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Exotic species in large lakes of the world ☆

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Abstract

Many of the large lakes of the world have been exposed to the introduction of exotic species. We have reviewed here the introduction of aquatic species in 18 large lakes on five continents (Laurentian Great Lakes, African Great Lakes, several Canadian lakes, Lake Titicaca, Lake Baikal, Lake Ladoga, Gatun Lake, and Lake Biwa). We found that human activities, social preferences, and policy decisions are often associated with the spread of species in these large lakes. However, the spread and resulting ecological effects of introduced species varied among the case studies reviewed (ranging from the failure of brown trout introduction in Lake Titicaca to successful introduction of Nile Perch in Lake Victoria). Those species that did establish successful populations often had major impacts upon the ecosystems of these lakes via a variety of processes, including predation, disturbance, habitat modification and competition. Although introduction of predators often negatively impacted native species (e.g. Nile perch in Lake Victoria, peacock bass in Lake Gatun), species introduced to lower trophic levels (e.g. sardine in Lakes Kariba and Kivu, rainbow smelt in Canadian Lakes) affected fisheries and altered food web structure as well. Exotic species in large lakes of the world were not limited to fish species: plants (e.g. in Lakes Baikal and Biwa), invertebrates (e.g. in Lake Ladoga), and parasites and pathogens (e.g. in Lake Titicaca) have been introduced, but it was often difficult to discern the food web and ecosystem effects of these organisms. Exotic species also impacted socio-economic systems, having both positive (e.g. Lakes Victoria, Titicaca, Kivu, and Kariba, and the Laurentian Great Lakes) and negative (e.g. Lakes Victoria and Titicaca, and the Laurentian Great Lakes) repercussions for humans who depended upon these lakes for food and income. Unfortunately, our understanding of the impacts and extent of introductions on large lake ecosystems often remains speculative at best. The introduction and spread of exotic species will continue to threaten large lakes of the world into the twenty-first century. Exotic species introductions are a global problem that deserves global attention and understanding.

Keywords: Introduction of exotic species; Large lakes; Human activity in lakes

1. Introduction

Exotic species represent the most significant threat to indigenous biota throughout the world (Elton, 1958; Mooney and Drake, 1989; Office of Technology Assessment, 1993). The earth's biota is rapidly becoming homogenized due to the spread of non-indigenous species outside their native range (Heywood, 1989). For plants, exotics typically represent 10–30% of the flora of most regions, and within these regions, exotic plants may comprise 90% or more of the plant biomass (Heywood, 1989). The impact of these biological invasions on native species can be significant and wide-ranging. Exotic species not only have direct and indirect effects on the structure and function of aquatic and terrestrial ecosystems, they have economic impacts, they can impact food supplies

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and human health, and prevention and control of their growth can be extremely costly.

Centuries of colonization and commercial development have set the stage for fundamental biological alterations and modifications of ecosystems worldwide. In the United States alone, more than 30,000 nonindigenous species are estimated to have been introduced since Columbus first landed (Pimentel et al., 2000). More than 4500 exotic species have successfully established populations in the United States, including more than 2000 plant species, more than 2000 insect species, 239 plant pathogens, 142 terrestrial vertebrate species, 91 species of freshwater mollusks, and 70 species of fish (Office of Technology Assessment, 1993). Some of these exotic species have caused severe economic losses and environmental damage, while for most others the impacts are unknown.

In this review we focus on introduction of exotics into large aquatic ecosystems. Worldwide, exotic species have been introduced into aquatic ecosystems, for a variety of reasons that generally fit into the following categories (Welcomme, 1984, 1986, 1988; Courtenay and Taylor, 1986; Mills et al., 1993, 1994): (1) sports or recreation, to establish suitable sporting species in waters in which they were absent, often involving assortment of salmonids and centrarchids; (2) aquaculture; (3) ecological manipulation and improvement of wild stocks, attempts to fill vacant niches in fish communities, or to substitute for species judged commercially or recreationally inferior; (4) control of unwanted organisms, involving control of vector organisms (i.e. mosquitoes), control of aquatic vegetation in lakes and canals, and control of phytoplankton; (5) as ornaments, particularly goldfish (*Carassius auratus*), and for the aquarium fish trade; and (6) accidental transfers, including transfer of juvenile fishes with intended transfer of exotics, release from aquaria or by breeders, diffusion, ballast transport and construction of canals or other water diversions.

Exotic species have been introduced in aquatic ecosystems in countries throughout the world. Welcomme (1988), who compiled a register of international transfers of inland fishes and some crustaceans for the Food and Agriculture Organization of the United Nations, found that, since the 1960s, international introductions of exotic fishes and crustaceans have declined worldwide. Geographically, Welcomme (1988) indicated that introductions were more numerous in South America, Europe, and Africa, and less numerous in Middle East and North America. This work has not been updated in the 1990s so we do not know if these trends remain accurate. Regardless, the impacts of exotics on aquatic ecosystems are numerous and can be summarized into ecological impacts, including (1) habitat alterations, often caused by fishes and plants; (2) competition and predation; (3) disease and pathogens; and (4) hybridization and gene pool deterioration (Hoffman and Shubbert, 1984; Welcomme, 1984, 1988; Kohler and Courtenay, 1986; Mills et al., 1993, 1994).

In addition to biological and ecological impacts, exotic species in aquatic ecosystems have had strong socio-economic impacts world-wide which should not be overlooked. These include: (1) costs of prevention and control; (2) economic costs and benefits, on short-term and, perhaps more importantly, on long-term timescales; and (3) sociological impacts, including interruptions to subsistence lifestyles and unequal benefit sharing.

The economic costs of aquatic exotic species is significant. Pimentel et al. (2000) estimated conservative economic costs for exotic fishes alone cost Americans more than US$ one billion annually. Damage caused by and control of zebra mussel (*Dreissena polymorpha*), Asiatic clam (*Corbicula fluminea*) and the European green crab (*Littorina littorea*) cost Americans US$ 4.44 billion per year, purple loosestrife control costs US$ 45 million per year and aquatic weed control costs US$ 110 million per year (Office of Technology Assessment, 1993). Thus, these conservative estimates reveal that the economic costs of controlling exotic species in aquatic ecosystems is not trivial.

The objective of this paper is to synthesize case histories of the effects of exotic species introduced into large lakes of the world. Our approach was to focus on published literature. We did not exhaustively examine impacts of introductions of exotic species; instead, we intend this paper to serve as a springboard for further discussion and research into exotic species issues in large lakes and other systems throughout the world. We followed definitions of introduced species after Kohler and Stanley (1984) and Kohler (1986) '... a plant or animal moved from one place to another

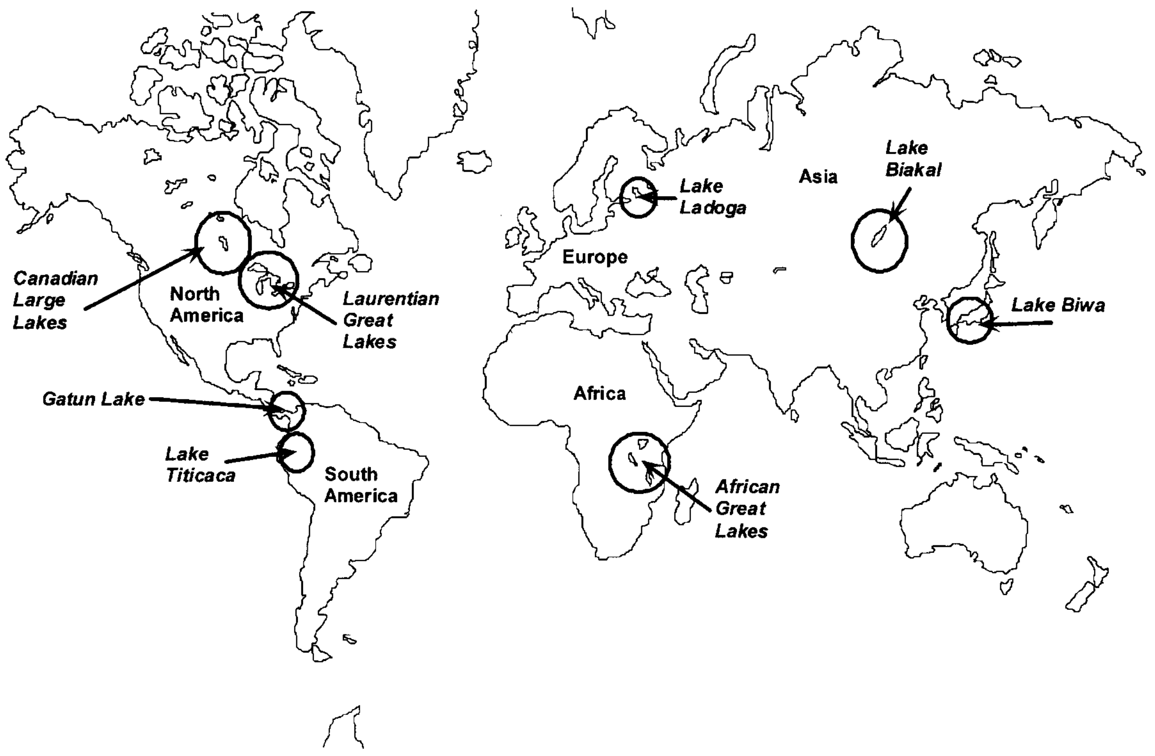

Fig. 1. Global map indicating location of large lakes discussed in text.

by man (i.e. an individual, group, or population or organisms that occur in a particular locale due to mans' actions)...' and after Welcomme (1988): 'Any species intentionally or accidentally transported and released by man into an environment outside its present range.' We define 'large' lakes rather loosely, ranging from truly large lakes, such as the Laurentian Great Lakes and the African Great Lakes, to smaller water bodies, such as Gatun Lake, Panama and Lake Biwa, Japan. These lakes represent a spectrum (both in terms of size and geography) of large and nationally important bodies of water (Fig. 1).

Our review concentrates on the spread and impacts of exotic species in the Laurentian Great Lakes (Lakes Erie, Huron, Michigan, Ontario, and Superior), African Great Lakes (Lakes Victoria, Kariba, Kivu, Malawi, and Tanganyika), several large Canadian lakes (Winnipeg, Manitoba, and Winnipegosis), Lake Titicaca (Peru–Bolivia), Gatun Lake (Panama), Lake Baikal (Russia), Lake Ladoga (Russia), and Lake Biwa (Japan) (Fig. 1). In each of these lakes, the impacts of exotic species have been noted. Combined, these lakes comprise over 62% of the world's freshwater lake resources, by volume (total volume of world's lakes = 125,000 km^3) (Wetzel, 1983; data from this review). Large scale modifications of these ecosystems caused by exotic species affect a majority of the world's lake resources. Thus, we feel the impacts of introductions of exotic species in these ecosystems deserve significant attention from scientists, managers and policy makers.

1.1. The Laurentian Great Lakes: a history of introduced species

The Laurentian Great Lakes, collectively the world's largest freshwater resource, provide perhaps the best documented case studies of the ecological and economic impacts of introductions of exotic species in large lakes of the world. The five Laurentian Great Lakes are among the largest lakes in the world (Table 1); they include: Lake Superior, Lake Huron, Lake

Table 1
Physical characteristics (surface area, volume, mean depth, and maximum depth) of and extent of exotic fish species introductions into Laurentian Great Lakes (data from Mills et al., 1993)

Lake	Surface area, volume, mean depth, maximum depth	Number of native species	Number of non-indigenous species	Percent introduced
Superior	82,100 km^2, 12,100 km^3, 147 m, 406 m	67	14	17
Michigan	57,800 km^2, 4,920 km^3, 85 m, 282 m	114	14	11
Huron	59,600 km^2, 3,540 km^3, 59 m, 229 m	99	16	14
Erie	27,500 km^2, 484 km^3, 19 m, 64 m	113	17	13
Ontario	18,960 km^2, 1,640 km^3, 86 m, 244 m	112	15	12

Michigan, Lake Erie and Lake Ontario (Fig. 2). Since the 1800s, some of the greatest ecological disasters in the Laurentian Great Lakes have resulted from exotic species. Furthermore, the cumulative effects of many exotic species on the natural structure of the Great Lakes ecosystems have compromised their biological integrity, and several species, such as the sea lamprey (*Petromyzon marinus*) and the zebra mussel

Fig. 2. Map of Laurentian Great Lakes.

