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Non-indigenous species in the Great Lakes: were colonization and damage to ecosystem health predictable?

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Abstract

The Great Lakes ecosystem is home to at least 139 non-indigenous species of fauna and flora which have become established following invasions or intentional introductions. About ten percent of the exotic species have caused economic or ecological damage to the system. A sample of this group is reviewed to determine if ecological concepts are useful in helping to predict colonization and impacts to ecosystem health. Successful colonization by most of the species reviewed was predictable from habitat requirements and behaviour. Ecosystem disturbance was a factor in the success of some of the colonists but was not an overriding ecological requirement. Perturbations to ecosystem health are more difficult to predict and in most cases were not readily apparent from knowledge about the ecology of invaders or native communities. The main damage to ecosystem health by the species reviewed resulted from competition, predation and habitat modification. Difficulties in predicting both invasions and damage from successful colonists point to the need to prevent non-indigenous species from reaching the Great Lakes basin.

1. Introduction

Interest in the introduction of non-native species and their impacts on endemic species of flora and fauna has been increasing globally. The world-wide dispersal of non-indigenous species (NIS) has been accelerated by human activities, particularly shipping (Carlton, 1985). In North America, interest in NIS has been sparked by recent introductions of invertebrates and fishes. Elton (1958) was one of the first to review and analyse invasions from an ecological viewpoint. He described 241 instances of species introductions world-wide and reviewed some of the worst invasions in terms of economic and ecological damage. The Office of Technology and Assessment (U.S. Congress, 1993) reported on 4542 NIS which have become successfully established in the USA. Included are more than 2000 plant species, more than 2000 insect species, 239 plant pathogens, 142 terrestrial vertebrate species, 91 species of freshwater molluscs and 70 fish species. Since 1980, 205 species have been introduced or detected, 59 of which are causing economic or environmental harm. Potential economic loss from just 15 worst-scenario species has been estimated at $134 billion (US). Included in this group are the zebra mussel (*Dreissena polymorpha*) and purple loosestrife (*Lythrum salicaria*).

As a pathway for settlement and the development of agriculture, industry and commerce in central North America, the Laurentian Great Lakes have been vulnerable to invasions by, and introductions of, NIS for several centuries. Since the early 1800s, at least 139 species have become successfully established (Mills *et al.*, 1993a). The number of unsuccessful invasions and introductions is unknown.

Elucidation of questions surrounding predictability of success or failure of establishment of NIS and their potential to do ecological and economic harm has been attempted (Elton, 1958; Mooney & Drake, 1986; Groves & Burdon, 1986; Pimm, 1991) although invasion theory is not well developed. It is the purpose of this paper to discuss some examples of successful NIS in the Great Lakes and their damage to the health of the ecosystem in light of ecological concepts. The concept of ecosystem health has been defined and discussed at length in the context of the Great Lakes ecosystem by Ryder (1990) and Evans *et al.* (1990) and will not be further elaborated here.

2. Introductions and ecological concepts

At least 139 NIS have colonized the Great Lakes basin (Mills *et al.*, 1993a). Undoubtedly, many more species failed to become established. Why are some invasions and introductions successful while others are not? Why are some systems more vulnerable to colonization than others? Why are some colonists more disruptive than others? Can we predict whether a colonist will displace a native species?

Many ecological concepts, particularly those concerning communities, have been explored to explain success or failure of introductions and invasions (Pimm, 1991). Elton (1958) referred to 'ecological resistance' to invasion. He found that most of the invasions that he reviewed occurred in disturbed habitats and hypothesized that ecological resistance is lowered in a disturbed system. Sharples (1983) also found that disturbed areas, like islands, are particularly vulnerable to invasion and reasoned that the simplified biota associated with those situations are less resistant. A clear example is the successful invasion of plants from Europe and Asia into North America. Of 124 common weeds of Canada (Mulligan, 1987), 74 percent were introduced, almost all from Europe and Asia (Table 1). Moreover, 87 percent of weeds on the noxious list of the 1988 Weed Control Act for Ontario are invaders (Government of Ontario, 1988). Many of these colonists became established when the land was being cleared for agriculture which represented a highly disturbed system with reduced native flora.

