645–651.

LAKES

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Lakes are essential resources for and are extensively exploited by human populations, which has resulted in a number of perturbations including introduction of nonindigenous species (NIS). Once established, some NIS spread in a series of secondary introductions to new lakes by either natural or human-mediated mechanisms. Nonindigenous species are associated with a wide array of physical, chemical, and biological impacts. Management efforts for invertebrates and fishes have focused principally on preventing new invasions and curtailing the spread of established NIS to new lakes, while programs for macrophytes are directed at both prevention and in-lake control.

SPECIES DISPERSAL TO LAKES

Species may enter lakes by natural or human-mediated dispersal. Because lakes provide drinking and industrial water, food, recreation, hydroelectricity, and transportation, their condition is of paramount importance. One consequence of this extensive use has been the introduction of many NIS to lakes, particularly macrophytes, fishes, and invertebrates (Fig. 1). The human-mediated introduction of species can cause severe industrial impairment and disrupt ecological and aesthetic qualities of lakes. For this reason, the comparative rate of introduction of NIS by humans versus natural dispersal is of interest. Ecologists dating to Darwin have assumed that natural dispersal was widespread and reflected by the semi-cosmopolitan distribution of zooplankton species in lakes. Recent analyses have indicated that the rate of human-mediated species introduction may exceed the background rate by 10,000 times for some species. This exceptional difference has focused attention on the need to prevent new invasions. Before this goal can be achieved, however, it is necessary to understand how species can be transported to lakes.

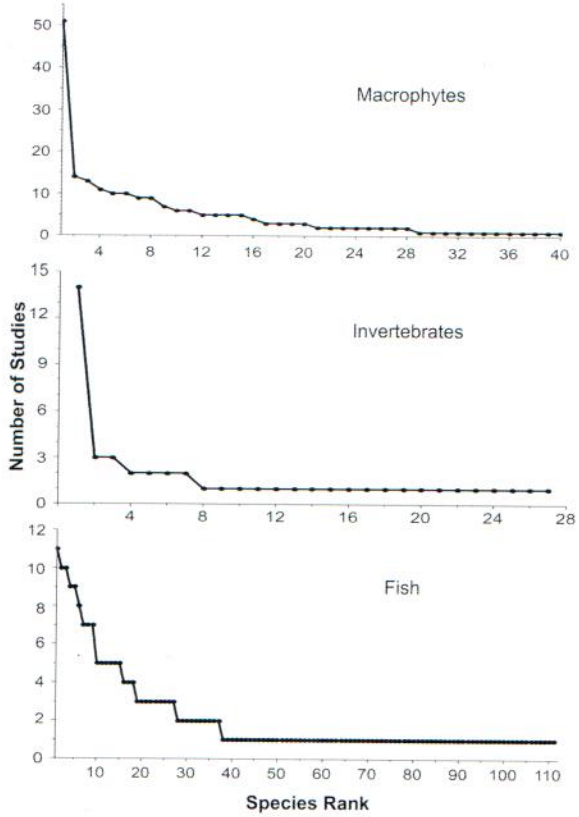

FIGURE 1 Relative dominance in published studies on lakes of nonindigenous macrophytes, invertebrates, and fishes based upon ISI Web of Science searches. In each case, searches consisted of combining searches for six synonyms for *nonindigenous* ("introduced," "exotic," "alien," "colonizing," "nonnative") with "lake" and with a taxon identifier. A seventh term, "invasive," was used in addition to the six terms for *nonindigenous*, and results were used only if the study considered the species as nonindigenous. Taxon identifiers were "macrophytes or aquatic plants," "invertebrate," or "'fish or Pisces." Searches were conducted from 1965 through August 12, 2009, for macrophytes and invertebrates, and for 2006 and 2007 for fish, because the latter are much better studied than either of the other groups. The best-studied nonindigenous macrophytes in lakes include *Myriophyllum spicatum* (51 studies), *Hydrilla verticillata* (14), *Elodea canadensis* (13), *Potamogeton crispus* (11), and *Lagarosiphon major* and *Eichhornia crassipes* (10 each). The best-studied nonindigenous invertebrates in lakes include *Bythotrephes longimanus* and *B. cederstroemi* (18 studies), *Dreissena polymorpha* and *D. rostriformis bugensis* (12 studies), and *Cercopagis pengoi* (3 studies). The best-studied nonindigenous fishes in lakes include *Cyprinus carpio* (11 studies), *Oncorhynchus mykiss* and *Salmo trutta* (10 studies each), and *Lepomis gibbosus* and *Neogobius melanostomus* (9 studies each).

Natural Dispersal Mechanisms

Unlike Darwin, we are now aware that the distribution of many lake species is limited to specific continents, and often to specific regions within continents. These large-scale patterns suggest that constraints on dispersal have strongly limited the distribution of life in lakes across the globe. A variety of natural mechanisms are available for NIS to enter lakes. In the simplest case, species extend their ranges by streams or rivers that connect colonized and uncolonized lakes. This form of advective introduction is notable in that it typically occurs in a single direction only, downstream from the source population. This mechanism can introduce virtually all species present—ranging from viruses and bacteria to fishes—in bulk transfers of water. This mechanism was undoubtedly important to initial dispersal of lake species following retreat of continental glaciers. For example, the opossum shrimp *Mysis diluviana* (formerly *relicta*) extended its range to deep lakes around the Great Lakes following glacier retreat at the end of the Pleistocene Epoch. The importance of advective dispersal diminishes strongly over time, as all lakes that can be colonized through the rivers connecting them eventually become so. In cases where a new NIS is introduced by humans, however, advection can be a major mechanism for subsequent spread of the species (see below). Advection influences only regional spread and cannot account for long distance transfers, including between continents. Advection has played an important role in the secondary spread of species including zebra mussels *Dreissena polymorpha*, quagga mussels *D. rostriformis bugensis*, fanwort *Cabomba caroliniana* in North America, and many Ponto-Caspian species in the Rhine River (see below).

A second mode of natural dispersal is wind. Large windstorms blowing from arid regions—such as the Sahara-Sahel region in Africa—contribute billions of tons of aerosolized dust to the atmosphere each year and can be important agents of long-range dispersal of bacteria, viruses, fungi, and plant pollen. Unlike the spatially constrained dispersal that may occur using stream connections, dispersal of species by wind (and rain) can occur over a broad region to lakes unconnected to one another. This mechanism also is strongly unidirectional. The importance of wind is inversely dependent on the size of the species, with small organisms such as bacteria and fungi being moved readily and larger species such as fishes being moved rarely and only by water spouts or gale-force winds. Over time, the importance of wind dispersal is likely to diminish, as species able to disperse will have already colonized downwind areas. However, if climate change alters wind patterns, then species that have not yet spread may have an opportunity to do so.