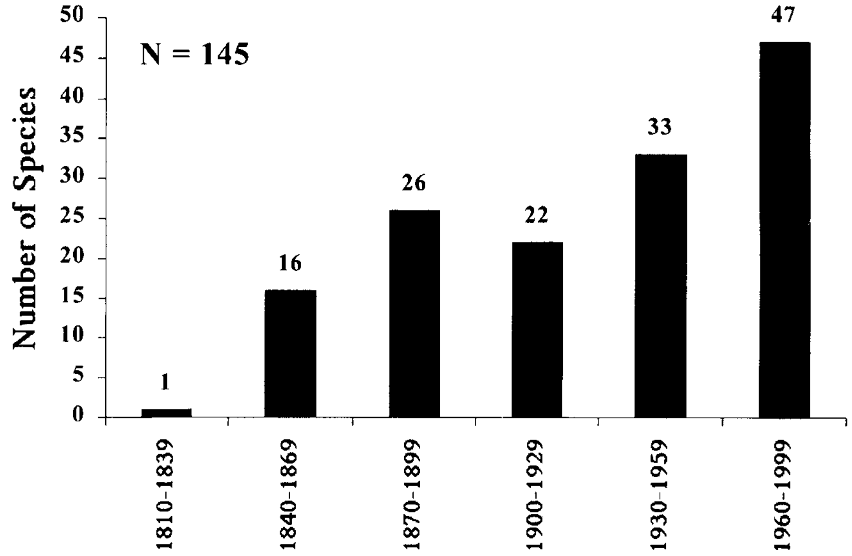

Fig. 3. Timeline of the introduction of exotic species into the Laurentian Great Lakes, 1810–1997 (from Mills et al. 1993).

(*Dreissena polymorpha*) have caused substantial economic hardship and ecological instability (Mills et al., 1993, 1994; Leach et al., 1998). The Laurentian Great Lakes play a major role in the economies of the eight states (United States) and one province (Canada) bordering their shores. Thus, both their ecological and economic well-being is important, and the harm caused to the systems by exotic species should serve as a warning to other nations with large lakes (Mills et al., 1993, 1994; Leach et al. 1998).

1.2. History of Great Lakes introductions and invasions

Introductions of exotic species into the Laurentian Great Lakes and the historical and present-day human activities are intricately intertwined. Exploration of the Great Lakes basin by Europeans commenced about four centuries ago and was followed by clearing of forests, settlement, and commercial development (Leach et al., 1998). The Great Lakes became the principal transportation route for this region of the United States and Canada, and large cities grew around strategic ports. The transport of goods was enhanced through the construction of canals (e.g. the Erie (1825) and the Welland (1829)) built to improve navigation for commerce and immigration into unsettled areas and to provide more direct transportation routes (Mills et al., 1999). By the late 1800s, a vast network of canals were constructed in northeastern North America, thereby dissolving natural barriers to the dispersal of freshwater organisms into the Laurentian Great Lakes (Mills et al., 1993). In 1959, construction of the St. Lawrence Seaway and hydroelectric facility was completed, allowing transoceanic ships to access the largest freshwater resources in North America (Mills et al., 1999). Almost one-third of the exotic species in the Laurentian Great Lakes have been introduced in the last 30 years. This surge corresponded with the opening of the St. Lawrence Seaway (Fig. 3; Mills et al., 1993).

All these lakes have been invaded by exotics, and each lake has experienced significant adverse effects. Exotic fish species now comprise 11–17% of the fish fauna of each of the Laurentian Great Lakes (Table 1). The sea lamprey (*Petromyzon marinus*) and the zebra mussel (*Dreissena polymorpha*) have caused significant ecological and economic impacts. Since the early 1800s, the Laurentian Great Lakes have been host to 145 known non-indigenous fishes, invertebrates, fish disease pathogens, plants and algae (Mills et al., 1993). Since some taxonomic groups have been well studied, while other groups have not, the true number of freshwater exotics in the Great Lakes is certainly more than 145. To date, plants and algae account for 60% of new species entering the Laurentian Great

Table 2
Number of invasive and introduced species established in the Great Lakes by taxonomic group and time period (data from Mills et al., 1993; Leach et al., 1998)

Period	Fishes	Invertebrates	Disease pathogens, parasites	Algae	Plants	Total
1810–1849	1				9	10
1850–1899	6	4			23	33
1900–1949	7	8	1	6	18	40
1950–1997	12	21	2	18	9	62
Total	26	33	3	24	59	145
Percent	18	23	2	17	40	100

Lakes basin since 1810, followed by invertebrates (22%) and fishes (18%) (Table 2; Leach et al., 1998).

1.3. Origins and entry vectors

Exotic species in the Laurentian Great Lakes are native to Europe and Asia (considered here as Eurasia), the Atlantic and Pacific Coasts of North America, the southern United States and the Mississippi River drainage system (Mills et al., 1994). Most exotic species in the Laurentian Great Lakes are native to Eurasia (57%) and the Atlantic Coast (13%). The large number of organisms introduced from Europe is most likely associated with the transport of goods by Europeans to the basin and the similar North-temperate climates in both Europe and the Laurentian Great Lakes region (Mills et al., 1994).

The entry mechanisms which have acted singly or jointly in the movement of organisms into the Great Lakes basin include: unintentional release (escape from cultivation, aquaculture and aquaria, and accidental releases due to fish stocking and from unused bait); deliberate releases (for example, the deliberate introduction of fish species to enhance fisheries); and canals, shipping, and disturbance linked to the construction of railroads and highways (Fig. 4).

The overall rate of establishment of new exotics to the Great Lakes for the past 30 years has been high (ca. 1.6 species per year) and continues to be high. The chronology of exotic species introductions since the 1800s indicate the importance of certain entry

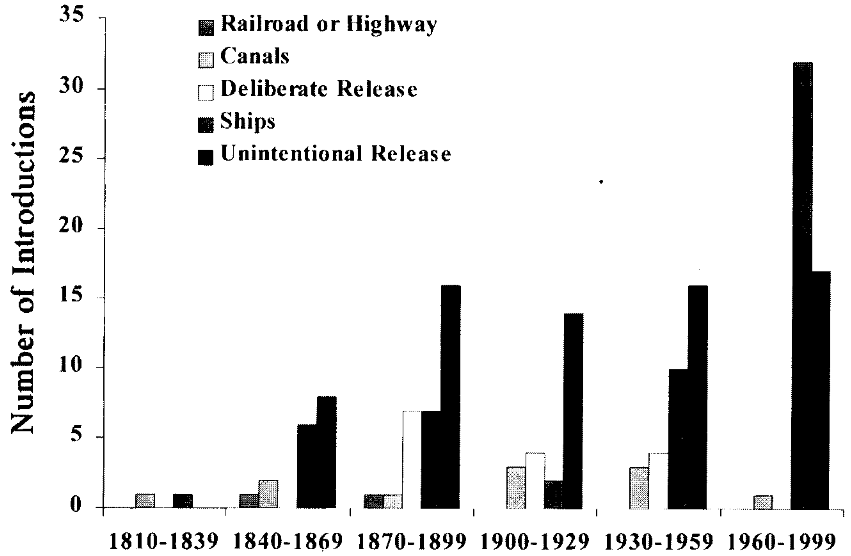

Fig. 4. Timeline of entry vectors of exotic species into the Laurentian Great Lakes (from Mills et al., 1993).

Table 3
Time of colonization and mechanism(s) impacting Great Lakes ecosystems resulting from unplanned species introductions (after Mills et al., 1993; Leach et al., 1998.)

Non-indigenous species	Origin	Time of colonization	Distribution[a]	Mechanism[b]			
				Habitat modification	Competition	Predation	Diseases and Parasites
Sea lampery	Atlantic	1830s	A	X		XX	
Purple loosestrife	Eurasia	1869	A	XX	XX		
Alewife	Atlantic	1873	A		XX	X	
Chinook salmon	Pacific	1873	A	X	XX	X	
Rainbow trout	Pacific	1876	A	X	XX	X	
Common carp	Asia	1879	A	XX	X		
Brown trout	Europe	1883	A	X	XX	X	
Aeromonas salmonicida	Unknown	1902					XX
Rainbow smelt	Altantic	1912	A		X	X	
Coho salmon	Pacific	1933	A	X	XX	X	
White perch	Atlantic	1950s	A		XX	X	
Eurasian milfoil	Eurasia	1952		XX	X		
Glugea hertwigi	Eurasia	1960					XX
Eurasian ruffe	Eurasia	1986	S		XX	X	
Dreissena spp.	Eurasia	1988	A	X	XX	X	
Round goby	Eurasia	1990	A		X	?	

[a] All Great Lakes (A), Superior (S).
[b] XX = major damage; X = minor damage; ? = uncertain.

Table 4
Degree of impact on ecosystem health of taxa of non-indigeneous species in the Great Lakes (data from Mills et al., 1993)

Degree of impact	Fishes	Invert	Disease pathogens, parasites	Algae	Plants
Very harmful	2	2	2		1
Harmful	4	3		1	2
Potentially harmful	4	3	1		9
Harmful and beneficial	7				
Unknown	10	24		23	47

vectors (Fig. 4). Historically, ships played an important role in the transfer of aquatic organisms, particularly in the late 1800s with the release of aquatic plants and invertebrates in the solid ballast materials. The surge in ship-related introduced species in recent times (particularly after the opening of the St. Lawrence Seaway to large ocean-going ships) has been associated with ballast water. Through ships, large volumes of foreign water and associated organisms have inoculated the Great Lakes. For all introduced species into the Great Lakes since the early 1800s, deliberate releases have declined, canal introductions have remained consistently low, railroad and highway migrations have been sporadic and unintentional introductions have been consistently high (Fig. 4).

1.4. Impacts of non-indigenous species on ecosystem health

The mechanisms for damage to Great Lakes ecosystems resulting from unplanned species introductions are many, including habitat modifications, competition, predation, associated disease pathogens and parasites and genetic effects (Krueger and May, 1991; Li and Moyle, 1993; Leach et al., 1998). For non-indigenous species having a significant impact (Table 3), competition involving introduced salmonids, alewife (*Alosa pseudoharengus*), white perch (*Morone americana*), Eurasian ruffe (*Gymnocephalus cernuus*), dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*) and purple loosestrife (*Lythrum salicaria*), has been a major factor impacting Great Lakes native species (Mills et al., 1993; Leach et al., 1998). Major changes in habitats of the Great Lakes have been linked with common carp (*Cyprinus carpio*) through disturbance of nearshore benthic habitats, and with the plants Eurasian milfoil (*Myriophyllum spicatum*) and purple loosestrife, through displacement of native plants (Table 3).

Several taxa have caused adverse predator–prey interactions on native species including sea lamprey, alewife, white perch and salmonids (Tables 3 and 4). The sea lamprey, a parasitic fish, has had a catastrophic impact on native lake trout (Lawrie, 1970). In the late 1960s, alewife populations accelerated the collapse of coregonid populations (e.g. lake whitefish (*Coregonus clupeaformis*) and bloater (*Coregonus hoyi*)), and negatively impacted yellow perch (*Perca flavescens*) and other native species (Smith, 1970; Brandt et al., 1987). The white perch gained access to the Laurentian Great Lakes through the Erie Canal (Christie 1973; Hurley 1986) where it has had substantial impacts on native fish species and community stability (Boileau, 1985). The introduction of salmonids, either deliberately to enhance the sport fishery or unintentionally, as in the case of pink salmon (*Oncorhynchus gorbuscha*), has had significant and permanent ecological (predation on native salmonids and other fishes and the introduction of parasites and diseases) and genetic effects (caused by interbreeding with native fishes) (Table 3). Most recently, these ecosystems have been invaded by a European amphipod (*Echinogammarus ishnus*; recently identified in Lake Erie; Witt et al., 1997) and blueback herring (*Alosa aestivalis*; MacNeill, 1998; Owens et al., 1998), and the fishhook water flea (*Cercopagis pengoi*; MacIsaac et al., 1999).

