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Exotic Species in the Hudson River Basin: A History of Invasions and Introductions

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ABSTRACT: We compiled information about the distribution of exotic organisms in the fresh waters of the Hudson River basin. At least 113 nonindigenous species of vertebrates, vascular plants, and large invertebrates have established populations in the basin. Too little was known about the past or present distributions of algae and most small invertebrates to identify exotic species in these groups. Most established exotic species in the Hudson River basin originated from Eurasia or the Mississippi-Great Lakes basins, and were associated with vectors such as unintentional releases (especially escapes from cultivation), shipping activities (especially solid ballast or ballast water), canals, or intentional releases. Rates of species invasions of fresh and oligohaline waters in the basin have been high (ca. one new species per year) since about 1840. For many well-studied groups, introduced species constitute 4% to nearly 60% of the species now in the basin. Although the ecological impacts of the invaders in the Hudson River basin have not been well studied, we believe that about 10% of the exotic species have had major ecological impacts in the basin. Since the rates of entry and composition of exotic species in the Hudson basin are similar to those observed previously for the Laurentian Great Lakes, invasions tended to occur earlier in the Hudson basin, probably reflecting the earlier history of human commerce. While most exotics have had negative impacts on local flora and fauna, some fish species have provided unique angling opportunities and important economic benefits.

Introduction

One of the most damaging impacts of man on the world's ecosystems is the introduction of exotic species (Elton 1958; Mooney and Drake 1986). Exotic species are numerous in many ecosystems, and individual exotic species can have enormous economic and ecological effects (Office of Technology Assessment 1993). Nevertheless, despite some classic studies (especially Elton 1958), species invasions have been regarded until recently (e.g., Mooney and Drake 1986; Drake et al. 1989) as a series of isolated ecological catastrophes rather than a coherent problem suitable for formal analysis.

The purpose of this paper is to describe and analyze the history of invasions of fresh waters in the Hudson River basin by exotic species. We are specifically concerned with the numbers of species invasions into the basin, the taxonomic and ecological composition of the invasive assemblage, the origins of the invaders, and the ecological impacts of the invaders. We also will compare the history of species invasions into the Hudson basin with that of the well-studied Laurentian Great Lakes (Mills et al. 1993). We believe that studies of entire biotas, rather than individual exotic species, will be helpful in developing generalizations about the numbers of exotics in various ecosystems, the nature of taxonomic and ecological selection imposed by human movements of species, and the kinds and magnitudes of ecological impacts of exotics in various ecosystems. In the case of this study, we provide specific information about the biota of the Hudson River basin. This paper is a summary and further analysis of the data presented by Mills et al. (in press), which contains the documentation and further details of our results.

New species have been introduced into the Hudson River basin at least since European explorations in the early sixteenth century. By the early seventeenth century, Europeans were visiting the basin regularly, bringing with them plant seeds in solid ballast and livestock feed, and fouling organisms on ship hulls. Shipping activity into the basin from around the world has continued to this day.

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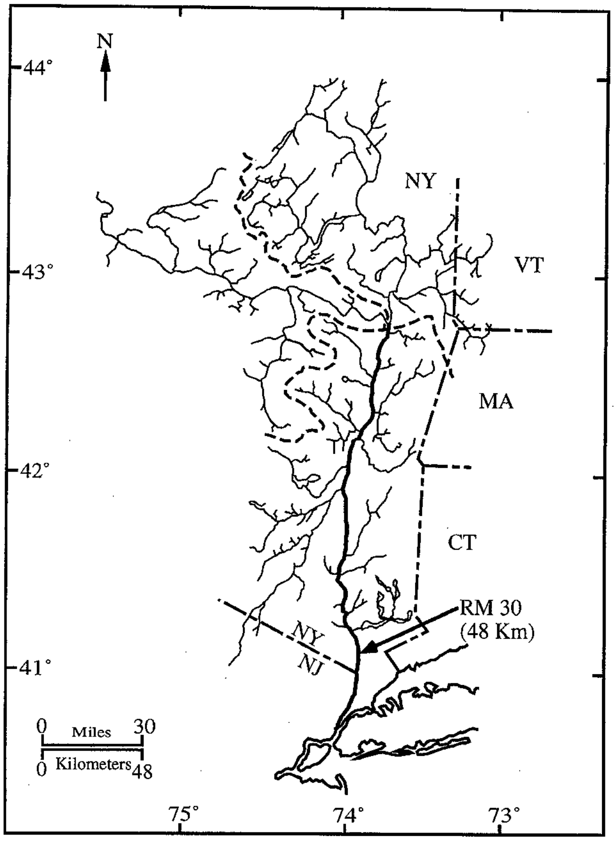