Two attributes favor dispersal of many aquatic taxa: asexual reproduction and production of resting stages. Asexual reproduction is advantageous because colonization by a single parthenogenetic female can be followed by repetitive cycles of asexual reproduction, resulting

in rapid population growth, high population density, and a reduced probability of local extinction. Aquatic plants like the highly invasive Eurasian watermilfoil *Myriophyllum spicatum* exhibit extreme flexibility with respect to reproduction. This and many other invasive macrophyte species can reproduce sexually, resulting in seed production, or asexually by production of stolons or fragmentation of parental tissues. The latter vegetative capability poses a severe challenge for mechanical control of introduced plant populations (see below). A second reproductive attribute that favors colonization by many NIS is production of small, light, diapausing stages (e.g., cysts, gemmules, statoblasts, resting eggs, ephippia) that resist adverse conditions including desiccation. If these stages are carried aloft to aquatic habitats with favorable conditions, they may ex-cyst or hatch into larger, heavier free-living adult stages that are far less likely to be transported by wind. As with adults, the larger and heavier the resting stage, the less likely it is to be transported by wind.

Experimental studies show that large numbers of lake-dwelling species are transported by wind and rain. Two groups of taxa tend to dominate these colonization studies: crustacean zooplankton and rotifers. A study in South Africa identified 17 taxa of invertebrates that were collected in windsocks. Most of these specimens were resting eggs of cladoceran crustaceans, although anostracans, turbellarians, copepods, and branchiopods were also collected. Another study revealed dispersal by wind or rain of 13 rotifer species, two copepods, and seven cladoceran species to experimental mesocosms from which animal vectors were excluded. Other groups that colonized mesocosms included water mites, flatworms, and ostracods. Colonization can occur very rapidly, but in some cases, it can be delayed by up to a year. Early colonists tend to be asexual rotifer species. A suite of other zooplankton species may never colonize, highlighting the stochastic nature of colonization. Other studies on experimental ponds have had similar results, with colonization of some zooplankton species occurring within days or weeks, particularly those over short distances. As distance from the source increases, colonization tends to decline.

Colonization of a pond by one species may positively or negatively alter establishment by subsequent invaders. These so-called "priority effects" have been demonstrated in both laboratory cultures of lake phytoplankton and with zooplankton in experimentally created ponds. Priority effects are potentially important in terms of community composition of lakes and ponds, because different community assembly trajectories and species assemblages may result depending on the order in which species invade. Recent work suggests that priority effects may extend to genotypes as well, with early colonizing genotypes producing sufficiently large propagule banks as to saturate the environment and repel future invasions by other genotypes of the same species.

The application of molecular markers has helped to identify sources and frequencies by which lake species such as crustaceans and bryozoans disperse to lakes. These studies provide information that is otherwise unobtainable from studies that employ experimental pools, mesocosms, or newly created ponds. Initial studies of genetic composition of colonizing species were limited to allozyme differences between source and destination populations, although these markers have largely been supplanted by mitochondrial and microsatellite markers that provide greater resolution. For example, spread of the fishhook waterflea *Cercopagis pengoi* to the Great Lakes was traced using a mitochondrial gene to a population living in the Baltic Sea, which itself was introduced from a Ukrainian port on the Black Sea. Mitochondrial markers have also been used to examine the spread of many other NIS that have spread to lakes in Europe and North America, including mysid shrimp *Heimysis anomala* and *Limnomysis benedeni*, round goby *Neogobius melanostomus*, tubenose goby *Proterorhinus semilunaris*, spiny waterflea *Bythotrephes longimanus*, and amphipod *Echinogammarus ischnus*. Microsatellite markers provide the highest resolution and have recently been used to survey introduced populations of spiny waterfleas, zebra and quagga mussels, round goby, sockeye salmon *Oncorhynchus nerka*, lake trout *Salvelinus namaycush*, northern pike *Esox lucius*, sculpin *Cottus* spp., whitefish *Coregonus*, and common reed *Phragmites australis* in lakes across Europe and North America.

ANIMAL-MEDIATED DISPERSAL Interactions between species may play a pivotal role in the dispersal of lake species. Animals transfer other species either externally (ectozoochory) or internally (endozoochory). While vectors for spread could potentially involve any species that uses shoreline or lake habitat and thereafter moves to another lake (e.g., moose, beaver), most attention has focused on waterbirds and fish vectors. Nonindigenous species could be transferred live or as resting stages. Local movements by waterbirds could disperse NIS regionally, while long-distance migrations have the potential to effect long-distance dispersal. Studies dating back to Darwin demonstrated that some species (e.g., molluscs) disperse between lakes on the external surfaces of waterfowl, notably their

legs, feet, bills, and plumage. More recently, live-captured sanderling *Calidris alba*, dunlin *Calidris alpina*, and curlew sandpiper *Calidris ferruginea* have been observed with cockles *Cerastoderma edule* attached to their digits, confirming Darwin's hypothesis.

Plumage may offer an even more inviting opportunity for dispersal of aquatic NIS. It is not clear how many lake-dwelling species can be moved alive in waterfowl plumage. Some bryozoans produce statocysts with hooks that could easily attach to waterfowl plumage. Resting eggs or plant seeds that float also would be most likely to get tangled in waterfowl plumage. Fishhook and spiny waterfleas are two invasive NIS that have colonized the Great Lakes from Europe over the past 30 years (Fig. 2). One study has confirmed fishhook waterfleas in plumage of a dead lesser scaup *Aythya affinis* that was dipped into Lake Ontario during the summer when the waterflea was present. In addition, "foam" consisting of millions of spiny waterflea carcasses—some with resting eggs—has been observed on the leeward shoreline of Lake Huron on windy days. These eggs could easily attach to the plumage of foraging dabbling ducks, with the possibility of secondary transfer to other lakes. It is not clear how important this mechanism has been in spread of spiny waterfleas around the Great Lakes, as patterns of spread are more consistent with human than waterfowl vectors (see below).

Dispersal of invertebrate resting stages and plant seeds by their predators is a growing avenue of interest. Several studies have demonstrated that resting stages and or seeds may pass through the digestive tracts of predators—mainly ducks and shorebirds—and remain viable. Experimental studies have identified a range of invertebrate species (e.g., gastropods, crustaceans), strictly aquatic plants (*Chara*, *Riella americana*, diatoms, cyanophytes, *Najas marina*), and wetland plants (*Potamogeton natans*, *Scirpus paladosus*, and 23 other species) that may be ingested and survive passage through duck digestive tracts. Germination success is higher for seeds that are hard or otherwise difficult to digest, and following passage through ducks with smaller gizzards. Many resting eggs of the spiny waterflea are destroyed by passage through ducks, although even a small proportion (<4%) surviving can have important consequences for dispersal in light of the enormous populations of migrating waterfowl that may carry the species. The distance these eggs are carried will vary according to the flight speed of the bird, the composition of other foods ingested, and the size of the eggs. Available studies suggest that endozoochory could contribute to dispersal of plants and animals over short (<300 km) distances.