1.5. Management strategies and future invasions

The long history and high rates of biological invasions clearly indicate that the Great Lakes continue to be vulnerable to invasion. Consequently, future management strategies involving prevention and control of introduced species into the Laurentian

Table 5
Summary of reviewed case studies of introduction of exotic species into large lakes of the world, excluding Laurentian Great Lakes

Lake, Country	Surface area, volume, mean depth, maximum depth	English and Latin names of introduced species and date (if known)	Reasons[a]	Documented impacts (conclusive or speculative)
Lake Victoria (Kenya, Uganda, and Tanzania)	68,385 km^2, 2,700 km^3, 20 m, 79 m	Nile perch (*Lates niloticus*), 1950s and early 1960s	S, M	Decline of native cichlid species flocks (potentially 200 + species) Collapse of fishery from 100s to 3: Nile perch, *Rastrienobla argentea*, and exotic Nile tilapia (*Oreochomis niloticus*) Food web alterations: replacement of cichlids by prawn *Cardinia nilotica* and *R. argentea* Cyanobacteria blooms and severe periods of deoxygenation in the hypolimnion Various other ecosystem impacts Creation of industries, concommitant decline of subsistence fishery, and local deforestration
		Tilapias *Oreochromis nilotica*, *O. leucosticus*, and *Tipapia zillii*	M	*O. niloticus* replaced native *O. esculentus* offshore *O. leucostictus* thrived in low-oxygen areas *T. zillii* out-competed native *O variabilis* for nursery areas
Lake Kariba	5,364 km^2, 156.5 km^3, 29 m, 120 m	*Limnothrissa miodon*	M	Creation of pelagic fishery where none had existed previously (providing jobs and protein) Alteration of zooplankton community (species composition, mean size, and biomass) Potential competition with characid *Brycinus lateralis* Spread of *L. miodon* downstream of Lake Cahora Basa
Lake Kivu (Congo and Rwanda)	2,699 km^2, 583 km^3, 285 m, 485 m	*L. miodon* (possibly *Stolonthrissa tanganicae*), 1958–60	M	Creation of pelagic fishery where none had existed before (providing jobs and protein) Alterations of zooplankton community (species composition, mean size, and biomass) Potential *L. miodon* cannibalism
Lakes Winnipeg, Manitoba, and Wininpegosis	23,750 km^2, 284 km^3, 12 m, 36 m; 4,610 km^2, 22.8 km^3, 4.9 m, 37 m 5,510 km^2, 19.8 km^3, 4.2 m, 18.3 m, respectively	Rainbow smelt (*Osmerus mordax*), early 1990s	N	Provide prey for co-existing predators yielding potentially higher growth rates but potentially increased mercury uptake by piscovores Varying predation levels upon larvae of native fishes, particularly lake whitefish (*Coregonus clupeaformis*) and lake herring (*Coregonus artedii*) Competition: evidence is unclear Food web shifts likely
Lake Titicaca (Peru, Bolivia)	8,100 km^2, 893 km^3, 107 m, 281 m	Rainbow trout (*Salmo gairdneri*) and brown trout (*S. trutta*), 1935	S,M	Rapid expansion and collapse of rainbow trout fishery; promotion of cannery industry, closed in 1969 Reduction of species in pelagic zone to two (currently *Orestias ispi* and exotic *B. bonariensis* [below]) and role in extinction of *O. cuvieri* Outbreak of epizootic protozoan *Ichthyophthirius multifiliis*, impacting fishes (particularly *Orestias agassii*)

Table 5 (*continued*)

Lake, Country	Surface area, volume, mean depth, maximum depth	English and Latin names of introduced species and date (if known)	Reasons[a]	Documented impacts (conclusive or speculative)
		Pejerry (*Basilichthys bonariensis*), before 1955	U	Predation (particularly upon fingerlings) and competition (for food resources) effect upon rainbow trout, possibly causing decline of species
Gatun Lake (Panama)	425 km^2	Peacock bass (*Cichla ocellaris*), 1967	N, S	Elimination of six common species, significant reduction of 7th Altered food web structure (impacting zooplanktivores, tertiary consumers, primary consumers, and possibly primary producers) Resurgence of native fishes from refuge in Changres River, and from alternative prey source (exotics common carp (*Cypinus caprio*) and Nile tilapia
Lake Biakal (Russia)	31,550 km^2, 23,000 km^3, 740 m, 1741 m	Macrophyte *Elodea canadensis*, mid-1970s and early 1980s	N,	Covers bottom of many harbors, shallow bays, and sors Potential impacts upon native vegetation
Lake Ladoga (Russia)	18,135 km^2, 908 km^3, 51 m, 230 m	Amphipod *Gmelinoides fasciatus*	N (M)	High densities negatively impact native amphipod *Gammarus* and isopod *Asellus aquaticus* High probability of spread to other lakes as food for aquarium fishes
Lake Biwa (Japan)	674 km^2, 412 m, 110 m	Macrophytes *Elodena nuttallii* and *Egeria densa*, 1961 and 1969 (respectively)	U	Became dominant macrophytes in Biwa Impact upon limnological factors (light attenuation, nitrogen and phosphorus, B-group vitamins, chlorophyll *a*, and phytoplankton production in littoral zone
		Largemouth bass (*Micropterus salmoides*) and bluegill sunfish (*Lepomis gibbosus*)	N, S	Preyed upon native littoral fishes Reduced diverse community of native littoral fishes to three

[a] Reasons for introduction exotic species. S = Sport or recreational; A = Aquaculture; M = Ecological manipulation and improvement of stocks; C = Control; N = Non-purposeful or accidental transfers; and U = Unknown or not documented.

Great Lakes must learn from lessons of the past (i.e. the science) and develop policies that will reduce the risk of unplanned invaders.

The identification of ship ballast water as a major vector transporting unwanted organisms into the Laurentian Great Lakes has motivated control efforts (Leach et al., 1998). In 1990, the United States Congress passed the Nonindigenous Aquatic Species Act and by 1993, the first and only ballast water law in the world was adopted. The law required that ships that have operated outside the waters of the United States and Canada, and that intend to enter the Laurentian Great Lakes with ballast water, must have exchanged that water on the high seas (Mills et al., 1994). In the Water Resources Act of 1992, the ballast water exchange requirement was extended to ships entering the Hudson River (which connects the Laurentian Great Lakes via the Erie Canal). Ballast water exchange reduces the risk of invasion but does not totally eliminate future invaders (Leach et al., 1998). For example, while full saline salt water may kill freshwater organisms, it may not kill brackish or estuarine water species. The recent introduction of the amphipod *Echinogammarus ischnus* and the waterflea *Cercopagis pengoi* to the Great Lakes illustrate this point as they are native to the Ponto-Caspian region and they possess broad salinity tolerance (MacIsaac and Grigorovich, 1999). Future invaders can also enter the Great Lakes in ships with no ballast on board or when in-lake ballasting and deballasting disturbs/suspends and ejects residual sediments. Ships that contain sedimented material in the hull can pose a potential threat, as resting spores of foreign freshwater organisms are known to remain viable in these sediments (Hallegraeff and Bolch, 1992; Kelly, 1993). Reports in 1994 of specimens of the non-reproducing Chinese mitten crab (*Eriocheir sinensis*) and European flounder (*Platichthys flesus*) in the Laurentian Great Lakes point to the fact that current ballast water management strategies only reduce risk. As a result, ballast water management strategies in the future should consider alternative or complementary strategies such as ship design, thermal, microfiltration, ultraviolet treatment and use of ozone to remove organisms destined for the Laurentian Great Lakes.

Mills et al. (1993) have shown that nearly two-thirds of non-indigenous species established in the Laurentian Great Lakes have arrived via two vectors: unintentional releases (34%) and shipping activities (31%). Since 1960, these two entry mechanisms have been responsible for 98% of all new introductions. Mills et al. (1993) suggest that vector management is important in order to make progress toward preventing unwanted organisms from becoming established in the Laurentian Great Lakes. Both shipping activities and unintentional introductions in the private sector will need to be addressed by policy makers and lawmakers in the future.

2. Great Lakes of Africa

2.1. Lake Victoria

'Complex ecosystems, with their many species and rich interaction structure, are considered to be, in general, dynamically fragile. Although the communities in these ecosystems are considered to be able to thrive in predictable, resistant environments, they are likely to be more vulnerable to perturbations imposed by man than are communities in relatively simple but more robust systems' (May, 1975).

In the past, Lake Victoria had a species and interaction rich ecosystem, but man has significantly altered this dynamically fragile lake. Lake Victoria is the largest tropical lake and the third largest lake in the world (Table 5), and it is a crucial economic resource for over 30 million people inhabiting its shores in Kenya, Uganda and Tanzania (Fig. 5).

2.1.1. Lake Victoria prior to introduction of exotic fish species

Lake Victoria, like its East African neighbors Lakes Malawi and Tanganyika, exhibited rapid, endemic, and presumably monophyletic speciation of the family Cichlidae (Greenwood, 1974; Meyer et al., 1990; Goldschmidt et al., 1993). The flock of 300 + species occupied a great variety of niches in the lake (Witte et al., 1992a), and an assemblage of haplochromine cichlids exploited each habitat type (Barel et al., 1985; Witte et al. 1992a; the review in Goldschmidt et al., 1993). Cichlids occupy a wide range of trophic specialization but a narrow range of reproductive guilds (Balon, 1975; Bruton, 1990). Cichlids typically invest heavily in relatively few young, exhibit extended parental care, defend nests and young, have limited dispersal abilities, and have strong site attachment (Bruton, 1990). In theory, these characteristics should make them vulnerable to extinction (Jablonski, 1986; Gaston and Lawton, 1990; Kaufman, 1992). However, cichlids are also aggressive, behaviorally and physiologically adaptable, and phenotypically plastic (Fryer and Iles, 1972). Furthermore, they can alter the duration and timing of ontogenetic events to shift from altricial to precocial homeorhetic states so that these fishes are quite flexible, and the effects of biotic and abiotic factors in their environment determine the behavior that they exhibit (Bruton, 1990).

Prior to the introduction of exotics, native fisheries in Lake Victoria were impacted by overfishing and lack of regulations, promoting their decline. Early surveys (Worthington, 1929 and Graham, 1929, in Ogutu-Ohwaya, 1990a) showed that tilapiine cichlid species *Oreochromis esculentus* and *Oreochromis variabilis* dominated native commercial fisheries; other important species included *Protopterus aethiopicus*, *Bagrus docmac*, *Clarias gariepinus*, *Barbus* spp., mormyrids and *Schilbe mystus* (Ogutu-Ohwaya, 1990a). Haplochromine cichlids were common in catches but usually not heavily exploited on a large scale (Ogutu-Ohwaya, 1990a). The earliest subsistence fisheries consisted of locally made basket traps, hooks and seine nets of papyrus. Although pressure upon fisheries stocks was originally low, the introduction of more efficient gill nets in 1908 (Ogutu-Ohwaya, 1990a) permitted increased and more efficient fishing effort. Stocks of *Oreochromis esculentus* declined significantly by 1920 as development of urban centers and improved communication created increased demand for fish from Lake Victoria (Ogutu-Ohwaya, 1990a). Despite early efforts to manage the fisheries of Lake Victoria (via mesh restrictions on gill nets), the fishing industry continued to expand as markets and communication continued to improve (Ogutu-Ohwaya, 1990a). When catches declined in gillnets of standard mesh sizes, fishermen began to shift to smaller meshed nets, soon followed by removal of mesh restrictions in the three neighboring countries altogether (Ogutu-Ohwaya, 1990a; Reidmiller, 1994), thereby ending uniform management policy for the entire lake.

As stocks of the larger fish species of Lake Victoria declined, fishermen directed increased effort at smaller species, particularly for *Rastrineobola argentae* and haplochromine cichlids. However, the biology of haplochromines prevented the species flocks from withstanding and recovering quickly from heavy commercial fishing pressure (Ogutu-Ohwaya, 1990a). Consequently, unregulated fishing pressure on native fisheries, including cichlid species flocks, probably contributed to (but did not fully cause) their decline in Lake Victoria.

2.1.2. The introduction of fish species into Lake Victoria

The Nile perch *Lates niloticus* and several tilapiine species, *Oreochromis niloticus*, *Orechromis leucostictus* and *Tilapia zillii* were introduced into Lake Victoria in the 1950s and early 1960s. *Tilapia zillii* was introduced to feed on macrophytes which were not being used by commercially valuable species, and *Oreochromis niloticus* and *Oreochromis leucostictus* probably were introduced to supplement stocks of overfished native *Oreochromis* (Ogutu-Ohwaya, 1990a). The colonial administrators of the countries surrounding Lake Victoria introduced *Lates niloticus* with the belief that it would feed upon haplochromine cichlids and convert them into a suitable 'table' fish (Ogutu-Ohwaya, 1990a). The officials who initiated stocking of *Lates niloticus* also found the piscivore favorable because it was large, easily caught and was preferred by anglers. Apparently, officials did not consider the potential value of haplochromine fishes as food for numerous local groups (Eccles, 1985; Barlow and Lisle, 1987) or the difficulties of preserving and marketing large perch caught by small, scattered fishing units (Eccles, 1985). Additionally, Lake Victoria was stocked before any rigorous analyses of similar stockings in Lake Kyoga or Lake Nabugabo (Barlow and Lisle, 1987) were completed. As well, the stockings occurred despite significant scientific debate surrounding them (e.g. Fryer, 1960). Although caught in only small quantities throughout the 1960s and 1970s, populations of Nile perch rapidly expanded in the early 1980s (Barel et al., 1985; Hughes, 1986; Ogutu-Ohwaya, 1990a–c; Ochumba, 1995). The proportion of Nile perch in commercial catches increased from 1.1% of total landings in 1977 to 69.1% of total landings in 1987 in the Kenyan part of Lake Victoria (Fig. 6), and total landings increased from 19,000 tonnes in 1977 to as high as 225,000 tonnes in 1989 (Ochumba, 1995).