Two general hypotheses have been put forward (Simberloff, 1986; Baltz & Moyle, 1993) to help explain invasion resistance:

(a) Environmental resistance hypothesis (e.g. inability of a species to adapt to physical and/or chemical characteristics of the environment);

(b) Biotic resistance hypothesis (e.g. competition and/or predation interaction with native species).

Some of the characteristics which may influence the success or failure of a colonist to overcome habitat or biotic resistance are listed in Table 2. In general, none of the characteristics may be essential or sufficient by itself to account for colonization.

Table 1. Numbers of native and non-indigenous species of common weeds of Canada (from Mulligan, 1987)

Family	Native species	Non-indigenous species
Composite	14	27
Mustard	1	12
Buckwheat	2	6
Grass	2	6
Others	13	41
Total	32	92
Percent	26	74

Similar climate is a broad first ecological requirement for successful introductions. For example, zebra mussels occur between latitudes 30° and 60° in Europe which provides a rough latitudinal range of possible distribution in North America. However, suitable habitat within a similar climate is also important for zebra mussels. Habitat requirements in the water, such as calcium concentration and pH, might preclude establishment within a broad climatic scale (Neary & Leach, 1992, Fig. 8). In the dispersal of zebra mussels in the Canadian province of Ontario (Neary & Leach, 1992), climate and habitat are more important than the existence of other fauna. This observation agrees with a hypothesis put forward by Simberloff (1986) who disagrees with the 'disturbed system' theory of Elton (1958) and others. Simberloff hypothesized that 'each potential invader has a probability of successfully colonizing each site, and this probability rests largely on the nature of its habitat requirements and habitat availability at the site, and only secondarily on what other species are present'.

Groves & Burdon (1986) suggested that inoculation rate, the rate at which NIS are brought into the ecosystem, determines the vulnerability of an ecosystem to invasion. However, Simberloff (1986) found that many successful introductions of insects resulted from an inoculation of few individuals, often from one site.

Pimm (1991) found, as a generality, that increased species richness and connectance (i.e., the actual, divided by the possible number of interspecific interactions) decrease the chances of invasion. He explained that competition for resource use increased directly with connectance in a community and with more competition there was less opportunity for invasion. Consequently, species-poor communities will have a greater

Table 2. Attributes of habitats, invading species and communities which may contribute to success of colonization by non-indigenous species

Habitats	Invading species	Communities
Climate similar in donor and receiving habitats	High fecundity	Species-poor
Disturbance	Short generation time	Low complexity
Suitable physical and chemial characteristics	Rapid dispersal	Stressed native populations
Available substrata	Eurybiont	Trophic opportunities available
	Polyphagous	Reduced competition and predation
	High genetic variability	from native species
	High inoculation rate	
	Affiliated with *Homo sapiens*	

Table 3. Number of native fish species and number and percent of non-indigenous fish species in the Great Lakes (from Ryder, 1972; Mills *et al.*, 1993a)

Lake	Number of native species	Number of non-indigenous species	Percent introduced
Superior	67	13	16
Michigan	114	13	10
Huron	99	15	13
Erie	113	17	13
Ontario	112	14	11

proportion of invaders than species-rich communities. This follows for Great Lakes fishes where Lake Superior has the fewest native species and the highest percentage of NIS (Table 3). On the other hand, Baltz & Moyle (1993) found that undisturbed California streams, with species-poor fish communities, continuously resisted invasion by introduced species. Also, the endemic fish community of Lake Victoria in Africa with over 300 species was easily invaded by Nile perch (*Lates* sp.) with the loss of about two-thirds of the native cichlid species (Lowe-McConnell, 1994).

The 'empty' niche concept in relation to success of introductions has been discussed at length by several authors (see Herbold & Moyle, 1986; Li & Moyle, 1993). There has been considerable confusion concerning niche definition (Kerr & Ryder, 1977) and this has led to intentional introductions of species to fill niches considered vacant, usually with disastrous results (Herbold & Moyle, 1986). The concept of an 'empty' niche is not particularly useful for prediction of success or failure of colonization because a niche must be occupied to be recognized (Pimm, 1991). Richard A. Ryder (personal communication) has proposed 'trophic opportunity' as a more realistic and useful descriptor. Pimm (1991) concluded from his extensive review of invasions that 'communities are sometimes resistant to introduced species but most often are not'.