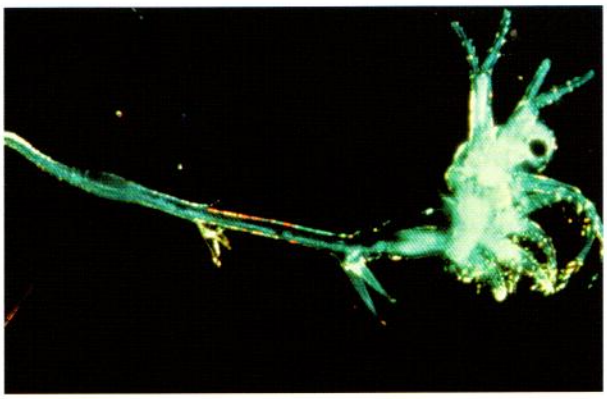

FIGURE 2 Native to northern Europe, the spiny waterflea (*Bythotrephes longimanus*) was first discovered in 1982 and had spread to all of the Great Lakes by 1987. Scientists think international cargo ships first carried the spiny waterflea to North America in their ballast water. The species has changed the food webs of the Great Lakes by causing declines in native zooplankton through direct predation, thus impacting sport and commercial fisheries. (Photograph courtesy of United States Environmental Protection Agency, Great Lakes National Program Office.)

The importance of endozoochory to long-distance dispersal is likely quite low because migrating waterbirds will completely evacuate their digestive tracts long before they reach their destination.

Evidence of endozoochorous dispersal by fishes in lakes is more limited. The waterflea *Daphnia lumholtzi* is native to parts of Australia, Southeast Asia, and Africa, and was first reported in North America in a reservoir in Missouri in 1991. The most plausible hypothesis for its introduction is via ephippia carried in the digestive tract of Nile perch *Lates niloticus* introduced to the same reservoir in 1983.

It is also possible that secondary dispersal of the spiny waterflea has been facilitated by fish predators. Many spiny waterflea resting eggs consumed by Great Lakes' fish remain viable following passage through the digestive tract. Migrations of these fishes between connected lakes could disperse the species. Some of the fish species that ingest spiny waterfleas are collected and sold commercially as bait. If these were used on lakes that have not yet been invaded by the waterflea, then viable eggs released in feces could potentially establish a new population.

Human-mediated Introductions to Lakes

Natural dispersal has resulted in a slow but consistent spread of NIS to lakes within continents for millennia. This background process of natural species colonization of lakes by fishes, invertebrates, and macrophytes has been joined by the much faster process of human-mediated introductions. For example, human introduction of fishes

increased steadily after 1860 and dramatically between 1950 and 1980. Human-mediated introductions to lakes can be classified into two categories: intentional and inadvertent. Intentional releases include species stocked as food for humans or other species, for sport fishing, for biocontrol, and for pet, aquarium, or ornamental purposes (Table 1).

INTENTIONAL RELEASES Intentional stocking of lakes with fishes or with species intended as fish food is widespread. Aquaculture, sport fishing, and fishery improvement have been responsible for more introductions than any other mechanisms. A Web of Science search revealed that the top three fish species introduced to lakes were common carp *Cyprinus carpio*, rainbow trout *Oncorhynchus mykiss*, and brown trout *Salmo trutta*, all of which were introduced for human food. Common carp has been introduced worldwide to more than 117 countries as either a food or sport fish. While originally stocked as a human food source, the species is now widely considered an ecological menace because it destroys macrophyte beds, thereby adversely affecting species associated with these plants as well as increasing water turbidity. Rainbow trout have been introduced globally as a sport or human food fish to at least 80 countries, while brown trout were introduced and have established in at least 28 countries. Both trout species are used in aquaculture (e.g., Chile, Argentina), owing to their high commercial value, and both are associated with strong, adverse ecological effects on native communities. Other fishes introduced commonly to lakes for human food or sport include largemouth bass (*Micropterus salmoides*; successfully introduced to 58 countries), brook trout (*Salvelinus fontinalis*; 40 countries), Nile tilapia (*Oreochromis*

TABLE 1
Possible Dispersal Mechanisms for Species Introduced to Lakes.

Mechanism	Mode	Examples
currents	N	macrophytes, zebra mussels
birds	N	invertebrate resting stages, plant seeds
other animals (e.g., fish)	N	zebra mussels
canals	A	sea lamprey, blueback herring, zebra mussels
ballast water	A	zebra and quagga mussels, phytoplankton, round and tube nose gobies, New Zealand mud snail, and many others
vessel hulls	A	*Enteromorpha flexuosa, Bangia atropurpurea*
vessel interiors	A	zebra mussels
fishing boat live wells	A	zebra mussels
recreational boat bilge water	A	zebra mussel larvae
recreational boat engine water	A	zebra mussel larvae
recreational boat trailers	A	macrophytes and associated fauna (e.g., zebra and quagga mussels)
navigation buoys	A	zebra mussels
marina/boatyard equipment	A	zebra mussels
fishing equipment/cages	A	zebra mussels
fish stocking water	A	zebra mussels
bait and bait bucket water	A	zebra mussels
commercial products	A	zebra mussels
marker buoys and floats	A	zebra mussels
fire truck water	A	zebra mussels
float planes	A	zebra mussels
recreational equipment	A	zebra mussels, New Zealand mud snails
litter (garbage)	A	zebra mussels
scientific research	A	zebra mussels
pet/aquarium releases	I	water hyacinth, cabomba, hydrilla, Canadian waterweed, Egeria waterweed, catfish, mollies, bullfrog, salvinia, and many more
human food	I	salmonids, bass, walleye, Nile perch, Nile tilapia, common, bighead, grass and silver carp, catfish, crayfish, and many more
food for other species	I	mysids, amphipods
ornamental	I	macrophytes
sport fishing	I	salmonids
biocontrol	I	grass, silver, bighead and black carp, mosquitofish, and many more

NOTE: Mode refers to what the mechanism is: N = natural colonization, I = intentional human transfer, A = inadvertent human transfer. Modified from Carlton's (1993) list for zebra mussels.

niloticus niloticus; 75 countries), and bighead carp (*Hypophthalmichthys nobilis*; 43 countries).

A number of species have been introduced to facilitate growth of other species, usually fish, that are exploited for human benefit. Some of these introductions have occurred with spectacular unintended consequences. For example, both mysid and amphipod crustacean species have been stocked into lakes to enhance fisheries in lakes in Soviet Russia, Scandinavia, and western North America. The opossum shrimp *M. diluviana* was introduced to Flathead Lake, Montana, and Kootenay Lake, British Columbia, to enhance kokanee salmon *Oncorhynchus nerka* production. While opossum shrimp can be eaten by adult fishes, the mysids outcompete kokanee fry for zooplankton prey, resulting in a "bottleneck" in survival of young fish. Adult populations of kokanee subsequently collapsed in both systems.