The reproductive and feeding biology of Nile perch largely explains their dramatic numeric increase in Lake Victoria. A mature female Nile perch can produce as many as 8–11 million eggs, and high fecundity permitted rapid establishment in favorable conditions (Ogutu-Ohwaya, 1988). Additional biological characteristics such as size of first maturity, favorable sex ratios, prolonged breeding seasons, a fast growth rate, and a long lifespan favored Nile perch. Numerous large areas of shallow, oxygenated inshore areas in Lake Victoria also provided optimal habitat for Nile perch (Ogutu-Ohwaya, 1988). Furthermore, large numbers of vulnerable prey, particularly haplochromine cichlids, inhabited inshore areas (Ogutu-Ohwaya, 1988).

2.1.3. Impact of introduced Tilapias and Nile Perch

Introduced tilapias and Nile perch had major impacts upon the ecosystem of Lake Victoria. The introduced tilapias (*Oreochromis niloticus*, *Oreochromis leucostictus* and *Tilapia zillii*) replaced the two endemic tilapia species (*Oreochromis. variabilis* and *Oreochromis esculentus*). This displacement occurred through a variety of mechanisms. *Tilapia zillii* out-competed *Oreochromis variabilis* for nursery areas. *Oreochromis leucostictus* thrived in suboptimal habitat in inshore areas where dissolved oxygen was lowest, and *Oreochromis niloticus* replaced *Oreochromis esculentus* offshore (Welcomme, 1964, 1966; Reinthal and Kling, 1994).

We have chosen to focus upon the impacts of Nile perch, however, which were more catastrophic and more thoroughly documented. As Nile perch densities increased, a fish community of more than 400 species collapsed into just three co-dominants: the introduced Nile perch and Nile tilapia, and a single indigenous species, *Rastrineobola argentea*. The cichlid populations monitored in the Mwanza Gulf of Lake Victoria drastically declined (Okemwa, 1984; Barel et al., 1985; Hughes, 1986; Ogutu-Ohwaya, 1990a–c; Witte et al., 1992a), mostly between 1977 and 1982 (Kaufman, 1992; Witte et al., 1992a). Some dispute over the cause of the decline existed (review in Witte et al., 1992a): critics argued that overfishing was a major cause of the decline. While overfishing has probably some effect on haplochromines (Marten, 1979; Witte, 1981), high fishing pressure on haplochromines existed only locally in the littoral and sub-littoral zone near densely populated areas (Witte et al., 1992a). Furthermore, the haplochromine fishery never resulted in the complete eradication of a haplochromine community in any habitat, although it did cause the local disappearance of certain species (Marten, 1979). In contrast, the lake-wide Nile perch boom coincided with the disappearance of complete communities, even in areas where fishing pressure was absent (Witte et al., 1992a). Thus, predation pressure from Nile perch was a major cause of decline of native fish species (Witte et al., 1992a,b; Goldschmidt et al., 1993). Over 200 species had been eradicated or were threatened with extinction following the introduction of Nile perch (Witte et al., 1992a).

The food web of Lake Victoria and the diets of Nile perch changed as haplochromine cichlids were replaced by *Caridina nilotica*, *Rastrineobola*, and Nile perch. In sublittoral regions of Lake Victoria, detrivorous, phytoplanktivorous, and zooplanktivorous cichlids once constituted more than 56% of the demersal fish mass (Witte et al., 1992a). These groups were replaced by the native detritivorous atyid prawn *Caridina nilotica* and by the native, zooplanktivorous, and highly fecund cyprinid *Rastrineobola argentea* (Ligtvoet and Witte, 1991; Goldschmidt et al., 1993). Blooms of cyanobacteria in some areas of the lake accompanied the loss of phytoplanktivorous haplochromines and increased nutrient loadings into the lake (Witte et al., 1992b; Goldschmidt et al., 1993). Additionally, the diet of Nile perch shifted from haplochromines, which were their major prey, to *Caridina*, *Rastrineobola*, and its own young (Ogutu-Ohwaya, 1990c).

These changes radically simplified Lake Victoria's food web. The loss or reduction of species from highly interrelated ecosystems such as Lake Victoria's tightly linked food web often has cascading effects (Bruton, 1990). For example, haplochromines tightly recycled nutrients and moved biomass and nutrients via vertical and horizontal migrations (Kaufman, 1992). Nile perch may have decoupled the nutrient cycling capacity of Lake Victoria by converting cichlid biomass into Nile perch biomass (Kaufman, 1992). It has not been established that the links from detritus to *Caridina* to Nile perch are indeed less ecologically and energetically efficient than the previous, complex foodweb (Kaufman, 1992). However, decoupled biological recycling capacity of the lake, combined with a long-term increase of nutrients into the lake (and subsequent algal growth), may have caused a buildup of biomass on the bottom of the lake's deeper waters. Because of high oxygen demand in these regions, the formerly well-mixed, well-oxygenated hypolimnion of Lake Victoria has shown frequent, severe deoxygenation periods (Kaufman, 1992). Thus, haplochromines faced intense predation pressure from Nile perch and loss of habitat in hypoxic waters (Kaufman, 1992).

The introduction of exotic species into Lake Victoria has clearly been an ecological disaster, but expectations were high from a fisheries management and socio-economic perspective. High yields of Nile perch attracted investors and provided a basis for a lucrative business (Kaufman, 1992). In Uganda and Kenya, industries have been established to process Nile perch (Bruton, 1990; Kaufman, 1992; Kitchell et al., 1997), and Nile perch is the most profitable and important fishery in the Tanzanian part of Lake

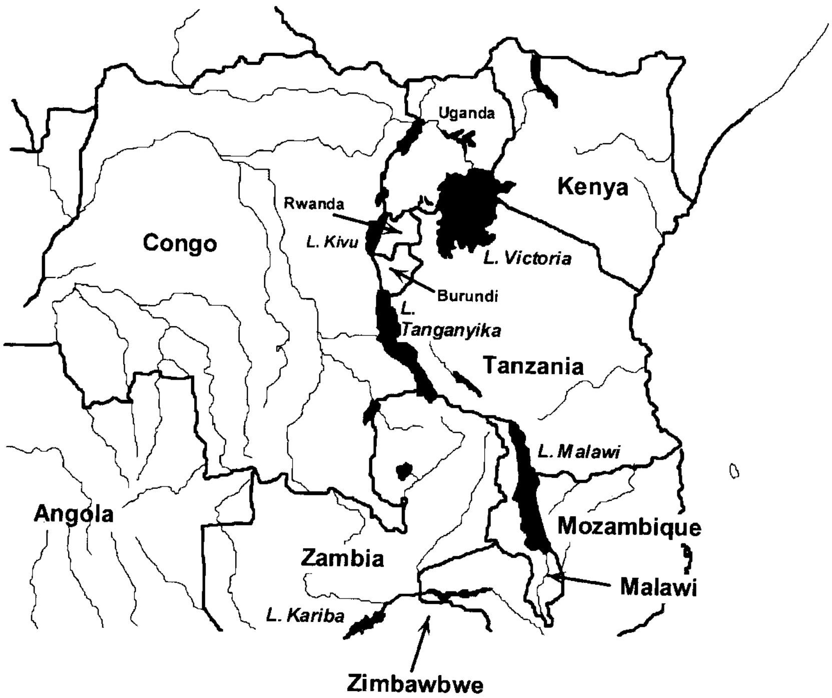

Fig. 5. Map of Central Africa, showing African Great Lakes discussed in text.

Victoria (Bruton, 1990; Kaufman, 1992). Wealthy individuals with sufficient capital to purchase larger, stronger, and more expensive nets to capture and refrigerate Nile perch have benefited (Barel et al., 1985; Kaufman, 1992; Reidmiller, 1994). The Nile perch fishery produced 150,000 new jobs and threefold net economic benefits to the region, particularly in areas where unemployment was high (Greboval, 1990; Kitchell et al., 1997). But social and economic benefits of the Nile perch fishery harmed others (Reidmiller, 1994; Kitchell et al., 1997). For instance, because of the large size and oily nature of *Lates*, local people harvested trees to smoke their catches, creating local deforestation problems in surrounding areas (Barel et al., 1985; Reidmiller, 1994). Previously, the traditional artisan fishery depended upon sun-dried tilapia and haplochromines, but these fishermen have not been able to compete (Reidmiller, 1994). Thus, the lake has become an unpredictable support base for subsistence and artisan fishermen in one of the world's most rapidly growing human populations (Bruton, 1990).

2.1.4. Current status of Lake Victoria fisheries

It is clear that the ecosystem of Lake Victoria cannot be restored to ancestral condition because many endemic species are extinct, habitats have changed due to continuing cultural eutrophication, and the inertia of the current fishery is enormous (Kitchell et al., 1997). It is difficult to make predictions about the future status of haplochromine fishes because the ecosystem is currently ecologically and limnologically unstable (Witte et al., 1992a). Anecdotal evidence suggests an increase of phytoplankton, macrophytes (e.g. *Ceratophyllum demersum* and the exotic *Eichornia crassipes*, whose spread has unknown effects), mollusks, chironomids and chaoborids, snails and diseases which accompany them, and oligochaetes, and the decrease of bordering papyrus swamps (Kaufman, 1992; Witte et al., 1992; Ogutu-Ohwaya, 1994, in Chapman et al., 1996; Chapman et al., 1996; Kitchell et al., 1997). These changes effect existing organisms in various ways, often creating large fish kills in the lake associated with deoxygenation of the hypolimnion and blooms of cyanobacteria (Ochumba and Kibaara, 1989;

Kaufman, 1992; Kitchell et al., 1997). Reportedly, haplochromines have reappeared in the shallow littoral areas of Lake Victoria (Ogutu-Ohwaya, 1990b), perhaps aided by structure and low-oxygen refugia provided by surrounding wetlands (Chapman et al., 1996). Survival of sub-littoral and deepwater fish assemblages seems less probable (Witte et al., 1992a). Meanwhile, Nile perch catches, which had peaked during the 1985–1990 period, are now declining despite increases of fishing effort (Fig. 6) (Pitcher and Bundy, 1994; Reidmiller, 1994; Kitchell et al., 1997). Little data exists on Nile perch abundance and age distribution, so estimates of fisheries yield are not available (Reidmiller, 1994; Kitchell et al., 1997).

Several conservation measures have been proposed for Lake Victoria and its haplochromine cichlids by Bruton (1990). They include: (1) captive propagation, which requires sufficient funding and amelioration of the current problem and involves dangers of artificial and relaxed selection and genetic bottlenecks; (2) reduction of Nile perch stocks (but the intensive fishing effort that is required to sufficiently reduce Nile perch stocks is not thought to be possible); and (3) closure of the trawl fishery to reduce overfishing on haplochromines. As well, (4) establishment of nature reserves on remote, lightly fished areas may provide refugia from fishing mortality. However, the philopatry and stenotrophy of many cichlids permits conservation of only local cichlids. There is a need for increased, internationally supported research of a lack of fundamental data, both quantitative and qualitative, relative to the biological effects of Nile perch, Nile tilapia, and other introductions upon Lake Victoria. Modeling efforts such as Kitchell et al. (1997) should continue. Ogutu-Ohwaya (1990a) has proposed that enforced regulations and effective management of Lake Victoria's fisheries should be a crucial part of conservation efforts.

2.2. Lake Kivu and Lake Kariba

2.2.1. Lake Kariba

Lake Kariba is a large man-made lake (Table 5) located on the Zambezi River and forming the border between Zimbabwe and Zambia (Fig. 5). Before it was created, managers believed that none of the indigenous riverine fishes would colonize Kariba's pelagic waters (Jackson, 1961, in Marshall, 1991). Subsequently *Limnothrissa* was introduced from Lake Tanganyika into Kariba, colonized the entire lake by 1970, and spread into the Zambezi River and the Canhora Basa Reservoir (Marshall, 1991). By 1973, commercial fishing for *Limnothrissa* began, and the fishery grew rapidly (Marshall, 1991). Annual yields exceeded 20,000 tonnes by the mid- to late 1980s, providing the most substantial fishery in the lake (Marshall, 1991), a million dollar industry (Harris et al., 1995) and room for continued exploitation (Pitcher and Bundy, 1994; review in Harris et al., 1995). Thus, the introduction of *Limnothrissa* into Kariba brought economic development and job creation where none had existed previously (Marshall, 1991). Consequently, from a socio-economic perspective, some considered the introduction of the sardine into Lake Kariba to be a success (Marshall, 1991).