The other principal question concerns our ability to predict whether a colonizing species will affect the health of the receiving ecosystem. Will habitat and/or native communities be negatively perturbed? Will indigenous species be displaced or driven to extinction?

From data collected in the United States, the United Kingdom, and the Laurentian Great Lakes, the percentage of successful colonists considered to be harmful is surprisingly uniform (Table 4). In the United Kingdom, Williamson & Brown (1986) found no significant differences in the proportion of 'pests' in three broad groups of invaders: vertebrates, insects, and vascular plants. In the United States, the percentage of high-impact species ranged from 4 to 19 in five groups of NIS (U.S. Congress, 1993). Terrestrial vertebrates, insects and molluscs were uniformly high at 18 to 19 percent; plant pathogens and fishes were lower at 11 and 4 percent respectively. Of the 139 NIS established in the Great Lakes basin (Mills *et al.*, 1993a), 20 percent of fishes, 21 percent of invertebrates and diseases, and only 5 percent of algae and aquatic plants are considered harmful to ecosystem health. Impacts of non-indigenous flora at the population or community levels in the Great Lakes have not been well observed or documented and consequently could be much higher than indicated.

The main mechanisms for ecosystem damage by colonizing species include habitat modification, competition, predation, associated diseases and para-

Table 4. Number of successful colonists and percent considered to be harmful to ecosystem health in the United States, the United Kingdom and the Laurentian Great Lakes drainage basin

Study area	Number of species of successful colonists	Approximate percent considered harmful	Reference
United States	>4500	15	U.S. Congress (1993)
United Kingdom	>600	10	Williamson & Brown (1986)
Great Lakes	139	10	Mills *et al.* (1993a)

sites, and genetic effects (see Li & Moyle, 1993 for overview). All have been instrumental in degrading the health of the Great Lakes ecosystem and will be discussed below in relation to individual colonizing species.

The ultimate measure of harm by a NIS is local extinction of native species. Simberloff (1981) reviewed 10 studies involving 850 introductions of plants and animals and concluded that less than 10 percent of NIS caused extinctions of native species. Of the 71 extinctions, predation was the main cause with 51, habitat change was considered responsible for 11 and competition for three.

The degree of ecosystem impact by NIS in the Great Lakes is variable and ranges from very harmful to harmful/beneficial (Table 5). However, effects of almost three-quarters of the colonists are virtually unknown. Moreover, it is difficult to predict how native communities and habitats will react to a new species. In some cases ecological effects of a colonist are evident from its behaviour in its native environment.

3. Examples from the Great Lakes

The following examples of NIS in the Great Lakes are selected from Mills *et al.* (1993a). There is a bias in the selections which favours fish species, largely because more is known about them which, in turn, is a reflection of their economic importance.

3.1. *Sea lamprey*

The origin of the sea lamprey (*Petromyzon marinus*) in Lake Ontario (first records in the 1830s) as a glacial relict or canal immigrant is uncertain (Lark, 1973; Christie, 1973; Emery, 1985). It was first recorded in Lake Erie in 1921, Lake Huron in 1932, Lake Michigan in 1936, and Lake Superior in 1946. The species never proliferated in Lake Erie due to lack of suitable spawning and nursery areas although it is now sufficiently abundant to threaten survival of planted lake trout (*Salvelinus namaycush*). In the upper Great Lakes it became abundant and depleted stocks of lake trout and other native species (Lawrie, 1970).

Invasion of Lake Erie and the upper Great Lakes by sea lamprey was predictable. In fact, the danger of an introduction to Lake Erie through the Welland Canal was suggested as early as 1851 (Christie, 1973). The importance of disturbance in the system as an aid to invasion is uncertain but probably not a major factor. All of the Great Lakes were experiencing cultural perturbations at the time (Loftus & Regier, 1972), but habitat quality in the upper Great Lakes and tributaries was much superior to that of Lake Erie. Most of the tributaries to Lake Erie were degraded to the point where they could not sustain lamprey spawning and development of ammocoetes. Lack of suitable hosts for the parasitic adults was also a factor in the failure of the sea lamprey to proliferate in Lake Erie.