The amphipod *Gmelinoides fasciatus* is native to the Lake Baikal region of Siberia but has been intentionally stocked into a series of lakes and reservoirs in order to enhance production of fish predators. The species was stocked into Gorkovskoye Reservoir on the Volga River cascade in the 1960s, after which it spread upstream and downstream to other major reservoirs on the river. It was also stocked into lakes on the Karelian Isthmus in northwestern Russia, which resulted in its eventual colonization of lakes Ladoga and Onega, which are among the largest lakes in Europe and are 5,000 km west of Lake Baikal.

Other amphipods have also been transferred between continents. The North American estuarine amphipod *Gammarus tigrinus* was stocked as fish food into the salt-contaminated Werra and Weser rivers in Germany. The species was also introduced to Europe via ballast water. Its introduced distribution in Europe and North America now includes a number of freshwater lakes, including Lough Neagh in Northern Ireland and the Laurentian Great Lakes.

Other crustaceans, notably crayfishes, have been stocked as human food. European stocks of crayfish were devastated prior to 1900 by the introduction of crayfish carrying a fungal disease (*Aphanomyces astaci*). Disease-resistant stocks of other species were subsequently introduced, including a number of North American species (*Pacifasticus leniusculus, Orconectes limosus, Procambarus clarkii, Procambarus zonangulus*). Transfer of crayfish within continental Europe has also occurred fairly commonly (e.g., *Astacus leptodactylus, Astacus astacus*). Within North America, rusty crayfish *Orconectes rusticus* has been moved between lakes through its use as a sport-fishing bait, often with adverse ecological effects.

It has recently become increasingly popular to introduce species to lakes for biocontrol purposes. Western mosquitofish (*Gambusia affinis*; 73 countries) and eastern mosquitofish (*Gambusia holbrooki*; 29 countries) have been widely introduced globally for mosquito control, although only the former species has demonstrated effectiveness, and both species have adverse ecological impacts on invaded lakes. Black carp (*Mylopharyngodon piceus*; 16 countries) have been introduced to aquaculture ponds for control of snails, which are intermediate hosts of trematode parasites of cultivated fishes. Silver carp (*Hypophthalmichthys molitrix*; 58 countries) have been introduced to aquaculture ponds and lakes for control of algal blooms, while grass carp (*Ctenopharyngodon idella*; 67 countries) have been introduced to lakes and reservoirs both to control aquatic vegetation and to serve as a food source. Black, silver, and bighead carp raised in aquaculture facilities in the southern United States escaped confinement and have migrated up the Mississippi River, with the last two posing a current invasion risk to the Great Lakes via the Chicago Ship and Sanitary Canal.

Other biocontrol agents have been introduced to eliminate undesirable vegetation. For example, water hyacinth *Eichhornia crassipes* was stocked into many waterways as an ornamental species despite its reputation as a highly invasive NIS. The species was reported in Lake Kyoga, Uganda, in 1988 and in Lake Victoria, the world's second largest lake, in 1989. Water hyacinth severely impedes nearshore boat travel and fishing in Lake Victoria, adversely affects water intakes for municipalities around the lake, dramatically increases evapotranspiration, and greatly transforms the ecology of colonized areas. The weevils *Neochetina bruchi* and *Neochetina eichhorniae* were successfully introduced from their native range in South America to Lake Victoria to feed on and control water hyacinth. Hyacinth aerial coverage has declined from its maximum of 178,374 ha in 1998–1999 to less than 2,000 ha by 2001, at least in part due to weevil herbivory.

Giant salvinia *Salvinia molesta* is a highly invasive aquatic fern sold as an ornamental for use in aquariums and garden ponds. Like water hyacinth, this species has been released into lakes around the world, where it can completely cover the surface, impeding boaters and adversely affecting lake communities. Giant salvinia has been successfully controlled using another herbivorous weevil, *Cyrtobagous salviniae*, from the plant's South American native range.

Eurasian watermilfoil *Myriophyllum spicatum* is an introduced invasive macrophyte in the United States and

Canada. Work on biological control of watermilfoil is much less well established than for the previously mentioned macrophytes, although a native North American weevil, *Euhrychiopsis lecontei,* has some potential. Use of native species in biological control of NIS holds great appeal because no additional NIS would be introduced—with their attendant risks—to the system. Other methods currently employed to control invasive macrophytes include mechanical harvesting and herbicide application. Mechanical harvesting can clear lakes of standing biomass, although fragments created or left behind can allow recolonization or dispersal. Some jurisdictions have implemented laws banning sale, possession, or shipment of invasive macrophytes.

Aquarium trade, water garden, and human food species also are introduced intentionally to lakes. Fishes are by far the most commonly established introduced aquarium species, followed by gastropods and aquatic plants. Enhancing establishment success of these species is the fact that they are often released as large, healthy, mature individuals. Indeed, aquarium fishes are typically discarded because their owners tire of them, or because they become too large or prolific. For example, the red-bellied piranha *Pygocentrus nattereri* is a South American fish very popular in the aquarium trade. Two large individuals were captured from a reservoir in Oahu, Hawaii, and otolith analysis indicated that one fish originated from aquarium stock before being released. In some cases, aquarium and water garden pathways can be the dominant mechanism by which species are introduced to lakes. For example, in Australia, 22 of 34 nonindigenous fish species originated from the aquarium or ornamental trades. Fishes that are more commonly sold in stores are more likely to be introduced to and established in lakes than are rare species. Analyses of aquarium stores around the Laurentian Great Lakes revealed six families commonly for sale: Cichlidae (e.g., cichlids), Poeciliidae (e.g., guppies, mollies, and swordtails), Characidae (e.g., tetras), Cyprinidae (e.g., goldfish, koi), Beloontiidae (e.g., Siamese fighting fish, gourami), and Loricaridae (e.g., armored catfish). One of the fishes most likely to colonize this region successfully is the white cloud mountain minnow (*Tanichthys albonubes*), which has moderate "propagule pressure" from aquarists and can survive environmental conditions around the Great Lakes.

A number of invasive aquatic plants, including Eurasian watermilfoil, Canadian waterweed *Elodea canadensis*, and Egeria waterweed *Egeria densa*, are available in aquarium shops or by Internet sale. Surveys of aquatic plants purchased from pet stores and biological supply houses have revealed that contamination with epiphytic animals is very common. Such "fellow travelers" pose a significant introduction risk if the water in which the desired species is shipped is discarded directly into local waterways.

A number of other taxa are also available in aquarium shops. For example, a parthenogenetic crayfish (*Procambarus* "Marmorkrebs") is sold in human food markets in Madagascar and aquarium shops in Germany. This species recently colonized aquatic ecosystems in Madagascar, where it is expected to have adverse ecological effects on the country's highly endemic flora and fauna. Unlike most of the animal species sold in the aquarium trade that are introduced to lakes in low numbers, and which can suffer from Allee effects owing to a scarcity of potential mates, this asexual crayfish has a very high reproductive potential.