Despite the socio-economic benefits of *Limnothrissa* in Lake Kariba, its introduction has impacted the lake ecosystem. For instance, *Limnothrissa* does compete with a characid species, *Brycinus lateralis*, for zooplankton (Marshall, 1991). It is possible that *Brycinus* may have filled the empty pelagic niche now dominated by *Limnothrissa* (Marshall, 1991). However, *Byrcinus* may have been limited by a lack of suitable breeding habitat regardless of the presence of *Limnothrissa* (Marshall, 1991). Furthermore, *Brycinus* is not a particularly desirable commercial fish species, and its populations are still abundant in nearshore areas where the species occupies a niche separate from the sardine. Additionally, increased populations of *Limnothrissa* may have indirectly caused a rapid decline of the floating fern *Salvinia molesta* (Marshall, 1991). After the creation of Kariba in the 1960s, an outbreak of *Salvinia* covered 22% of the lake (Machena and Kautsky, 1988; Marshall, 1991). *Salvinia* played an important role in retaining plant nutrients and may have restricted nutrient availability to other communities (Machena and Kautsky, 1988; Marshall, 1991).

Perhaps more importantly, the planktivorous *Limnothrissa* impacted Kariba's zooplankton community (Marshall, 1991). Before the introduction of sardines, larger cladocerans, such as *Ceriodaphnia* and *Diaphanosoma*, and diaptomid copepods dominated the zooplankton community. *Chaoborus* larvae

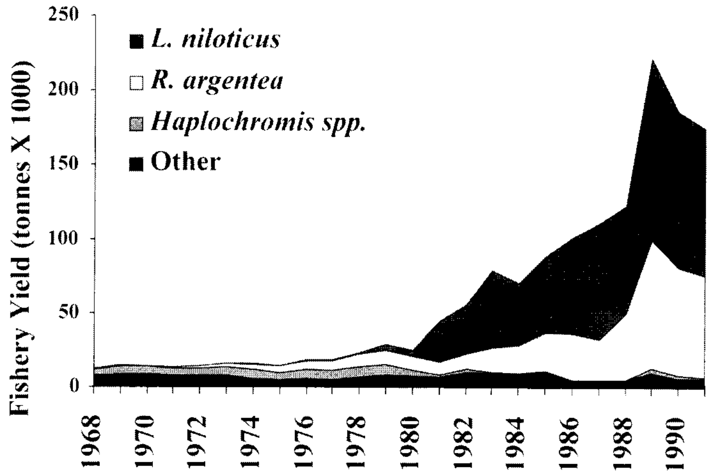

Fig. 6. Total catch (tonnes) of fishes from the Kenyan part of Lake Victoria. "Other" fishes consist of tilapiines, Clarias, Bagrus, and Protopterus (From Ochumba 1995).

were the major predators upon zooplankton, and small cladocera and rotifers were relatively unimportant to the community. Since the introduction of sardines, *Chaoborus* has become extinct in the lake, presumably because of size-selective predation by sardines (Lynch, 1979; Marshall, 1991). The larger cladocerans and diaptomids also declined rapidly, with smaller species and copepod nauplii becoming increasingly important (Marshall, 1991). Additionally, biomass of zooplankton declined dramatically throughout the pelagic areas of the lake (Marshall, 1991). Associated changes in the zooplankton community of Lake Kariba would be expected to cause changes in lower trophic levels (e.g. Carpenter et al., 1987; McQueen et al., 1989), but data are insufficient to make such conclusions (Marshall, 1991).

Despite impacts upon zooplankton communities, the introduction of *Limnothrissa* into Lake Kariba has created little criticism. Except for perhaps *Brycinus*, none of the 40 species of indigenous fish in Kariba seem to be affected either directly or indirectly by the introduction of *Limnothrissa*. Instead, overall inshore fish production varies with fluctuations in hydrologic regime and subsequent nutrient loadings (Karenge and Kolding, 1995). The introduction of *Limnothrissa* did impact the food web structure of this large man-made lake but also produced a productive fishery that has had positive socio-economic benefits (Marshall, 1991). The species will likely be considered for introduction into African impoundments in the future (Pitcher, 1995).

2.2.2. Lake Kivu

More debate surrounds the establishment of *Limnothrissa* into Lake Kivu (Table 5). Located in the western Rift Valley, Lake Kivu forms a natural border of more than 100 km between Zaire and Rwanda. Kivu is a relatively young lake, formed by a volcanic dam 20,000 years ago (De Inough et al., 1995) (Fig. 5). Due to steep shores, the littoral zone is relatively less important than pelagic areas of the lake (Beadle, 1974).

The relative paucity of Kivu's fauna made introduction of exotic fish species seem attractive to managers. The impoverished fish community of Lake Kivu resulted from Kivu's ecological immaturity and from waterfalls which prevented migration of fishes from Lake Tanganyika (De Inough et al., 1995). Until 1980 the fauna consisted of only 16 species of fish, belonging to the families Cyprinidae and Clariidae, and had little similarity to the fauna of ancient Rift Valley lakes, such as Lake Tanganyika (De Inough et al., 1995). Several niches of the ecosystem of Lake Kivu were not occupied; for instance, the absence of pelagic zooplanktivores and their predators implied to managers that zooplankton resources were not being used (De Inough et al., 1983; Verbeke, 1957a, in De Inough et al., 1995).

Consequently, between 1958–1960, thousands of clupeid sardines (*Limnothrissa miodon* and perhaps *Stolothrissa tanganicae*) from Lake Tanganyika were transported to Lake Kivu, and in 1976 an expedition recorded the presence of *Limnothrissa* throughout the lake (De Inough et al., 1983; Frank et al., 1977, in De Inough et al., 1995).

Since its introduction, adult *Limnothrissa* have impacted the pelagic ecosystem of Lake Kivu. In 1953, the zooplankton community consisted of relatively large, distinctly pigmented Copepoda and Cladocera (average size 0.6 mm, maximum 1.5 mm), and was dominated by *Daphnia curvirostris* (Dumont, 1986). Mean yearly biomass of plankton was estimated at 7.5 g m^{-3} dry weight. By 1981, the zooplankton community had shifted from *Daphnia curvirostris* (which disappeared) to at least eight species of smaller bodied rotifers and four small species of Cladocera (De Inough et al., 1995). However, most species of copepods (i.e. *Tropocyclops confinis*, *Thermocyclops consimilis*, and *Mesocyclops* sp.) remained in the lake (De Inough et al., 1983). Despite the increase of the number of zooplankton species, the mean annual biomass had decreased to 0.05–0.15 g m^{-3} dry weight, while average size declined to 0.2 mm (Dumont, 1986; De Inough et al., 1995). These impacts were interpreted as the result of heavy size-selective predation on the zooplankton by *Limnothrissa* (Dumont, 1986; Marshall, 1991; De Inough et al., 1995). Furthermore, cannibalism is frequently recorded by *Limnothrissa* in Kivu (e.g. De Inough et al., 1983; Dumont, 1986). Dumont (1986) concluded that stocks of *Limnothrissa* had become unstable (due to overgrazing of resources and cannibalism) and that the stocks would collapse. However, this collapse has not yet been documented (De Inough et al., 1995).

The introduction of *Limnothrissa* into Lake Kivu created an artisanal fishery and has had notable socio-economic effects. Beginning in 1976, an artisanal light-fishing technique developed with average yields per fishing unit of 43.6 kg per night and production increased from 66.5 tonnes in 1981 to 370.1 tonnes in 1987 with maximum sustainable yield estimates ranging from 2250 tonnes to 11,300 tonnes to 30,000 tonnes (De Inough et al., 1995). The socio-economic benefits of the sardine exploitation have been the development of labor-intensive fisheries in areas with high unemployment, and a protein source in densely populated and protein-deficient Rwanda. Increased extension and awareness campaigns need to be undertaken to promote use of the fishery (particularly after the disruptions caused by recent war) (De Inough et al., 1995). However, introduction of semi-industrial fisheries and purse seining may reduce the benefits to the artisanal fishery in the future (De Inough et al., 1995).

2.2.3. Lake Malawi

Lake Malawi is the third largest lake in Africa (Table 5; Lowe-McConnell, 1993; Fig. 5). Malawi is thought to have over 500 cichlid species, the highest diversity of cichlid fishes in any African lake (Kaufman, 1992). Malawi also has a flock of four endemic tilapias, a unique flock of at least 12 species of clariid catfish (*Dinopterus* spp.), endemic cyprinids, some large cyprinids (*Barbus* spp., *Labeo* spp., and *Opsaridium* spp.), and the endemic cyprinid *Engraulicypris sardella*, which supports a pelagic fishery (Lowe-McConnell, 1993). Lake Malawi currently has no documented examples of introduced species (Pitcher and Hart, 1995).

Local national governments have considered stocking Lake Malawi with two clupeid fish species, *Limnothrissa miodon* and *Stolothrissa tanganicae*, from Lake Tanganyika. Turner (1982) in Marshall, (1991) believed that the presence of *Chaoborus* in Malawi indicated an inefficient transfer of energy from zooplankton to native zooplanktivorous fish compared with the transfer of energy to *Limnothrissa* in Tanganyika, where *Chaoborus* were absent (presumably due to predation or competition). Thus, he promoted stocking Lake Malawi with *Limnothrissa* and *Stolothrissa* to more efficiently use zooplankton resources wasted by indigenous fishes (Eccles, 1985; McKaye et al., 1985).

It is unlikely, however, that introduced fishes would increase total fisheries yield in Lake Malawi. Current yields of pelagic fishes, such as the endemic cyprinid *Rastrineobola sardella*, cichlids *Rhamphochromis*, and the catfish *Synodontis* currently are higher than that modeled for *Limnothrissa* (Pitcher, 1995). Furthermore, the discovery of large, numerous, and truly pelagic and zooplanktivorous *Diplotaxodon* species confirms that there are no trophic opportunities for *Limnothrissa* (Turner, 1994, 1995; Pitcher, 1995). Production of pelagic fishes is limited by production of zooplankton, reducing the probability that an introduced sardine could improve current ecological efficiency (Pitcher, 1995). Introduction of predatory species (such as Nile perch) to convert smaller fish into larger fish would not increase the total production of the fisheries of Lake Malawi, because of a huge loss of energy (91.8%) (Pitcher, 1995) in the conversion of biomass between trophic levels (Turner, 1995).

However, pressure to introduce species and increase fish yields from Lake Malawi may increase. The ethical case against fish introductions can be based on the intrinsic value of endemic species flocks. However, a large, rapidly growing (3% per year in addition to refugees from the war in Mozambique) and undernourished populations surrounding the lake are pitted against such ethical arguments. Yet, the existing lake fisheries already supply 50% of the animal protein in the country (Pitcher, 1995). Pitcher (1995) suggested that a sustainable Nile perch catch could produce between 13,000 and 60,000 tonnes, potentially worth US$ 16–73 million. These figures are 1.5–4 times higher than the current fishery yield, and the fishery would provide foreign currency (Pitcher, 1995). However, Nile perch most likely would drastically alter the ecosystem, could collapse existing fisheries (possibly excluding pelagic planktivores, which survived in Lake Victoria following *Lates* introduction), would not alleviate current food and protein shortages, and could cause major socio-economic changes. Consequently, the balance of costs and benefits favors neither a sardine nor a Nile perch introduction into Lake Malawi (Pitcher 1995).

2.2.4. Lake Tanganyika

Similar to Lake Malawi, Lake Tanganyika has no documented introduced species (Pitcher and Hart, 1995). Lake Tanganyika drains westward via the Lukaga River to the Zaire system and is the second deepest lake in the world (Table 5; Lowe-McConnell, 1993; Fig. 5). It is permanently stratified and has an anoxic hypolimnion (Lowe-McConnell, 1993). The lake has more families of fishes than any other lake in the world. It has over 287 species of fish, 220 + which are endemic, and 172 of which are cichlids, nearly all endemic (Lowe-McConnell, 1993). Tanganyika's cichlids have differentiated more greatly than those of other African lakes, reflecting the older age of the lake (Lowe-McConnell, 1993). Of the 115 non-cichlids, 53 are endemic (Lowe-McConnell, 1993).

In contrast to Lakes Victoria and Malawi, Tanganyika's fisheries are supported by six pelagic species. These species include two clupeid sardines (*Limnothrissa miodon* and *Stolothrissa tanganicae*) and four predators *Lates mariae*, *Lates angustifrons*, *Lates microlepis* and *Lates stappersi* (Lowe-McConnell, 1993; Pearse, 1995). Since industrial-scale exploitation of fisheries stocks in 1959, only *Stolothrissa tanganicae* and its predator *Lates stappersi* remain important in pelagic catches (Pearse, 1995).

Lessons learned from the Laurentian Great Lakes and Lake Victoria would favor management strategies that discourage the introduction of species in order to maintain the ecological integrity of Lake Tanganyika. The ethical argument for the preservation of the endemic cichlid fauna is strong (Pitcher, 1995). Furthermore, all niches in the lake are currently occupied (Pitcher, 1995). Instead of relying upon introduced species, fisheries managers should try to increase the endemic fish while simultaneously regulating against symptoms of overexploitation (Pitcher, 1995).