Fig. 1. Map of the Hudson River drainage basin. Dashed lines within the basin denote the divisions between the Upper Hudson, Mohawk-Hudson, and Lower Hudson watersheds.

In the early nineteenth century, humans opened another gateway into the basin by constructing canals that linked the Hudson basin with surrounding drainage systems: the Champlain Canal (Lake Champlain basin, 1819), the Erie Canal (lakes Erie and Ontario basins, 1825, enlarged 1918), the Delaware and Hudson Canal (Delaware River basin, 1829), the Chenango Canal (Susquehanna River basin, 1837), and the Black River Canal (Lake Ontario basin, 1839–1855).

Materials and Methods

We define an exotic species as one that was absent from the study area in pre-Columbian times, was brought into the area through some type of human activity, and has established reproducing populations. For this study, we consider the Hudson River and its watershed as the freshwater tidal reach north of River Mile (RM) 30 (48 km) (Fig. 1). The entire Hudson River basin drains parts of five states (New York, New Jersey, Massachusetts, Connecticut, and Vermont) as well as six physiographic regions (the Canadian Shield, the Folded Appachachians, the Catskills, the Hudson Highlands, the New England Upland, and the New Jersey Lowland) (Kammen 1975). Although exotic species are numerous in the terrestrial and more saline parts of the basin, these areas are beyond the scope of our study.

Data on species distributions and histories were gathered from published sources, museum and herbarium records, and interviews with experts. This list includes fishes, invertebrates, and aquatic plants that have entered the Hudson River basin since the early 1800s. Our list did not include terrestrial plants nor aquatic mammals and marine invaders that occur south of RM 30 (48 km). We realized that a gray area existed between terrestrial and aquatic plants and, therefore, used Gleason and Cronquist (1991) and Godfrey (1979, 1981) as a basis for determining whether a plant was aquatic or not. Because data on algae and small invertebrates were so scarce, our study includes only vascular plants, vertebrates, mollusks, crayfish, and a few other conspicuous invertebrates. For each exotic species, we recorded the date of first appearance in the basin, the mechanism (vector) through which it entered the basin, and the geographic origin of the colonizers. Date of appearance includes the first recorded release, the date of the first sighting or collection, or the date of the earliest publication that mentions the species in the basin (if the actual date of collection cannot be established). Following Carlton (1989, 1992, 1993) and Mills et al. (1993), we divided entry mechanisms into five broad categories: i) *intentional releases,* which were intended to establish a wild population of the species; ii) *unintentional releases,* which includes aquarium releases, escapes from cultivation, release of baitfish or nontarget organisms with stocked fish, and other accidental releases; iii) *shipping activities,* including transport of solid or water ballast as well as fouling organisms on hulls; iv) *canals,* which includes here only the active movement of organisms though canals (as opposed to passive movement on barge hulls); and v) *multiple vectors,* for any species that used more than one entry vector. The following regions were recognized as sources of exotics: Eurasia, Asia, North American Atlantic Slope, North American Interior Basin (i.e., the Mississippi or Great Lakes basins), the Southern United States, and the North American Pacific Slope. Further details on methods were given by Mills et al. (1993, in press).