INADVERTENT HUMAN INTRODUCTIONS Many mechanisms exist by which humans introduce or spread NIS inadvertently (Table 1). Principal among these are the release of contaminated ballast water, the creation of canals, and the movement of recreational boats on trailers. Not all species in an area have the same likelihood of dispersal via these vectors. For example, planktonic organisms may have a higher probability of being loaded into ballast water than strictly benthic ones, and motile species such as sea lamprey *Petromyzon marinus* and blueback herring *Alosa aestivalis* may use canals to colonize systems like the Great Lakes while less vagile species are unable to do so.

Ballast water is a potent mechanism for the introduction of NIS to coastal marine habitats because of the tremendous volume of water moved and because nearly entire communities may be transferred at once. Ballast water plays a much smaller role in introducing NIS to freshwater systems because transoceanic vessels usually do not load and discharge ballast into freshwater habitats on the same trip. One exception to this pattern is provided by the North American Great Lakes, where up to 70 percent of species invasions over the past 50 years are attributable to ships. Many of these species originated in western Europe or the Ponto-Caspian basin. Virtually all life forms have been successfully introduced to the Great Lakes by contaminated ballast water, including notorious species such as zebra and quagga mussels, round gobies, fishhook waterfleas, and bloody red shrimp, all of which are Ponto-Caspian natives. Many of the NIS introduced by ballast water are first reported in the corridor between Lake Huron and Lake Erie or in areas surrounding major ports. Many of these species then spread

through a combination of natural and human-mediated mechanisms to other Great Lakes and to inland lakes. The dominance of ballast water as a vector of NIS introductions resulted in policy changes by the U.S. (2008) and Canadian (2006) governments that require all transoceanic vessels to exchange filled ballast water tanks or flush empty ones while operating on open ocean prior to entering the lakes. This policy change is expected to dramatically reduce propagule pressure associated with freshwater species in the ballast vector.

Canals have been instrumental in spreading NIS around the world. This importance is highlighted by Europe, where a network of an estimated 28,000 km of rivers, lakes, and canals has been established over the past few centuries. This system has facilitated north–south and east–west spread of many species. One of the most dramatic of these invasions was the spread of the ctenophore *Mnemiopsis leidyi* from the Black and Azov seas to the Caspian Sea. This invasion was facilitated by discharge of contaminated ballast water by a ship that traveled through the Volga-Don canal, which was opened in 1952 to link the Black-Azov and Caspian seas.

Once canal connections have been established, many species will spread downstream in currents. An entire guild of Ponto-Caspian invertebrates including amphipods (*Echinogammarus trichiatus, Chelicorophium robustum, Dikerogammarus villosus, Dikerogammarus haemobaphes*), mysids (*Limnomysis bendeni, Hemimysis anomala*), ispods (*Jaera istri*), water mites (*Caspihalacarus hyrcanus danubialis*), flatworms (*Dendrocoelum romanodanubiale*), oligochaetes (*Potamothrix vejdovskyi*), polychaetes (*Hypania invalida*), leeches (*Caspiobdella fadejewi*), and bivalves (*Dreissena rostriformis bugensis*) spread from the Danube River into the Rhine River via the Main-Danube canal after it was reopened in 1992. This canal is fed by Danube River water, allowing species to spread downstream. Once these species establish beachheads in major freshwater ports like Rotterdam and Antwerp, ships may carry them all over the world. In this manner, these ports can serve as hubs for invasions far removed from western Europe.

While zebra mussels have spread across much of continental Europe over the past 200 years, the quagga mussel has only recently begun to spread outside of its native range in the Black Sea basin using the Danube-Rhine and Volga-Don canal systems to invade the lower Rhine and upper Volga rivers, respectively. Canals and rivers have dispersed zebra and quagga mussels in both Europe and North America.

Two dramatic invasions illustrate the importance of trailered recreational boats to the spread of NIS. Zebra mussels were first found in Ireland in 1997 in Lough Derg. DNA fingerprinting and field surveys suggest that the species was introduced to Ireland, fouled on the hull of a recreational boat ferried from England, owing to a highly unusual combination of events: enhanced licensing requirements for secondhand vessels implemented in England, elimination of value-added taxes on secondhand vessels in Ireland, and favorable exchange rates. Since the initial invasion, the mussel has spread widely across Ireland through a combination of natural dispersal in rivers and canals as well as by pleasure craft fouled with mussels.

An even more dramatic example of jump dispersal occurred with the discovery of the quagga mussel in Lake Mead, Nevada, in 2007, some 2,700 km from the closest known source population in Lake Michigan. Adult mussels fouling an exterior surface of a trailered pleasure boat were likely responsible for this invasion, although many other boating mechanisms can transport veliger larvae or adult individuals (Table 1). This invasion reveals the highly unpredictable nature of long-range dispersal, as successful colonization required mussel survival while the boat was trailered across semi-desert environments. Only slightly less impressive was the dispersal of zebra mussels to reservoirs in Colorado and California from eastern North America, illustrating that functional vectors exist for transcontinental movement of both mussel species.

Movement of trailered recreational boats between lakes is a potent mechanism for the spread of invasive macrophyte species. Surveys of trailered boats departing Lake St. Clair, Michigan, revealed that 33–36 percent were fouled by stranded macrophyte species, many of which are nonindigenous to the lake. The human role in spreading nonindigenous macrophyte species was highlighted by a New Zealand survey that found NIS in 83 percent of lakes used for boating or fishing but 0 percent in lakes without these activities. Trailers appear to be the predominant vector for moving nonindigenous macrophytes, rather than the boats themselves, likely because submerged trailers are highly conducive to fouling by floating plants. Inspections at lakes in British Columbia found Eurasian watermilfoil on 4.3 and 0.06 percent of trailers and pleasure boats, respectively. Other NIS likely to be transported by recreational boats include *Hydrilla verticillata* and *Cabomba caroliniana*, although many other macrophyte species could be transported by this mechanism.

Boaters and anglers may congregate on particular lakes, and if these lakes become invaded, they can serve as hubs for secondary spread to other systems. As an example, *Hyrdilla verticillata* recently colonized Pongolapoort Dam, a large reservoir in South Africa. This reservoir hosts the largest fishing competition in the southern hemisphere. Trailered boats departing this lake pose a clear risk of introducing *Hydrilla* to other systems in South Africa unless preventative measures are implemented to ensure the trailers are cleaned before they depart from the reservoir. Trailered boats pose an additional risk of spreading "fellow traveler" invertebrates that colonize nonindigenous plants in lakes.

Reservoirs are formed when rivers are dammed. In some parts of the world, reservoirs are the dominant standing water bodies. Reservoirs have played a central role in spreading some NIS. For example, after the waterflea *Daphnia lumholtzi* first colonized a reservoir in Texas in 1990, it spread across the southeastern, midwestern, and southwestern United States, with most populations becoming established in reservoirs. Dispersal of this species most likely involved inadvertent transport in recreational boats (e.g., live well or bilge water) or on fishing gear of anglers associated with major fishing competitions. Reservoirs have also been implicated in serial invasions by the copepod *Eurytemora affinis*.