3. Exotic species in other lakes

3.1. Lake Winnipeg and other large Canadian lakes

Rainbow smelt *(Osmerus mordax)* have invaded and continue to invade large lakes of Canada, such as Lakes Winnipeg, Manitoba and Winnipegosis (Table 5). Rainbow smelt is an invasive species in Canada, considered a pest by some and a boon to fisheries by others. Several studies (i.e. Evans and Loftus, 1987; Evans and Waring, 1987) have identified the potential threat posed by rainbow smelt to existing sport and commercial fisheries. Rainbow smelt also have great potential as a colonist, and its spread is hard to predict (Evans and Waring, 1987; the review in Franzin et al., 1994), increasing the probability of their spread throughout large lakes of Canada.

3.1.1. Geographic spread

Rainbow smelt have already invaded the Hudson

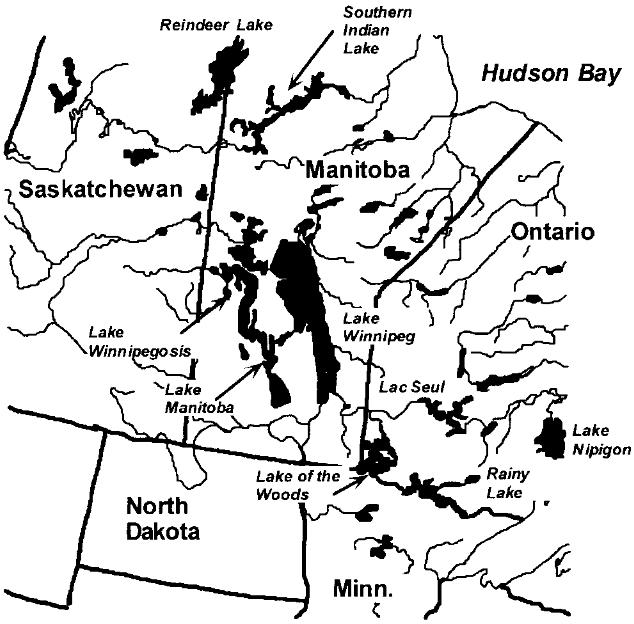

Fig. 7. Location of Lakes Winnipeg, Manitoba, and Winnipegosis in Manitoba, Canada.

Bay drainage waters of northwestern Ontario, southeastern Manitoba, and northern Minnesota, including Lake Winnipeg (Franzin et al., 1994) (Fig. 7). These waters eventually drain into Manitoba's large lakes, which have large and important commercial fisheries (Franzin et al., 1994). As of 1990, 32 lakes of the Lake Winnipeg drainage in Manitoba, northwestern Ontario, and northeastern Minnesota contained introduced rainbow smelt (Franzin et al., 1994). Stomachs of Lake Winnipeg walleyes (*Stizostedion vitreum*) collected during spring and fall in 1990 provided the first indication that rainbow smelt had invaded the lake (Campbell et al., 1991; Franzin et al., 1994). Smelt could have reached Lake Winnipeg by a variety of unintentional vectors, including movement downstream through the Winnipeg River, transportation by man from the English River system or directly into the lake, for example, via live bait left behind by anglers (Campbell et al., 1991). The practice of dumping unused live bait into lakes may be the most important single source of unauthorized introductions of exotic fishes, such as rainbow smelt, in both Canada and the United States (Campbell et al. 1991). Rainbow smelt do spread without human assistance (via migration in waterways), and probably will invade (or already have invaded) Lac la Croix, Namakan Lake, Rainy Lake, and Lake of the Woods, in Ontario and Manitoba, and in the larger, deeper, off-current main-stem lakes in the Winnipeg River system below Lake of the Woods (Franzin et al., 1994). Furthermore, Lake of the Woods could provide an important source of continual downstream migration of smelt in the Winnipeg system via the Winnipeg River (Franzin et al., 1994).

Humans activities, both accidental and deliberate, have been by far the most important agent in the spread of rainbow smelt (Franzin et al., 1994). Despite regulations and educational programs in Ontario, Manitoba and Minnesota, human introduction of the species is unlikely to stop, yielding most large lakes in Ontario, central and northern Manitoba, eastern Saskatchewan, and northern Minnesota at risk of rainbow smelt introduction (Franzin et al., 1994). Lakes that contain lake trout *Salvelinus namaycush* (Evans et al., 1988) and that are accessible by road or have substantial cottage development are at high risk for the introduction of exotics (Evans et al., 1988; Franzin et al., 1994).

3.1.2. Ecological impacts

Rainbow smelt are opportunistic feeders and can occupy various ecological roles (Franzin et al., 1994). Smelt serve as prey for almost all co-existing predators, including larger conspecifics (Evans et al., 1988; Franzin et al., 1994). Because they provide a food source for predators, rainbow smelt introductions or colonization frequently result in increased short-term growth rate of salmonids and possibly other fish species in various Canadian Shield Lakes and other systems (i.e. McCaig and Mullan, 1960). Increased levels of mercury in the white mussel of piscivorous fishes accompany these higher growth rates from feeding upon rainbow smelt (MacCrimmon et al., 1983; Mathers and Johansen, 1985).

Forecasts of the impacts of rainbow smelt are difficult to make and vary from lake to lake (Evans et al., 1988). Often, lake whitefish recruitment declines after invasion of rainbow smelt in already stressed lakes (i.e. a threatened status for lake whitefish in Lake Simcoe, Evans et al., 1988), although the mechanism is not clear. Predation by rainbow smelt is probably important (Crowder, 1980), particularly upon larval lake whitefish and lake herring *(Coregonus artedii)* (Loftus and Hulsman, 1986), although the magnitude of the predation effect depends upon the densities of prey and predator populations (Selgeby et al., 1978; Evans and Loftus, 1987). Evidence of competition is less clear (Evans and Loftus, 1987). A presumption of competition between rainbow smelt and other native species is based upon habitat and diet overlaps and on comparisons of change in growth, survival, and abundance of native species before and after rainbow smelt introductions (Evans and Loftus, 1987; Franzin et al., 1994). It is possible that rainbow smelt displace juvenile lake whitefish and cisco *(Coregonus artedi)* from preferred habitats and compete with both species for preferred food (Franzin et al., 1994), although some populations of species may increase in abundance after rainbow smelt introduction (Evans and Loftus, 1987; Evans and Waring, 1987). In some instances, rainbow smelt have not been considered harmful (i.e. rainbow smelt in Lake Superior, Selgeby et al., 1978).

3.1.3. Extent of spread and current status

Although rainbow smelt have reached Lake Winnipeg, unfavorable habitat in the lake may help discourage its further movement downstream. For instance, Lake Winnipeg may lack a suitable thermal habitat, particularly for adult smelt (Evans et al., 1988; Franzin et al., 1994). Additionally, Winnipeg is shallower, more turbid, and warmer in the summer than other large lakes (e.g. Lake Erie) where rainbow smelt have become established (Franzin et al., 1994). Winnipeg remains thermally unstratified during most of the ice-free period, precluding the development of cool-water refugia ordinarily sought by adult rainbow smelt in most lakes (Franzin et al., 1994). The presence of lake whitefish *(Coregonus clupeaformis)* in the north basin of the lake may indicate, however, that some refugia may be available (Davidoff et al., 1973; Franzin et al., 1994).

The range expansion of rainbow smelt to Lakes Winnipeg, Manitoba, and Winnipegosis can be expected to have negative impacts upon the lakes' important commercial fisheries. Predictions by Loch et al. (1979) in Franzin et al. (1994) state that rainbow smelt could cause a collapse of cisco populations in both Lakes Winnipeg and Manitoba, could have a major negative impact on the lake whitefish fishery in the north basins of each lake, and could have negative impacts upon walleye fisheries (particularly with increased mercury contamination). If rainbow smelt do indeed become abundant in Lakes Winnipeg, Winnipegosis and Manitoba, a decrease in commercial income due to reduced abundance of native species could be expected (Franzin et al., 1994). Until recently, Lake Winnipeg has not been exposed to many of the exotic species which appeared in the Laurentian Great Lakes. Introduced fish species have been limited to common carp *(Cyprinus carpio)*, black crappie *(Pomoxis nigromaculatus)*, and white bass *(Morone chrysops)* (Franzin et al., 1994). However, with the introduction of rainbow smelt, the Lake Winnipeg basin may now be approaching the threshold of ecological threats that were so dramatically illustrated in the lower Great Lakes 30 years ago.

3.2. Lake Titicaca (Peru–Bolivia)

The story of fishery development of Lake Titicaca provides an example of planned introductions of exotic species with unpredicted results. Lake Titicaca is a large (Table 5), high-altitude (3803 m above sea level), mesotrophic lake located in the Peruvian and Bolivian Andes. Like many other tropical lakes, the pelagic zone of Lake Titicaca was species-poor in comparison to its littoral fish assemblages (Vaux et al., 1988). Of the 30 native fish species known to inhabit the lake, 28 belong to the cyprinodont genus *Orestias* (Parenti, 1984); the remaining two native species are benthic catfish, *Trichomycterus dispar* and *Trichomycterus rivulatus*. Introduction of several exotic species have been attempted, with two species becoming established (Vaux et al., 1988).

3.2.1. History of introductions

In 1935, the federal governments of Bolivia, Peru, and the United States began a development project on Lake Titicaca to create a commercial fishery in one of the densest and poorest rural areas in the Andes and where only an Indian subsistence fishery had existed previously (Laba, 1979). Earlier scientific expeditions concluded that the pelagic zone of Lake Titicaca was unproductive (from a fisheries perspective) and could be improved by the introduction of exotic species (Laba, 1979). Following a survey conducted by the US Bureau of Commercial Fisheries, the introduction of lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), and cisco (*Coregonus* spp.) were cautiously recommended despite little ecological understanding of the lake (Laba, 1979). However, a fisheries technician failed to establish populations of lake trout and instead promoted the stocking of brown trout (*Salmo trutta*) and rainbow trout (*Salmo gairdneri*), directly conflicting with the Bureau's recommendations (Laba, 1979). The existing fishery rapidly changed without concomitant extension and management efforts (Laba, 1979). The pejerry, native of Argentina, was introduced by the government of Bolivia before 1955 (Everett, 1973; Laba, 1979). Like rainbow trout, pejerry is a shallow water species but spawns throughout the lake (thereby not limited to spawning in rivers, as is rainbow trout) and has a more varied diet (including zooplankton) (Laba, 1979; Vaux et al., 1988).

3.2.2. Results of introductions

Introductions of salmonids created a short-lived commercial fishery. The resulting catches of the commercially valuable salmonids promoted the development of foreign- and locally-owned canneries which exported their products to France, Germany, England, Italy, the United States and Australia (Laba, 1979). Although the socio-economic benefits of the fishery were broadcasted widely in the 1960s, the benefit to local fisherman and industry employees remained low (Laba, 1979). The fishery closed in 1969 (Everett, 1973; Laba, 1979).

The introduction of the brown and particularly rainbow trout had several biological consequences. Instead of occupying unproductive deep-water areas, rainbow trout, a relatively shallow water predator, most likely competed with and preyed upon native fish species (Laba, 1979). Additionally, the introduction of both trout species was not preceded by or followed by studies of its interactions with or impacts upon the native *Orestias* (Laba, 1979). It appears that trout followed a pattern common to many exotic fishes: a population boom followed by a rapid decline (Laba, 1979). The failure of trout to reproduce and become established was perhaps caused by a collapse of forage or the considerable increase of fishing effort (Everett, 1973). However, it resulted most likely from competition (for food resources) and predation pressure (particularly upon fingerling trout) of another exotic fish, the athernid pejerry (*Basilichthys bonariensis*).

The boom–bust cycles of the introduced salmonids and pejerry have impacted pelagic Lake Titicaca, primarily by shifting species abundance. Before 1980, three native species of *Orestias* (*Orestias ispi*, *Orestias pentlandii*, and *Orestias forgeti*), rainbow trout and pejerry were common in Lake Titicaca's pelagic zone. By the mid 1980s, only two species (*Orestias ispi* and *B. bonariensis*) were important and the only rainbow trout reported were captured by fishermen from depths of 50 m or more (Vaux et al., 1988). Harvests of existing pelagic fishes could be increased, however. By using an echo-sounding survey, estimates of pelagic biomass (species undefined) in Titicaca equal approximately 200 kg wet weight ha^{-1}, or a total of over 97,000 tonnes for the main basin of the lake (Vaux et al., 1988). Harvests of pelagic species were estimated at 6.5 tonne y^{-1}, although sustainable yields of the abundant pelagic species could be considerably increased (Vaux et al., 1988).