Results and Discussion

Number and Kinds of Invaders

One hundred thirteen exotic species were identified as established in the fresh waters of the Hudson River basin (Tables 1 and 2). Because too little

TABLE 1. List of nonindegenous fish and aquatic invertebrates in the freshwater portion of the Hudson River basin.

Taxon	Species	Common Name
Fish		
Petromyzontidae	*Ichthyomyzon unicuspis*	silver lamprey
Amiidae	*Amia calva*	bowfin
Clupeidae	*Dorosoma cepedianum*	gizzard shad
Sciaenidae	*Aplodinutus grunniens*	freshwater drum
Ictaluridae	*Noturus miurus*	bridled madtom
Cyprinidae	*Carassius auratus*	goldfish
	Pimephales promelas	fathead minnow
	Ctenopharyngodon idella	grass carp
	Cyprinus carpio	common carp
	Rhodeus sericeus	bitterling
	Scardinius erythrophthalmus	rudd
	Campostoma anomalum	central stoneroller
	Nocomis biguttatus	hornyhead chub
	Notropis atherinoides	emerald shiner
	Notropis stramineus	sand shiner
Salmonidae	*Oncorhynchus mykiss*	rainbow trout
	Salmo trutta	brown trout
Umbridae	*Umbra limi*	central mudminnow
Esocidae	*Esox lucius*	northern pike
	Esox lucius × *masquinongy*	tiger muskellunge
Poeciliidae	*Gambusia affinis*	mosquitofish
Percichthyidae	*Morone chrysops*	white bass
Centrarchidae	*Ambloplites rupestris*	rock bass
	Lepomis cyanellus	green sunfish
	Lepomis gulosus	warmouth
	Micropterus dolomieui	smallmouth bass
	Micropterus salmoides	largemouth bass
	Pomoxis annularis	white crappie
	Pomoxis nigromaculatus	black crappie
Percidae	*Percina caprodes*	logperch
	Percina peltata	shield darter
	Stizostedion vitreum vitreum	walleye
Mollusks		
Valvatidae	*Valvata piscinalis*	European stream valvata
Bithyniidae	*Bithynia tentaculata*	mud bithynia
Viviparidae	*Viviparus georgianus*	banded mystery snail
	Cipangopaludina chinensis malleatus	Chinese mystery snail
Pleuroceridae	*Elimia livescens*	liver elimia
	Pleurocera acuta	sharp hornsnail
Lymnaeidae	*Radix auricularia*	big ear radix
Unionidae	*Alasmidonta marginata*	elktoe
	Fusconaia flava	Wabash pigtoe
	Anodonta embecilis	paper pondshell
	Lampsilis cardium	plain pocketbook
	Leptodea fragilis	fragile papershell
	Anodonta grandis	giant floater
	Potamilus ulatus	pink heelsplitter
Sphaeriidae	*Sphaerium corneum*	European fingernail clam
	Pisidium amnicum	greater European pea clam
Dreissenidae	*Dreissena polymorpha*	zebra mussel
	Mytilopsis leucophaeata	dark false mussel
Mactridae	*Rangia cuneata*	Atlantic rangia
Crayfish		
Asticidae	*Orconectes immunis*	crayfish
	Orconectes obscurus	crayfish
	Orconectes rusticus	rusty crayfish
	Orconectes virilis	crayfish
Cambaridae	*Procambarus acutus acutus*	crayfish
Other Invertebrates		
Amphipoda	*Gammarus daiberi*	gammarid amphipod
Hydrozoa	*Cordylophora caspia*	European fouling hydroid
Hydrozoa	*Craspedacusta sowerbyi*	freshwater jellyfish
Naididae	*Ripistes parasita*	oligochaete

TABLE 2. List of nonindegenous aquatic plants in the freshwater portion of the Hudson River basin.