Sea lamprey damage in the upper Great Lakes was not predictable from its behaviour in Europe where measures have been taken to conserve the species (Maitland, 1980). The lamprey did not attract much attention as a predator on salmonids in Lake Ontario in the 1800s. Christie (1973) considered that more stream habitat became available to sea lamprey in Lake Ontario in the early 1900s through the removal and deterioration of dams. Abundance of lampreys and lamprey scarring had increased by the 1920s and it became evident later that the parasite was limiting the success of lake trout plantings. Despite the experience with lampreys in Lake Ontario, fisheries managers were not prepared for the severe damage which followed its successful colonization in the upper Great Lakes. Several important fish species have declined in abundance and sport and commercial fisheries have suffered many millions of dollars in damage (Fetterolf, 1980). Expenditures by the Great Lakes Fishery Commission (GLFC) for sea lamprey control and research up to 1993 amounted to $168 million (US) (R.L. Eshenroder, GLFC, personal communication). Partial success in controlling the sea lamprey population in the Great Lakes has been achieved with selective chemicals. The GLFC recognizes the need to reduce dependence on chemical controls and is currently supporting research that will lead, hopefully, to an integrated sea lamprey management program (Anon, 1992a).

Table 5. Degree of impact on ecosystem health by taxa of non-indigenous species in the Great Lakes (from Mills *et al.*, 1993a)

Degree of impact	Fishes	Molluscs	Other invertebrates	Diseases and parasites	Algae	Plants
Very harmful	2	2		2		1
Harmful	3	1	1		1	2
Potentially harmful	3	1	1	1		9
Harmful/beneficial	7					
Unknown	10	10	12		23	47

3.2. *Alewife*

Like the sea lamprey, the origin of alewives (*Alosa pseudoharengus*) in Lake Ontario is uncertain but they were established there by 1873. From allozyme variation studies, Ihssen *et al.* (1992) concluded that the species probably originated from the Hudson-Mohawk Rivers, and gained access to Lake Ontario through the Erie Canal. The species was first found in Lake Erie in 1931 (Dymond, 1932) and then spread rapidly upstream, colonizing Lake Superior in 1954. Invasion from Lake Ontario into the other Great Lakes was predictable with the completion of the Welland and Erie Canals. The species never became abundant in Lake Erie due to winter habitat restrictions (Colby, 1973). Ecosystem disturbance was a factor in the rise of alewife populations which increased dramatically, particularly in Lake Michigan, due to lack of predation by piscivores following the rise of the sea lamprey.

Ecosystem damage did not become apparent until after the populations of alewives exploded and, therefore, was probably not predictable. Obligate shallow-water planktivores and inshore stocks of facultative plantivore-piscivores declined at the peak of alewife population density (Smith, 1972). Species affected included the deepwater ciscoes (*Coregonus* spp.), lake herring (*Coregonus artedii*), deepwater sculpin (*Myxocephalus quadricornus*), emerald shiner (*Notropis atherinoides*), rainbow smelt (*Osmerus mordax*), yellow perch (*Perca flavescens*), and walleye (*Stizostedion vitreum*) (Smith, 1972; Schneider & Leach, 1979).

3.3 *Common carp*

The common carp (*Cyprinus carpio*) was intentionally introduced into the Great Lakes basin in 1879 as a food fish (Emery, 1985). The species is now ubiquitous in shallow waters (except in Lake Superior where it occurs but is not abundant) where its feeding activity destroys habitat for favoured fish species and waterfowl. Disturbance was unlikely a factor in colonization; however, nutrient enrichment favours proliferation of the species. Native species of fish that utilize inshore habitats have been impacted through competition for food and space and loss of habitat (Emery, 1985).

Ecosystem damage was not likely considered at the time of first plantings but was soon recognized and stocking was reduced by the late 1890s (McCrimmon, 1968). Commercial exploitation is limited due to low market value and the species is seldom sought by anglers. Expensive (and largely unsuccessful) eradication efforts have been ongoing for many decades.