The arrival of exotic species to Lake Titicaca also had another unforeseen effect upon the ecosystem, introduction of disease. An outbreak of the epizootic protozoan *Ichthyophthirius multifiliis* (commonly known as Ich) caused massive fish mortality in Lake Titicaca in 1981 (Wurtsbaugh and Tapia, 1988). The outbreak of Ich affected seven species of fish, but 93%

of the fish collected with the parasites were adult *Orestia agassii*, an abundant littoral fish representing 70% of the total fish yield in Lake Titicaca (Wurtsbaugh and Tapia, 1988). The estimated mortality of the species attributed to Ich was 193 tonnes, representing 6% of its annual yield to the fishery (Alfaro et al., 1982, in Wurtsbaugh and Tapia, 1988). Pelagic species were rare in the collections of Wurtsbaugh and Tapia (1988), most likely because spread of Ich requires a benthic cyst from which mobile infective stages develop (Wurtsbaugh and Tapia, 1988). The origin of *I. multifillis* in Lake Titicaca is unknown but likely arrived with exotic fishes, since both salmonids and athernids are carriers of the parasite (Wurtsbaugh and Tapia, 1988). Information on Lake Titicaca is so limited that we may never know the relative role of exotic fishes, diseases, and increased fishing pressure on the native fauna.

3.3. Gatun Lake, Panama

Gatun Lake provides a Central American example of the impact of an introduced piscivore into a tropical lake ecosystem. Gatun Lake, Panama, is a large (Table 5), man-made lake formed *ca.* 1910 by the damming of the Changres River as part of the Panama Canal (Zaret and Paine, 1973). In 1967, peacock bass (*Cichla ocellaris*) was inadvertently introduced into the Changres River, and by 1969 the piscivorous and highly valued peacock bass was established (Zaret, 1982). The introduction of this species provided a sport fishery in Gatun Lake but ultimately resulted in dramatic changes in the entire lake ecosystem (Zaret and Paine, 1973). Due to its predatory habits, *Cichla* contributed to the demise of six previously common fish species (*Astyanax ruberrimus*, *Roeboides guatemalensis*, *Aequidens coeruleopunctatus*, *Gobiomrous dormitor*, *Gambusia nicaraguagensis*, and *Poecilia mexicana*) and nearly 50% of a seventh (*Melaniris chagresi*) off of Barro Colorado Island (Zaret and Paine, 1973). At another study station, 13 of 17 common diurnal fishes were extirpated locally (Zaret, 1982). Additionally, *Cichla* altered and simplified the food web of the lake, significantly affecting populations of the important zooplanktivore *Melaniris*, tertiary consumers (such as tarpon, (*Tarpon atlanticus*), black terns (*Chidonias niger*); kingfishers and herons), primary consumers and possibly primary producers (Zaret and Paine, 1973).

All of the fish species which declined in Gatun Lake did not disappear from the environmentally variable Changres River (Zaret, 1982; Lever, 1996), however. Since *Cichla* is not well established in the Changres, species previously believed to be extinct have re-entered the lake from river refuges (Zaret, 1982; Welcomme, 1988; Lever, 1996). The situation is further complicated by intentional introduction of other exotic species, such as common carp and Nile tilapia, which provide *Cichla* with an alternative food source in Gatun Lake (Welcomme, 1988). The resulting annual resurgence of prey species from the river has provided an element of long-term stability of the whole system (Lever, 1996). Subsequently, Gatun Lake has returned potentially to an ecological equilibrium, largely due the importance of the Changres River and its inflowing tributaries on the ecosystem of Gatun Lake (Lever, 1996).

3.4. Lake Baikal, Russia

Exotic species in large lakes of the world are not limited to fish species: exotic plants can also alter and impact lake ecosystems. *Elodea canadensis*, a macrophyte species native of North America, invaded Lake Baikal between the mid 1970s and early 1980s (Kozhova and Izhboldina, 1993). Lake Baikal is one of the oldest and largest lakes in the world (Table 5; Kawanabe, 1996). Not much is known about the introduction of exotics in Lake Baikal, although it is likely that undocumented invasions have occurred for some time.

Several theories explaining the invasion of *Elodea* exist. *Elodea* probably entered Lake Baikal through expansion from the Irkutsk Reservoir or from the Selenga River and has been spread throughout by navigation (Kozhova and Izhboldina, 1993). Alternatively, aquarists or transport vehicles may have brought the species to Lake Baikal, or it may have been transported with fishes from the lakes of the Urals (which had large amounts of the plants since the turn of the century) (Kozhova and Izhboldina, 1993). Although it first appeared in the shallow bays and streams of Baikal, *Elodea* completely covered bottoms of harbors and shallow bays and sors; its spread into more open waters is possible (Kozhova and Izhboldina, 1993). Potential change to the structure of the community of macrophytes of the coastal-sor zone of Baikal (consisting of species of macrophytes and benthic algae including *Potamogeton perfoliatus*, *Potamogeton pectinatus*, *Ranunculus trichophyllum*, *Myriophyllum spicatum*, *Cladophora* spp., *Spirogyra* spp., *Oedogonium* spp. and *Mougeotia* spp.) is possible (Kozhova and Izhboldina, 1993). *Elodea* is a competitive species and is highly toxin-resistant. Consequently, Kozhova and Izhboldina (1993) suggested that the appearance of *Elodea* in Lake Baikal may indicate an unforeseen and unpredicted effect of eutrophication and pollution of the lake.

3.5. Lake Ladoga, Russia

Deliberate, large-scale introductions of many invertebrate species have been made into large lakes of Russia in order to enhance production of fish (Panov, 1996). Introduction of the small Baikalian amphipod *Gmelinoides fasciatus* was due in large part to its ability to adapt to variable environmental conditions in littoral zones and to its high productivity (Panov, 1996). Introduced widely in the 1960s and 1970s into several lakes and reservoirs in the European part of Russia and Siberia, the ability of *Gmelinoides* to migrate and its predatory habits were not considered when transferred (Panov, 1996). After its intentional introduction into some lakes on the Karelian Isthmkus proximate to the western shore of Lake Ladoga (Table 5), *Gmelinoides* spread to Lake Ladoga by upstream and downstream movements (Panov, 1996). In 1989–1990 collections, *Gmelinoides* reached maximum density in Lake Ladoga of 54,000 animals m^{-2} and biomass of 160 g (wet weight), exceeding typical maximum figures for *Gmelinoides* in other waters (Panov, 1996). Accompanying such high densities is a negative impact upon native *Gammarus* and the isopod *Asellus aquaticus*, possibly due to competitive advantages of *Gmelinoides* (Panov, 1996). *Gmelinoides* is likely to spread to other lakes in developing countries because it is being exported as live food for aquarium fish (Panov, 1996). However, further research is necessary to identify the impacts of *Gmelinoides* on the littoral communities of Lake Ladoga as well as to predict and control its spread (i.e. possibly by ballast water of ships?).

3.6. Lake Biwa, Japan

Lake Biwa, the largest (Table 5) and oldest lake in Japan (Kawanabe, 1996), has recently undergone dramatic changes in environmental conditions, including the introduction of exotic plant and fish species. Although decreasing, Secchi depths from Biwa range from 4 to 9 m. The lake is 5–6 million years old and has many endemic species (Kawanabe, 1996). Lake Biwa has undergone cultural enrichment since the 1950s and particularly within the past 10–20 years, resulting in freshwater red-tides (mainly from dinoflagellates) and large blooms of *Microcystis* and *Anabaena* (Nakajima and Nakai, 1994; Kawanabe, 1996). Destruction of the land-lake ecotone is another serious problem in a catchment currently home to 1.25 million inhabitants (Nakajima and Nakai, 1994). Additionally, more than 70% of the shore is developed and most hydrophyte zones are gone, eliminating important nursery grounds for many of Biwa's fishes (Kawanabe, 1996; Nakajima and Nakai, 1994).

Both deliberate and accidental introductions of exotic species have accompanied the environmental changes of Lake Biwa. Two submerged macrophytes, *Elodena nuttallii* and *Egeria densa*, are examples of exotic plants that have impacted Biwa. *Elodena* was first found in the lake in 1961 and became the dominant macrophyte in the late 1960s (Nakajima and Nakai, 1994). *Egeria* appeared in the lake in 1969, rapidly replaced *Elodena*, and is currently the dominant plant in the lake (Nakanishi et al., 1989; Nakajima and Nakai, 1994). The dominance of these exotic species, particularly of *Egeria*, can be explained by their higher tolerance to increased eutrophication of the ecosystem compared with native species, and their ability to actively photosynthesize in winter (Nakanishi et al., 1989; Nakajima and Nakai, 1994). *Egeria* has influenced directly and indirectly several limnological factors within the littoral zone, increasing light attenuation, dissolved inorganic nitrogen and phosphorus, and B-group vitamins, while decreasing chlorophyll *a* and phytoplankton productivity in the upper littoral zone (Nakanishi et al., 1989).

Exotic animals have been introduced into Lake Biwa as well. The list of attempted introductions of species includes 19 fishes, two mollusks, three crustaceans, and one frog; additionally, four other species of fish (including largemouth bass *Micropterus salmoides*, first found in the lake in 1974) and one crayfish entered the lake via unknown vectors (Nakajima and Nakai, 1994). Of the 25 intentionally introduced species, only three have established populations; they include bluegill sunfish *Lepomis macrochirus* (brought from the USA in 1964), the potomid shrimp *Macrobrachium nipponense* (from Ibarkaki Prefecture in the 1920s), and the bull frog *Rana catesbeiana* (from the USA in 1920). However, *Micropterus* and *Lepomis* densities are of largest concern and have affected the native fish community via predation upon native, littoral fishes (Nakajima and Nakai, 1994; Kawanabe, 1996). Although densities of *Micropterus* in Lake Biwa have declined in the late 1980s, (Kawanabe, 1996), the exotic *Micropterus* and *Lepomis* and three native species are the only fishes presently common throughout the lake (Kawanabe, 1996). Consequently, a decrease of native littoral fishes has occurred in Lake Biwa, a result of environmental degradation coupled with exotic species in the system (Nakajima and Nakai, 1994).

4. Discussion and conclusions

Many of the large lakes of the world have been exposed to introductions of exotic species. After review of literature concerning these large lakes, we observed several trends (review in text and summary in Table 5). Human activities, preferences, and decisions are crucial to the spread of exotic species in large lakes throughout the world. In the case of the Laurentian Great Lakes, transportation involving railroads, canals, and ships (particularly in dry and wet ballasts) provided significant vectors for the spread of exotics (Mills et al., 1993, 1994, 1999). Humans also deliberately introduced exotics: for instance, Pacific salmon were deliberately introduced into the Laurentian Great Lakes to prey upon alewife, another exotic species (Mills et al., 1993, 1994). In Lake Victoria, colonial administrators stocked Nile perch to convert 'unsuitable fishes', such as haplochromine cichlids, into 'suitable table' fish and because it was large, easily caught, and preferred by European anglers (Eccles, 1985; Barlow and Lisle, 1987; Ogutu-Ohwaya, 1990a). Human activities, both deliberate and accidental, have been instrumental to the spread of rainbow smelt to Canada's Lakes Winnipeg, Manitoba, and Winnipegosis (Franzin et al., 1994). The governments of Peru, Bolivia, and the United States introduced salmonids with the idea of creating a sport fishery (Laba, 1979). Human activities have also been directly and indirectly involved with the spread of *Elodea canadensis* in Lake Baikal (Kozhova and Izhboldina, 1993) and *Gmelinoides fasciatus* in Lake Ladoga (Panov, 1996).

The spread and resulting ecological effects of introduced exotics vary among the case studies considered. In many instances an introduced species never becomes established, disappears without a trace, or has an unknown status. For instance, in Lake Titicaca the management goal of establishing a fishery for brown trout never was realized because the species did not become established successfully (Laba, 1979). In other instances a species may become established (possibly even increasing rapidly in abundance and becoming a dominant element in the population) but later disappears. An example of this boom and bust pattern is seen in Lake Titicaca with the rainbow trout fishery (Everett, 1973; Laba, 1979). Many case studies provide examples of a species that becomes a significant or dominant element of the host fauna and remains so, perhaps to lesser extent following the boom period., Nile perch in Lake Victoria (Barel et al., 1985; Hughes, 1986; Ogutu-Ohwayo 1990a–c; Ochumba, 1995, and so on) and peacock bass in Lake Gatun (Zaret and Paine, 1973; Zaret, 1982) provide prime examples.