Reservoirs are good candidates for invasion because they have higher water flow than do nonconnected lakes; they also have large surface areas and high visitation rates by recreational boaters. Each of these factors may increase propagule pressure of NIS entering reservoirs. More controversially, reservoirs have high disturbance rates, high but more variable productivity, and human-constructed food webs, all factors linked to invasibility. Whatever the mechanism, the examples provided—*Daphnia lumholtzi*, *Eurytemora affinis*, *Dreissena polymorpha*, *D. rostriformis bugensis*, and *Hydrilla verticillata*—demonstrate that reservoirs may serve as stepping stones in serial invasions of landscapes once an invader first arrives.

Other mechanisms associated with human activities also spread NIS among lakes. The spiny waterflea first invaded North America (Lake Ontario) in 1982 and has since spread to more than 144 lakes in Ontario plus about a quarter as many in Great Lakes states. Natural dispersal may have played a role in some of these invasions (see above), as the species is found in and around a river and canal system that runs through the invaded range in Ontario. However, invaded lakes are significantly closer to roads than their nearest neighbor lakes that are not invaded, which suggests a role for human activity. These waterfleas can foul fishing lines that are trolled through invaded lakes, resulting in the formation of "knots" on fishing lines. Adult animals retrieved on fishing lines undoubtedly die shortly after immersion, but their resting eggs remain viable for an extended period. Mathematical models that use information on travel patterns of boaters leaving invaded lakes has allowed reconstruction of the invasion sequence. Lake Muskoka, an extremely popular recreational inland lake, was invaded relatively early (1989). Up to thirty-nine other lakes were either directly or indirectly invaded from Lake Muskoka, with a stepping-stone chain spanning at least five links. The number of lakes that may become directly invaded from Lake Muskoka has declined because many of the systems linked to this lake are already invaded.

Other lake systems with other NIS may behave similarly. For example, Lake Mead in California and Nevada will be a source of future dispersal of quagga mussels, because it has the highest boater visitation rate in the western United States. Lake Mead was identified as a strong candidate for invasion and hub status, and the "100th Meridian Initiative" was specifically designed to prevent *Dreissena* mussels from colonizing the western United States, yet the invasion still occurred. Efforts to manage invasions must initially focus on prevention, followed thereafter by preventing propagule transfer out of the lake if the system becomes invaded.

IMPACTS OF INVASIONS ON LAKES

Nonindigenous species may produce an array of direct and indirect changes in invaded lakes. These include altered physical and chemical characteristics, as well as changes in biological composition. In many cases, it is difficult to separate effects because physical changes may drive chemical or biological ones, or vice versa.

While impacts of introduced aquatic NIS are often negative, many instances exist in which species are intentionally stocked into lakes (see above). Lakes with high water clarity are desirable both because they have high aesthetic value and because they command high cottage prices. Impaired water clarity often can be improved by reducing loading of limiting nutrients, especially phosphorus. Aquatic ecologists have used two strategies that may involve introduction of NIS to achieve this objective. First, some lakes may be "biomanipulated" by stocking high densities of piscivorous fishes to reduce planktivorous fish abundance and thus enhance algal

grazing by large zooplankton. Favoring large zooplankton at the expense of planktivorous fishes can enhance overall grazing of phytoplankton and improve water clarity. An alternate strategy involves eliminating the entire fish community through netting or application of poisons, followed by stocking of piscivorous fishes. Problems with either method include attenuation of beneficial effects with each trophic level and the ephemeral nature of some benefits. Biomanipulation efforts ideally involve stocking native piscivores (e.g., northern pike, or pikeperch *Stizostedion lucioperca*), although concern about introducing nonindigenous predators (e.g., largemouth bass) is usually secondary to improving water quality.

A second example of biomanipulation involves stocking mussels into systems with poor water quality. Introduced zebra and quagga mussels—and a South American analog, the golden mussel *Limnoperna fortunei*—filter silt, sediment, edible and inedible phytoplankton, and small zooplankton from water, improving light transmission. Inedible particles are rejected as pseudofeces and tend to accumulate with feces around mussel colonies on the lake bottom. Dutch researchers have exploited this characteristic of mussel filtering to improve water clarity. The addition of zebra mussels to lakes and ponds suffering from eutrophication has generally improved water clarity and reduced algal biomass. In fact, there may be no stronger effect of zebra mussels on invaded lakes than improved water clarity. Despite this fact, in most parts of the northern hemisphere, the perceived drawbacks exceed the potential benefits, and zebra mussels are not intentionally stocked in lakes as a result. A number of jurisdictions in North America have banned live transport of the species, including Vermont, Indiana, New York, Minnesota, Kansas, Florida, California, and Manitoba, to reduce invasion risk.

Many introduced fishes have the opposite effect on water quality, particularly if the fish is benthivorous and adversely impacts macrophytes or resuspends sediments. For example, before-and-after comparisons of lakes in New Zealand in which fishes including rudd *Scardinius erythrophthalmus*, tench *Tinca tinca*, European perch *Perca fluviatilis*, brown bullhead *Ameriurus nebulosus*, goldfish *Carassius auratus*, and koi *Cyprinus carpio* were introduced demonstrated profound reductions in water clarity following the introductions. Key to changes in water clarity is the relative abundance of macrophytes and phytoplankton. If macrophytes are consumed or uprooted by benthivorous fishes, then the physical structure and habitat formerly associated with the plants is lost, as is the ability to stabilize lake sediments and reduce resuspension of sediments. Once macrophytes are lost, the lake may shift rapidly to an "alternative stable state" characterized by perpetual turbidity and enhanced phytoplankton production.

Introduced fishes are not the only species capable of inducing dramatic shifts in ecosystem state. Introduction of red swamp crayfish *Procambarus clarkii* into shallow Chozas Lake, Spain, switched the system from one rich with macrophytes, invertebrates, amphibians, and birds to a turbid system in which abundances of these groups were greatly diminished. Similarly, in North America, the rusty crayfish *Orconectes rusticus* is currently spreading in lakes around the Great Lakes. In some but not all invaded lakes, rusty crayfish directly or indirectly reduce macrophyte abundance and species richness through herbivory, destruction, or increased turbidity, and they reduce abundances of many invertebrate taxa as well. These lakes are also characterized by very low abundances of *Lepomis* sunfish, whose macrophyte habitat crayfish destroy. On the other hand, invaded lakes where macrophytes continue to flourish are often characterized by abundant sunfish, which regulate crayfish abundance through intense predation on juveniles.

Introduced common carp and red swamp crayfish change lake chemistry in addition to or in conjunction with physical and biological changes. Both species cause significant increases in organic and inorganic suspended solids and significant declines in macrophyte abundance. Carp also negatively affect ammonia concentration and chironomid abundance, while chlorophyll *a*, total phosphorus concentration, and rotifer and copepod abundances increase significantly. Crayfish increase total and ammonia nitrogen and total and orthophosphorus concentrations, but decrease populations of both chironomids and oligochaetes.