3.4. *Rainbow smelt*

Colonization of the upper Great Lakes by rainbow smelt is believed to have resulted from a deliberate release of eggs into a lake in the Lake Michigan drainage in 1912 (Emery, 1985). Earlier and later plantings in the St. Marys River failed (Dymond, 1944). Rainbow smelt in Lake Ontario is considered to be either native (MacKay, 1963) or to have migrated from the Atlantic drainage through the Erie Canal system (Scott & Crossman, 1973). Rainbow smelt is abundant in all of the Great Lakes where it is preyed upon by piscivores. It has been an important commercial species in Lake Erie since the 1950s but may have adversely affected walleye, blue pike (*Stizostedion vitreum glaucum*) and lake whitefish (*Coregonus clupeaformis*) (Leach & Nepszy, 1976; Schneider & Leach, 1979). In the upper Great Lakes it is believed to have perturbed lake herring and bloaters (*Coregonus hoyi*) and lake herring in Lake Ontario through competition and predation (Smith, 1970; Christie, 1973).

As with the alewife, rainbow smelt is a preferred prey of piscivores in the Great Lakes. Whereas alewife populations did not become abundant until after massive decreases in predators, the rainbow smelt flourished in the presence of predation. Rainbow smelt has been (intentionally or accidentally) released extensively into inland lakes in Ontario and has colonized almost 200 (Evans & Loftus, 1987). The lakes varied widely in morphology and fish species associations. In an analysis of the Ontario data, Pimm (1989) found that rainbow smelt were more likely to invade lakes where there were more predatory species. It is possible that smelt were introduced more often in lakes with more predators. However, Pimm (1991) also suggests, as a generality, that predators may reduce the competition that an invader faces by feeding heavily on resident species. In the Great Lakes the decline in piscivores may have benefited the success of colonizing smelt (Christie, 1974), but cultural disturbance was unlikely a major prerequisite to invasion.

Ecosystem damage by colonizing rainbow smelt was not foreseen by fisheries managers who stocked the species as prey, particularly for lake trout. Impacts on other species in the Great Lakes were very slow to be recognized, perhaps because perturbations from competition and predation were not always consistent (Evans & Loftus, 1987).

3.5. *Introduced salmonids*

Rainbow trout (*Oncorhynchus mykiss*) were first introduced intentionally into the Great Lakes basin in 1876. Colonization by this and later introductions were successful and the species has provided excellent sport fisheries. However, there is evidence (Ryder & Kerr, 1984) that, in culturally disturbed environments, rainbow trout may outcompete the native brook trout (*Salvelinus fontinalis*). Excellent sport fisheries have also been established in cold water environments with introductions of brown trout (*Salmo trutta*), coho salmon (*O. kisutch*), and chinook salmon (*O. tshawytscha*) (Carl, 1982). All three species are considered to have displaced native species through competition and predation (Ryder & Kerr, 1984; Krueger & May, 1991).

Damage to ecosystem health from these introductions was certainly not predicted by the management agencies responsible for the plantings and only recently has been recognized. The 'vacant niche' syndrome was a factor in the stocking of coho salmon and chinook salmon in the Great Lakes where larger piscivores were lacking or in low abundance. Rainbow trout and brown trout were stocked in all the Great Lakes to provide nearshore and tributary angler opportunities without regard to possible interactions with native species through competition. Although competition is considered to be the main mechanism for impacts on native salmonids, there is evidence of deleterious effects due to predation, habitat modification, associated parasites and diseases, and genetic effects (see Krueger & May, 1991 for overview).

3.6. *Ruffe*

The ruffe (*Gymnocephalus cernuus*) is currently established in western Lake Superior having been released in Duluth Harbour from ballast, possibly in 1986 (Pratt *et al.*, 1992). The species has expanded its range into the St. Louis River and eastward about 150 km along the south shore of Lake Superior and to Thunder Bay, Ontario on the north shore (Busiahn & McClain, 1995). The ruffe in Europe, where it is still expanding its range, has impacted yellow perch (*Perca fluviatilis*) and whitefish (*Coregonus lavaretus*) (Maitland *et al.*, 1983; Anon, 1992b). It appears to be affecting yellow perch and some other native species in the St. Louis River (Busiahn & McClain, 1995). There is concern that yellow perch in the Great Lakes (particularly Lake Erie where it is a major species) could be severely stressed by the ruffe (Anon, 1992b; Busiahn & McClain, 1995).