Once species do become established, they can have major impacts upon lake ecosystems. These alterations arise though a variety of processes, including predation, disturbance, habitat modification, and interspecific competition (Mills et al., 1993). Perhaps the most obvious are those cases in which an introduced piscivore reduces abundance of native prey fishes. Examples of such piscivores include rainbow trout and pejerry in Lake Titicaca (Everett, 1973; Laba, 1979; Vaux et al., 1988) and peacock bass in Gatun Lake (Zaret and Paine, 1973; Zaret, 1982). Peacock bass impacted the entire food web of Gatun Lake, affecting zooplanktivores, tertiary consumers, primary consumers, and possibly primary producers (Zaret and Paine, 1973). Largemouth bass and bluegill altered the littoral fish community of Lake Biwa (Nakajima and Nakai, 1994; Kawanabe, 1996). Lake Victoria provides one of the most infamous examples of the effects of an exotic piscivore, Nile perch. Nile perch eliminated potentially 200 + species of cichlids and contributed to the collapse of a fishery formerly comprised of hundreds of species into three (Greenwood, 1974; Barel et al., 1985; Hughes, 1986; Kaufman, 1992; Witte et al., 1992a,b; Lowe-McConnell, 1993).

The introduction of species occupying lower trophic levels also creates trophic repercussions in ecosystems of large lakes. *Limnothrissa miodon* significantly impacted the pelagic zooplankton communities of Lakes Kariba and Kivu (Dumont, 1986; Marshall, 1991; De Inough et al., 1995). *Limnothrissa miodon* may also be competing with native species in Lake Kariba and has definitely moved (unexpectedly) into another neighboring system (Lake Canhora Bassa) (Marshall, 1991). In Lakes Winnipeg, Manitoba and Winnipegosis, rainbow smelt is hypothesized to potentially increase accumulation of mercury in commercially and recreationally valuable piscivores, impact fishes such as lake whitefish and lake herring via predatory and/or competitive (possibly) effects, and alter food web structures (Selgeby et al., 1978; Crowder, 1980; MacCrimmon et al., 1983; Mathers and Johansen, 1985; Loftus and Hulsman, 1986; Evans et al., 1988; Franzin et al., 1994). Similar to *Limnothrissa miodon*, rainbow smelt is spreading throughout large and small lakes of Canada accidentally (as well as deliberately) (Evans et al., 1988; Franzin et al., 1994). Perhaps most spectacularly, Nile perch has been linked to dramatic food web alterations and major limnological changes throughout Lake Victoria (Ligtvoet and Witte, 1991; Kaufman, 1992; Witte et al., 1992a; Goldschmidt et al., 1993).

Exotic species are certainly not limited to fish species. In both Lakes Baikal (Kozhova and Izhboldina, 1993) and Biwa, exotic plant species have become dominant macrophytes and have displaced native species. *Elodena nuttallii* and *Egeria densa* impacted several limnological variables in the littoral zone of Lake Biwa (Nakanishi et al., 1989; Nakajima and Nakai, 1994). The amphipod *Gmelinoides fasciatus* has also established in Lake Ladoga, potentially impacting native species of amphipods and possibly impacting food web structures there (Panov, 1996). Finally, parasites and pathogens such as *Ichthyophthirius multifiliis* can be introduced along with exotic species (i.e. Wurtsbaugh and Tapia, 1988). Ich in Lake Titicaca has caused mass mortality of native fish species (Wurtsbaugh and Tapia, 1988).

In addition to impacting ecosystems, exotic species impact socio-economic systems, in positive and negative manners. In Lake Victoria, the Nile perch fishery was a boom to members of society with sufficient capital to efficiently exploit and distribute their catches (Barel et al., 1985; Bruton, 1990; Kaufman, 1992; Reidmiller, 1994). Artisanal and subsistence fisherman, lacking sufficient resources to harvest Nile perch, suffered from declines in species they had previously harvested (Reidmiller, 1994). Furthermore, localized deforestation became a significant issue as fisherman harvested trees to smoke Nile perch (Barel et al., 1985; Reidmiller, 1994). In Lake Titicaca, the short-lived rainbow trout fishery benefited wealthy members of society but did little to ameliorate the condition of impoverished, rural denizens proximate to the lake (Laba, 1979). However, introduction of *Limnothrissa* in Lakes Kivu and Kariba created a pelagic fishery where none had existed before and incurred few obvious socio-economic costs (Marshall, 1991; Pitcher and Bundy, 1994; De Inough et al., 1995; Harris et al., 1995; Pitcher, 1995).

Our understanding of the effects and impacts of even these documented exotic species remains incomplete and in some cases speculative in nature. For instance, although *Limnothrissa miodon* has been declared a 'success' story in Lakes Kivu and Kariba, we are not convinced that its impact has been thoroughly studied and published. We do know that *Limnothrissa* has impacted the pelagic zooplankton community of each lake (De Inough et al., 1983; Marshall, 1991; De Inough et al., 1995). However, has this effect had cascading trophic repercussions (e.g. Carpenter et al., 1987; McQueen et al., 1989)? Do *Limnothrissa* consume larval fish of other species as do alewife in Lake Ontario (i.e. Krueger et al., 1995)? Are the current yields of *Limnothrissa* in these lakes sustainable? These and many other questions are difficult to answer in both lakes because pre- and post-introduction data are scarce (De Inough et al. 1983, 1995; Marshall, 1991). Thus, declaration of successful' introductions in Lakes Kariba and Kivu may be premature from an ecological standpoint.

Large lake ecosystems such as the Laurentian Great Lakes continue to be vulnerable to invasion. Six of the most recent invaders to these ecosystems are native to the biologically-rich Ponto-Caspian region (MacIsaac and Grigorovich, 1999). The latest arrival, *Cercopagis pengoi*, was identified in Lake Ontario in 1998 and has aggressively invaded to other Great Lakes and inland lakes (Raloff, 1999). Predicting future invasions to the Great Lakes is difficult but knowledge of possible donor regions and potential high risk species should be important elements of a prevention program (Ricciardi and Rasmussen, 1998). Using this approach, Ricciardi and Rasmussen (1998) identified suspension feeding *Corophium* spp., several mysid shrimp, and a Caspian herring, the "tyulka", as three high risk candidate invasive Ponto-Caspian organisms that could invade the Great Lakes in the future. Using the Great Lakes as a model, an inventory of potential invasive pest species from donor regions for other large lakes of the world including information about their life history, ecological requirements, dispersal patterns, and methods of control should be an essential prelude toward proactive prevention and control.

We know even less about the full number and extent of exotic species in these lakes. The Laurentian Great Lakes continue to provide by far the most thoroughly documented review (if still incomplete) of introductions of exotic species into large lake ecosystems (Mills et al., 1993, 1994; Leach et al., 1998). Fishes comprise 18% of the 145 documented exotic species within the Great Lakes ecosystem (Table 2). However, the case studies in this review focused on 12 fishes, three plants, one invertebrate, and one pathogen (Table 5); fishes comprised over 70% of the species introduced to non-Laurentian Great Lakes. Do these lakes have comparable introductions of exotic fishes, plants, algae, invertebrates and pathogens as the Laurentian Great Lakes, indicating a bias towards reporting introductions of fishes? Is accidental transfer of species via various forms of transportation important in these other lakes? These questions are important to address in the future.

5. Recommendations and challenges

The purpose of this paper is not to examine exhaustively the impacts of introductions of exotic species in large lakes throughout the world. Instead, we want this paper to serve as a springboard for further discussion and research into exotic species issues in large lakes and other systems. We make the following recommendations and conclusions to provoke debate about exotic species issues.

1. *Increase research activities.* As this literature review shows, on whole we understand relatively little about the spread and impact of exotic species in 62% of the world's freshwater lake resources. Therefore, we encourage further research activities on the lakes we have documented in this paper. We suggest that these research efforts be published in scientific journals distributed globally. Many of the papers cited in this review were published 10–20 years ago. What is happening to these ecosystems now? Furthermore, we would like to know about the impacts of exotic species in lakes such as Lakes Balkhash, Issyk-Kul, and Tung Ting in Asia, Lake Maracaibo in South America, Great Bear Lake, Great Slave Lake, and Reindeer Lake in Canada, and Lakes Vener and Onega in Europe. Are these lakes being impacted by exotic species also? To what extent? Crucial to the success of this intensified research effort is improved communication between decision makers and scientists (Balon and Bruton, 1986). Decision makers need to have as much of the best information as possible and then use that information to guide their choices. Unfortunately, scientific recommendations have been ignored in the past (i.e. cases of Lake Victoria and Lake Titicaca in this review) (Balon and Bruton, 1986).
2. *Recognize, anticipate, and discuss tensions between ecological stability and socio-economic benefits and costs.* In many of the case studies (e.g. all of the African Great Lakes, Laurentian Great Lakes and Lake Titicaca), socio-economic preferences and decisions drive introductions of exotics (directly or indirectly) and have dramatic socio-economic repercussions. These effects include decline of an artisanal fish harvest and commercialization of fishery harvests in Lake

Victoria and Lake Titicaca, and cost of control of purple loosestrife and sea lamprey in the watershed of the Laurentian Great Lakes (both of which were unauthorized introductions). Socio-economic pressure to stock fishes into Lakes Tanganyika and Malawi could increase. As the economy of Russia improves (both public and private sector), will the integrity of Lake Baikal be jeopardized by releases of exotic species? We believe that socio-economic effects of introductions are quite important to consider, particularly considering that immediate and long-term socio-economic costs are often high.

3. *Establish a protocol for evaluating introductions of exotic species.* Clearly, the issue of exotic species introductions is inherently global in nature and is intimately involved with human activities and decisions. Humans continue to transport species from continent to continent, deliberately or accidentally. Large lakes frequently form borders between countries, and introductions by one nation can affect several nations. Consequently, we agree with authors who propose protocols to evaluate introductions (i.e. Kohler and Stanley, 1984; Kohler and Courtenay, 1986) and suggest that each nation adopt a similar procedure. Since introductions can create catastrophic ecological changes (i.e. Laurentian Great Lakes and Lake Victoria), biologists and managers should be required to demonstrate a clear need for an introduction (Courtenay and Taylor, 1986). Furthermore, introductions are more than just ecological issues: protocols could help to reduce or eliminate over-emphasis of political and socio-economic benefits at the expense of the ecological integrity of the receiving ecosystems (Courtenay and Taylor, 1986). Once these protocols are established, they must be strengthened with enforced, rigorous quarantine procedures and enforced restrictions (Welcomme, 1986). An example of such protocols is the Nonindigenous Aquatic Species Act of 1990 (United States) and the first and only ballast water law in the world, adopted in the United States in 1993. At present existing legislation in many countries is haphazard, in some cases is non-exist, or in other cases is full of loopholes that make enforcement of legislation difficult (Welcomme, 1988).
4. *Create a system to support international consultation and inventory.* Introductions of a species into lakes and rivers of one country can affect the aquatic resources of another, particularly considering large lakes often form international boundaries between nations. Establishing a mechanism for international consultation could directly confront the international aspects of species introductions. With an international consultation process, common agreement can be reached on whether to permit transfers of species that might spread beyond the confines of the introducing nations. Some relatively strong, existing organizations include the Joint Strategic Plan for Management of Great Lakes Fisheries (SGLFMP) and the Great Lakes Fisheries Commission (GLFC) for the Laurentian Great Lakes (Dochoda, 1991), the European Inland Fisheries Advisory Commission (EIFAC), Indo-Pacific Fisheries Council (IPFC), Commission for Inland Fisheries of Latin America (COPESCAL), and Committee for the Inland Fisheries of Africa (CIFA) (Welcomme, 1988). A key source of information for this consultation process should be an inventory list of possible pest invaders, their life history, ecological requirements, dispersal patterns, and methods of control. These inventory lists should be coupled with a clearing-house information network to disseminate potential recipient and donor nations worldwide.
5. *Consider world heritage sites.* Some large lakes of the world continue to have tremendous diversity of fauna and need to be protected from the influence of exotics and environmental degradation. Large ancient lakes like Baikal, Malawi, and Tanganyika would fall into this category. Protecting lake crown jewels of the world would require international funding and support beyond the countries that border these waters.

6. Concluding remarks

Unbiased evaluation of the value of introduction of exotic species into large lakes (or more generally, in all aquatic systems) is difficult because of many different perspectives on the relative importance of ecological and socio-economic benefits and costs. Ecological costs occur in ecosystems that can be providing simultaneously both immediate and long-term socio-economic benefits and costs (Welcomme, 1988). Attitudes concerning exotic species range from a preservationist paradigm (i.e. those reluctant to see any change in the status quo) to those with a more economically-oriented paradigm (i.e. those favoring introduction of a species and modification of ecosystems to maximize economic benefits, regardless of socio-economic and ecological costs). We recognize the existence of tensions along this spectrum and agree that it is sometimes difficult to make conclusions and judgments about introductions, depending on the weight of different criteria used for evaluation of exotics. However, we agree with the statement: 'Any manager who believes that simply the act of injecting another species or two in a community will provide a lasting answer for any significant part of his concerns is deluding himself' (Regier, 1968, in Courtenay and Taylor, 1986).

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