Intense colonization of nearshore areas of lakes by introduced macrophytes may partially or completely obstruct navigation by ferries and recreational boats, reduce lake mixing, and result in dramatic light attenuation. In turn, reduced light or shading affects processes including phytoplankton productivity and sediment chemistry. For example, the macrophyte swollen bladderwort *Utricularia inflata* has invaded lakes in the Adirondack Mountains in upper New York State. Growth of this plant just above the lake bottom decreases growth of native macrophytes and indirectly reduces sediment oxygen and redox potential while increasing pH, carbon dioxide, ammonia, total phosphorus, and iron.

As with many invaders, the magnitude and direction of change following macrophyte invasions depends

on species' functional roles. Prolific growth of introduced Eurasian watermilfoil can either benefit or harm fish populations. The plant can obstruct swimming by pelagic and piscivorous species, can reduce piscivory, and can reduce the availability of invertebrate prey by replacing native plants upon which these species live. In other systems, watermilfoil encourages invertebrate colonization and provides refuge from piscivores for young-of-year fishes. *Hydrilla verticillata* appears to perform a similar function in Lake Izabal, Guatemala, as biomass of the most important subsistence fish species is higher in the hydrilla habitat than in the five habitats with native plants. Beds of introduced African elodea *Lagarosiphon major* and Canadian waterweed in a New Zealand lake had higher standing stocks and production of epiphytes, higher diversity and abundance of invertebrates, and higher native fish abundance than did native plant beds. Consequently, certain functional groups appear to benefit from colonization of lakes by nonindigenous macrophyte species, although native plants may suffer from competition, and human access may be adversely affected.

Zebra and quagga mussels are prime examples of "ecosystem engineers." In addition to their effects on water clarity, they can cause a wide range of direct and indirect physical, chemical, and biological changes in the lakes they invade. For example, extensive accumulations of mussel shells—both living and dead—may be found in many lakes. These shells enhance the structural complexity of the lake bed, particularly where the substrate is mud or sand. Although not all species benefit, invertebrate species diversity and total nonmussel abundance is typically much higher in these shell beds than in adjacent soft sediment. Many invertebrates also benefit from the accumulation of rich organic wastes produced by mussel feces and pseudofeces. A number of groups clearly have been adversely affected by zebra and quagga mussel colonization of the Great Lakes. These species include native unionid mussels, which through both exploitative and interference competition, become very rare or absent in areas with large *Dreissena* populations. Lake whitefish *Coregonus clupeaformis* populations in lakes Huron and Michigan appear to have declined sharply in response to large quagga mussel populations in both lakes. Whitefish body condition has deteriorated concomitantly, reflecting a near collapse of its primary food source, *Diporeia* spp., in both lakes. Other fishes suffering steep population declines in Lake Michigan since 1999 include alewife *Alosa pseudoharengus*, bloater *Coregonus hoyi*, deepwater sculpin *Myoxocephalus thompsoni*, and slimy sculpin *Cottus cognatus*. Crustacean zooplankton abundance has also declined sharply in Lake Huron, possibly reflecting the focusing of predators on remaining plankton following collapse of the *Diaporeia* populations. Although the precise mechanisms by which these changes are occurring is not understood, they are linked to *Dreissena* expansion. Earlier workers had speculated that introduced *Dreissena* mussels cause a nearshore shunt of phosphorus through prolific population suspension feeding, locking this essential nutrient in nearshore sediments and away from open waters. Available evidence from some of the large deep Great Lakes is consistent with this hypothesis, as large-scale changes are no longer limited to the shallow lakes (Erie, St. Clair) for which the hypothesis was developed.

Adverse effects of *Dreissena* mussels are not limited to fish and plankton. In recent years, large numbers of waterbirds, including common loons *Gavia immer*, red-breasted mergansers *Mergus serrator*, and red-necked grebes *Podiceps grisegena*, among others, have died of botulism E on lakes Erie, Ontario, and Huron. The exact mechanism responsible for the growth of the bacteria *Clostridium botulinum* that produce the toxin, and the manner by which the birds acquire the toxin, is not yet clear, although it appears to be associated with consuming contaminated *Dreissena* by introduced round gobies. The gobies are, in turn, consumed by the waterbirds, which get sick and drown.

Introduced Predators

Perhaps the strongest adverse effects of NIS in lakes are associated with introduced predatory fish. Introduced species are the second leading cause of extinction for North American fishes (27 of 40 species) and for fishes worldwide (11 of 23 species). Nile perch is native to lakes in northern Africa but was introduced to Lake Victoria—the second-largest lake in the world—around 1960 to establish a fishery based upon biomass derived from the lake's many small-bodied species of cichlid fishes. The introduction has proven remarkably successful, and today Nile perch constitutes one of the major commercial fishes in the lake. However, the introduction has also caused extinction of hundreds of the cichlid fish species exploited by Nile perch in the lake.

Some of the best examples of species extinction following introduction have occurred in Central and South American lakes. In Lake Atitlán, Guatemala, introduction of largemouth bass was followed by extinction of two-thirds of the native fish species, and bass

possibly contributed to loss of the endemic Atitlán grebe *Podilymbus gigus* by preying on native crabs, one of the grebe's principal foods. Similarly, introduction of the peacock bass *Cichla ocellaris* to Gatun Lake from South America resulted in myriad changes, including the loss of six of eight previously common native fish species and a highly altered food web structure. Introduction of lake trout, sea trout *Salmo trutta*, and pejerey *Basilichthys bonariensis* into Lake Titicaca caused either direct (predation) or indirect (competition) suppression, and likely extinction, of a native endemic fish *Orestias cuvieri*, as well as causing declines in at least three other species. Introduction of a suite of 12 fishes into Lake Banyoles, Spain, was associated with an apparent loss of the fishes *Gasterosteus aculeatus* and *Tinca tinca*, and a decline of three others.

Fishless alpine lakes are extremely susceptible to species losses from fish introductions. The introduction of Arctic charr *Salvelinus alpinus* into a mountainous lake in Slovenia caused the elimination of the copepod *Arctodiaptomus alpinus* and the virtual elimination of *Cyclops abyssorum taticus*. A similar pattern unfolded in the mountains of Austria where high abundances of alpine charr *Salvelinus umbla* were stocked into a fishless lake. Within nine years, two copepods had virtually disappeared, and *Daphnia rosea* had become very rare. In a fishless mountain lake in western Canada, the introduction of brook trout resulted in the loss of two large crustaceans, the copepod *Hesperodiaptomus arcticus* and the cladoceran *Daphnia middendorffiana*. Following removal of the fish population, *Daphnia* recolonized the lake via ephippial eggs, while the copepod, which does not produce resting stages, did not recover. These differences highlight the importance of life histories in determining possible responses by impacted species once a stressor has been removed.