Colonization of Duluth Harbour and the St. Louis River was a surprise. However, invasion of the Great Lakes was predictable from what we know about risks associated with ballast. The occurrence of ruffe in Thunder Bay, Ontario in 1991 is considered to have resulted from ballast transported from Duluth Harbour (Anon, 1992b). This vector alone could easily transport ruffe to the other Great Lakes which have much more habitat suitable for colonization than Lake Superior. As a percid, the ruffe prefers waters that are shallow, warm, turbid, and moderately enriched. Using preferred thermal habitat criteria, Busiahn & McClain (1995) calculated the following multipliers for habitable area for ruffe over that in Lake Superior: Lake Michigan 6×, Lake Huron 11×, Lake Erie 31× and Lake Ontario 4×.

Cultural disturbance was probably a factor in the successful initial colonization by the ruffe as the Duluth Harbour-St. Louis River area was rebounding from pollution problems at the time of invasion (Anon, 1992b). The ruffe was considered by Leach *et al.*

(1977) to be better adapted to eutrophic conditions than indigenous percids. The enriched waters of western Lake Erie, Saginaw Bay, Green Bay and Bay of Quinte will probably provide an edge to the ruffe over native percids which predominate in those areas now. Damage to ecosystem health by the ruffe is predictable from the consequences of range expansion in Europe (Maitland, 1991).

3.7. *Gobies*

Two goby species, the round goby (*Neogobius melanostomus*) and the tubenose goby (*Proterorhinus marmoratus*) were first observed in North America in the St. Clair River in 1990 (Jude *et al.*, 1992). Both species were likely transported to the Great Lakes basin in ballast water from the Black-Caspian Sea area (Mills *et al.*, 1993a). The round goby has expanded its range through Lake St. Clair to the mouth of the Detroit River. Round gobies have been found in the Grand River, a tributary to Lake Erie, and in Grand Calumet River, a tributary to Lake Michigan (Jude *et al.*, 1995). Ballast water is considered to be the likely vector.

Invasion of the Great Lakes by these small species was not predicted; however, the Black and Caspian Seas have been the source of sufficient recent invaders to alert our suspicions of shipping traffic from that region. Further expansion of the range of gobies (at least the round goby) is predictable (Jude *et al.*, 1995). It is unlikely that cultural disturbance played a major role in the success of the invasion. The round goby, in particular, has characteristics (high fecundity, nest guarding, nocturnal feeding) which favour successful colonization in suitable habitats.

The extent of ecosystem damage at this stage is uncertain. Jude *et al.* (1995) recorded observations which indicated that round gobies were perturbing mottled sculpins (*Cottus bairdi*) in the St. Clair River through competition and perhaps predation. Similar activity has not been observed in tubenose gobies. The potential for ecological damage is apparent but both goby species have not been in the system long enough for a sustained evaluation of their predator-prey interactions.

3.8. *Dreissenid mussels*

The zebra mussel was first found in the Great Lakes in 1988 (Hebert *et al.*, 1989) and the quagga mussel (*Dreissena bugensis*) three years later (May & Marsden, 1992). The zebra mussel has dispersed rapidly throughout the Great Lakes basin and is found in major drainage systems including the Mississippi, Hudson, and St. Lawrence Rivers (New York Sea Grant, 1993). As biofoulers, dreissenid mussels colonize intake cribs and pipes serving water treatment plants, power generating stations and industries. Removal of the fouler and prevention of infestation by physical and chemical means are expensive. As efficient filter feeders, the mussels are capable of altering food webs (MacIsaac *et al.*, 1992; Leach, 1993). Some species of native unionid mussels are being eliminated from the benthic fauna of Lake Erie and Lake St. Clair (Schloesser & Kovalak, 1991; Mackie, 1991).

The invasion of the zebra mussel into North America was certainly predictable. The possibility of transport of *Dreissena* from Europe to North America was suggested by Johnson (1921) and more recently by Sinclair and Ingram (1961) and indicated by a study of ballast water organisms in trans-oceanic shipping (Bio-Environmental Services Ltd, 1981). The zebra mussel has many characteristics which favour colonization and rapid dispersal. Fecundity is high and a pelagic larval stage of several weeks aids dispersal downstream. The ability to attach to surfaces with byssal threads favours spread through boat traffic (in and out of water) and habitat utilization. It has a trophic advantage in that it is a strong polyphagous filter feeder (Maclsaac *et al.*, 1992).

Was cultural disturbance a factor in the successful colonization of the Great Lakes by zebra mussels? Probably not if we consider that substrata and trophic opportunities were open to an invader with ability to biofoul and filter feed. Competition for substrata is essentially lacking in the Great Lakes and, as a strong filter feeder, the zebra mussel can easily out-compete pelagic filter feeders (Maclsaac *et al.*, 1992). Both dreissenid species overlap in habitat and trophic requirements; however, the quagga mussel can occupy soft sediments, survive in deep offshore waters and reproduce at colder temperatures (Dermott & Munawar, 1993; Mills *et al.*, 1993c).

Damage to ecosystem health by dreissenids was predictable from the European literature (Clarke, 1952; Stanczykowska, 1977). Impacts on other mussels (unionids) have occurred in European lakes (Sebestyén, 1938; Arter, 1989).

3.9. *Purple loosestrife*

Mills *et al.* (1993a) reported 59 NIS of aquatic plants established in the Great Lakes basin. Only two species, purple loosestrife and Eurasian watermilfoil (*Myriophyllum spicatum*) were considered to have perturbed the Great Lakes ecosystem. Purple loosestrife reached North America from Europe in the early 1800s and the Great Lakes basin in 1869. As with many plant invaders, dispersal was aided by railroads, roadways, and canals and, therefore, its spread throughout the basin was predictable. The plant's later popularity as an attractive garden perennial also accelerated its dissemination in the basin. Intentional introductions are discouraged but continue. Disturbance of wetlands by human interference including water level fluctuations, sediment and nutrient loading, and physical restructuring (Patterson & Whillans, 1985) has likely aided colonization by purple loosestrife (Mal *et al.*, 1992). The plant is well adapted for dispersal as it can reproduce by sexual or vegetative means. Seed production is prolific; a single plant is capable of producing an average of 2.7 million seeds (Thompson *et al.*, 1987).

The species is a strong invader and can outcompete native wetland plants to form monocultures thereby decreasing diversity and eliminating rare species. Many common valuable wetland species such as cattails (*Typha latifolia*), sedges (*Carex* spp.) and smartweed (*Polygonum* spp.) are displaced which, in turn, affects adversely some species of waterfowl, mammals and fish (Skinner *et al.*, 1994). In some areas of North America, wildlife species are declining in the face of increases in purple loosestrife abundance (Mal *et al.*, 1992).

The damage to the ecosystem was not predictable from Europe where the superior competitive ability of *Lythrum* was considered to be beneficial (Mal *et al.*, 1992). Intentional introductions as a garden perennial have been ongoing in North America for decades. Recognition of ecosystem damage by purple loosestrife has been slow and consideration of control and 'eradication' methodology has been recent.

4. Discussion

Characterization of the foregoing introductions into the Great Lakes is summarized in Table 6 according to predictability of colonization and damage to ecosystem health. Three of the introductions were intentional and I consider that colonization by five of the remaining taxa reviewed was predictable from information available in the literature. Cultural disturbance was considered to be a definite aid to colonization in only two of the invasions but may have contributed to the success of several others. Some taxa (sea lamprey, *Dreissena* spp.) possess unique characteristics which permit them to successfully colonize pristine environments providing basic habitat requirements are met.

All of the colonists reviewed above are considered to have impaired ecosystem health in the Great Lakes although the extent of damage by gobies is uncertain at this stage. Impacts by the early colonists were not generally foreseen. Possible damage to native fish species was certainly not considered by managers responsible for plantings of salmonid and forage species. Predictability of ecosystem health impairment is associated with the more recent ballast water introductions.

For the taxa reviewed, competition has been a major mechanism for damage to indigenous species (Table 6). For some colonists (common carp, purple loosestrife), the major perturbations have been inflicted through habitat modifications and for the other taxa, predator-prey interactions have been important. Native species have been displaced in the Great Lakes by impacts from at least seven of the taxa. Perturbations from NIS (e.g. sea lamprey, purple loosestrife) have been implicated in local extermination of native species (e.g. lake trout, cattails) (Lawrie, 1970; Skinner *et al.*, 1994). However, the array of cultural stresses on the Great Lakes ecosystem (Francis *et al.*, 1979) preclude easy delineation of impacts by a specific perturbation.