Adverse effects of introduced fishes in mountain lakes also extend to amphibians. Introduced trout species now inhabit 90 percent of total lentic surface area in a mountainous region of Idaho. Water bodies inhabited by trout have significantly lower amphibian abundances than those that lack fish. Although it might appear that amphibians can persist in these remaining fishless areas, these habitats tend to be too shallow to support reproduction or overwintering.

Introduced Diseases

Introduced diseases can profoundly affect native populations in lakes. As many as 40 different game and sport fish species in the Great Lakes have been infected since 2003 by a strain of viral hemorrhagic septicemia (VHS) virus, a disease common in coastal marine waters and in farmed freshwater salmonids in Europe but never seen previously in the Great Lakes. Populations of muskellunge *Esox masquinongy*, smallmouth bass *Micropterus dolomieu*, northern pike, freshwater drum *Aplodinotus grunniens*, and round goby have substantially declined coincident with viral infection.

Parasites may be carried as "fellow travelers" with species that are either intentionally stocked or inadvertently introduced. For example, introduced round and tubenose *Proterorhinus marmoratus* gobies, introduced via ballast water to the Great Lakes, carried at least two and possibly up to four parasites from the Black Sea. Whirling disease is a myxosporean parasite *Myxobolus cerebralis* that infects salmonids, causing both skeletal and neurological problems and resulting in characteristic spiraling swimming behavior. It was first reported in introduced rainbow trout in Europe, but the disease is now common in salmonids in many countries. It arrived to North America in frozen rainbow trout imported from Europe. In Europe, introduced Asian topmouth gudgeon *Pseudorasbora parva* carries an infectious pathogen *Spaerothecum destruens* that increases mortality and causes reproductive failure in foy *Leucaspius delineatus*, an endangered native cyprinid species. Such "spillover" effects, in which an introduced species carries a nonindigenous pathogen or parasite that is even more harmful to native species, are not uncommon. Spillback effects, in which NIS serve as competent hosts for native parasites that can later infect other native hosts, can also occur. For example, introduced rainbow trout and brook trout in Lake Moreno, Argentina, acquire four of their five helminth parasites from native fish and account for almost 25 percent of total helminth egg production. The result is a larger reservoir of parasites available to colonize the native species. Another example is provided by introduced African cichlids (*Oreochromis*) in Lake Chichancanab, Mexico. Following cichlid introduction, six of seven native *Cyprinodon* species declined dramatically, and one was extirpated. The cichlids served as an intermediate host for transmission of the native parasite *Crassiphiala cf. bulboglossa*, and because these fishes were heavily preyed upon, they increased the transmission of infective stages to the bird host and, indirectly, to the definitive *Cyprinodon* hosts. Of course, many species other than fishes are vulnerable to introduced diseases. The crayfishes of Europe long ago sustained massive population declines and species extirpations resulting

from the co-introduction of North American crayfishes and their diseases.

Hybridization with Native Species

Introduction of nonindigenous species may result in hybridization with native species. Hybridization is a concern because it may adversely affect persistence of endangered species, jeopardize the legal status of these endangered species, or alter the ecological, behavioral, or genetic specialization of native species. Hybridization has contributed to 38 percent of native fish extinctions in North America over the past century. As introductions of species to lakes continue unabated, opportunities for hybridization should increase in the future.

In many cases, more than one factor is implicated in species extinctions. Hybridization can become an especially important factor when very small native populations interact with much larger populations of introduced species. For example, stocks of longjaw cisco *Coregonus alpenae*, deepwater cisco *C. johannae*, and blackfin cisco *C. nigripinnis* in lakes Michigan and Huron were severely depleted by overfishing, and, to a lesser extent, sea lamprey predation, following which remaining individuals are thought to have hybridized with common ciscoes. The last recorded finds of native individuals of these species were in 1967, 1951, and 1923, respectively.

While hybridization between introduced and native species poses the greatest conservation concern, hybridization involving multiple lineages within a species or between multiple nonindigenous species can also be a problem. For example, mitochondrial DNA analyses of common carp from Lake Biwa, Japan, uncovered an infusion of five separate European strains into the native population, jeopardizing the integrity of this ancestral population. In the Murray-Darling river system in Australia, hybrid carp became far more widely distributed than either of the introduced stock species from which it was formed. Two and possibly three feral tilapia (*Oreochromis*) species also form hybrids in parts of Australia.

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FURTHER READING

Carlton, J. 1993. Dispersal mechanisms of the zebra mussel (*Dreissena polymorpha*) (677–697). In T.F. Nalepa and D.W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Boca Raton, FL: Lewis Publishers.

Havel, J.E., C.E. Lee, and M.J. Vander Zanden. 2005. Do reservoirs facilitate invasions into landscapes? *BioScience* 55: 518–525.

Johnson, P.T.J., J.D. Olden, and M.J. Vander Zanden. 2008. Dam invaders: Impoundments facilitate biological invasions into freshwaters. *Frontiers in Ecology and the Environment* 7: 359–365.

Leung, B., J.M. Bossenbroek, and D.M. Lodge. 2006. Boats, pathways, and aquatic biological invasions: Estimating dispersal potential with gravity models. *Biological Invasions* 8: 241–254.

MacIsaac, H.J., J.V.M. Borbely, J.R. Muirhead, and P.A. Graniero. 2004. Backcasting and forecasting biological invasions of inland lakes. *Ecological Applications* 14: 773–783.

Padilla, D.K., and S.L. Williams. 2004. Beyond ballast water: Aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Frontiers in Ecology and Environment* 2: 131–138.

Rahel, F.J. 2007. Biogeographic barriers, connectivity and homogenization of freshwater faunas: It's a small world after all. *Freshwater Biology* 52: 696–710.

Ricciardi, A., and R. Kipp. 2008. Predicting the number of ecologically harmful species in an aquatic system. *Diversity and Distributions* 14: 374–380.

Vander Zanden, M.J., and J.D. Olden. 2008. A management framework for preventing the secondary spread of aquatic invasive species. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 1512–1522.

Ward, J.M., and A. Ricciardi. 2007. Impacts of *Dreissena* invasions on benthic macroinvertebrate communities: A meta-analysis. *Diversity and Distributions* 13: 155–165.

LAMPREY

SEE SEA LAMPREY

LANDSCAPE PATTERNS OF PLANT INVASIONS

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Natural landscapes can be viewed as microcosms of the global environment. At global scales, plant diversity is highest in warm-wet areas, with noticeable decreases in plant diversity in extreme environments: near the north and south poles, on cold mountaintops, and in deserts. Plant invasions generally follow the same predictable patterns at landscape scales. Many low-elevation meadows, riparian zones, and canopy gaps in zones of moderate climates contain the greatest native species richness and the greatest nonnative species richness. This "rich get richer" pattern of invasion often scales from landscapes to continents, as most species track favorable environmental conditions (e.g., high light, warm climates, ample precipitation, and high soil nutrients). Disturbances, such as fire, flooding, and insect