Our experience with Great Lakes colonists suggests that ecological theory on invasions has been slow in emerging. Questions about vulnerability of systems to invasion, predictions of success of colonization, and predictions of damage to ecosystem health are difficult to answer (Mills *et al.*, 1993b; Pimm, 1991). Ecology at best, may provide only generalizations which have low predictive capabilities and are of little use in the Great Lakes ecosystem because each invasion is a unique event. I agree with Simberloff (1986) who suggested that adequate predictive hypotheses are unlikely to emerge from current knowledge of population and community ecology.

Current management strategies for future introductions in the Great Lakes include prevention, containment and control (Mills *et al.*, 1993b). Historically, very little attention has been directed towards prevention of invasions and containment to prevent spreading when one occurs. Control measures to minimize impacts of an introduced species are usually difficult and expensive (e.g. chemical control

Table 6. Attributes of colonization and ecosystem health damage by selected non-indigenous species in the Great Lakes (Symbols: Y = yes; N = no; I = intentional introduction; P = partly; XX = major impact; X = minor impact; ? = uncertain)

Species	Colonization predictable?	Disturbance a factor?	Damage predictable?	Ecosystem health damage		
				Habitat modification	Competition	Predation
Sea lamprey	Y	N	N	X		XX
Alewife	Y	Y	N		XX	X
Common carp	I–Y	P	P	XX	X	
Rainbow smelt	I–Y	N	N		X	X
Introduced salmonids	I–Y	P	N	X	XX	X
Ruffe	Y	P	Y		XX	X
Goby species	N	N	N		?	?
Dreissenid species	Y	N	Y	X	XX	X
Purple loosestrife	Y	Y	N	XX	XX	

of sea lamprey larvae). Eradication of established introductions is usually impossible. Aquaculture, fish-stocking programs, and the baitfish and aquarium industries have all contributed unwanted introductions to the Great Lakes, primarily fish, invertebrates, plants and disease organisms. Legislation and policies aimed at prevention of introduction and migration of unwanted species are in place in Canada (Leach & Lewis, 1991) and the United States (Stanley *et al.*, 1991; Wingate, 1991). In Canada, the legislation has not been particularly successful in preventing and controlling the introduction of undesirable species partly due to insufficient commitment by jurisdictions to enforce regulations and obtain compliance (Leach & Lewis, 1991). Despite extensive federal and state legislation, the list of introduced fish species continues to grow in the United States (Crossman, 1991). Protocols and guidelines for evaluating proposed fish introductions have been suggested (Kohler & Stanley, 1984; Li & Moyle, 1993) and, if implemented by managers, could help to minimize problems resulting from intentional introductions.

Ballast water has been the vector responsible for invasion of the Great Lakes system by about 30 NIS. The recent increase in ballast water introductions including dreissenid mussels, ruffe, the spiny waterflea (*Bythotrephes cederstroemi*) and two species of gobies has spurred efforts to control this vector. Regulations are now in place in the United States under the Non-indigenous Aquatic Nuisance Species Prevention and Control Act of 1990 that call for the exchange of original ballast water in the open ocean before arrival in the Great Lakes. In Canada, similar regulations are under development and, in the meantime, voluntary guidelines for the exchange of ballast water are administered by the Canadian Coast Guard with about 90 percent compliance (Mills *et al.*, 1994). It is still too early to measure the overall efficacy of these actions in preventing unwanted introductions. Although the rate of invasion may decrease, it is likely that the Great Lakes system will continue to receive NIS, particularly from Eurasia (Mills *et al.*, 1993b; Carlton *et al.*, 1995). Mills *et al.* (1993b) have suggested that strategies be developed on a global scale for the prevention of spread and the control of invasive species. These include an inventory of potential invaders from other continents and a clearinghouse network among agencies in North America and donor regions worldwide to exchange information on ecological requirements and control methodologies. Efforts to improve our ability to predict new enemies and their potential damage to ecosystem health should be encouraged.

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