Taxon	Species	Common Name
Potamogetonaceae	*Potamogeton crispus*	curly pondweed
Najadaceae	*Najas minor*	minor naiad
Cabombaceae	*Cabomba caroliniana*	fanwort
Brassicaceae	*Rorippa nasturtium = aquaticum*	watercress
	Rorippa palustris var. *palustris*	common watercress
	Rorippa sylvestris	creeping yellow cress
	Cardamine pratensis	cucko-flower
Trapaceae	*Trapa natans*	water chestnut
Haloragaceae	*Myriophyllum spicatum*	Eurasian water-milfoil
Manyanthaceae	*Nymphoides peltata*	yellow floating-heart
Butomaceae	*Butomus umbellatus*	flowering rush
Poaceae	*Phragmites australis*	reed
	Echinochloa crusgalli	barnyard-grass
	Poa annua	low speargrass
	Poa nemoralis	meadow-grass
	Poa trivialis	rough-stalked meadow-grass
	Calamagrostis epigeios	feathertop
	Agrostis gigantea	black bent
	Alopecurus geniculatus	marsh-foxtail
Juncaceae	*Juncus inflexus*	rush
Iridaceae	*Iris pseudacorus*	yellow iris
Polygonaceae	*Polygonum caespitosum* var. *longisetum*	bristly lady's-thumb
	Polygonum convolvulus	black bindweed
	Polygonum hydropiper	water pepper
	Polygonum lapathifolium	dock-leaved smartweed
	Polygonum persicaria	lady's-thumb
	Rumex crispus	curly dock
	Rumex obtusifolius	bitter dock
Ranunculaceae	*Ranunculus acris*	common buttercup
	Ranunculus bulbosus	bulbous buttercup
	Ranunculus repens	creeping buttercup
	Ranunculus scleratus	cursed crowfoot
Lythraceae	*Lythrum salicaria*	purple loosestrife
Onagraceae	*Epilobium hirsutum*	hairy willow-herb
Primulaceae	*Lysimachia nummularia*	moneywort
	Lysimachia vulgaris	garden-loosestrife
Boraginaceae	*Myosotis discolor*	yellow and blue scorpion grass
	Myosotis scorpioides	water scorpion grass
Labiatae	*Stachys palustris*	hedge nettle
	Lycopus europaeus	European water-horehound
	Mentha gentilis	red mint
	Mentha piperita	peppermint
	Mentha spicata	spearmint
Solanaceae	*Solanum dulcamara*	bittersweet
Rubiaceae	*Galium aparine*	cleavers
Asteraceae	*Bidens tripartita*	beggar-ticks
	Helenium flexuosum	southern sneezeweed
	Boltonia asteroides var. *recognita*	boltonia
	Sonchus arvensis	field-sow-thistle
Salicaceae	*Salix alba*	white willow
	Salix fragilis	crack willow
	Salix purpurea	purple osier

was known about the past and present distributions of algae and most small invertebrates for us to identify the exotic species in these groups, the true number of freshwater exotics in the basin is certainly far more than 113. Exotic species now constitute a large (and rising) proportion of the freshwater biota of the Hudson River basin (Table 3); for many well-studied groups, introduced species constitute 4% to nearly 60% of the species now in the basin. These figures are well above the 2–8% given as typical for the United States as a whole (Office of Technology Assessment 1993). Although it seems likely that the difference in scale of the two investigations is responsible for some of the difference (studies of geographically small parts of the continent might be expected to report a larger proportion of exotics than studies of the entire continent), it appears that the Hudson has been

TABLE 3. Numbers of native exotic freshwater species in various well-studied groups in the Hudson River basin.

Taxon	Native	Exotic	% Exotic
Aquatic mammals	5	1	17
Aquatic birds[a]	20	4	17
Aquatic reptiles	8	0	0
Aquatic amphibians	25	1	4
Fish	70	29	29
Crayfish	4	5	56
Mollusks	75	20	21
Aquatic vascular plants[b]	164	33	17

[a] Regular breeders only.

[b] Because of the difficulty in listing all "aquatic" plant species in the basin, this estimate refers to only a single community: the plants found below the high tide mark in the middle part of the tidal Hudson River (Kiviat 1978).

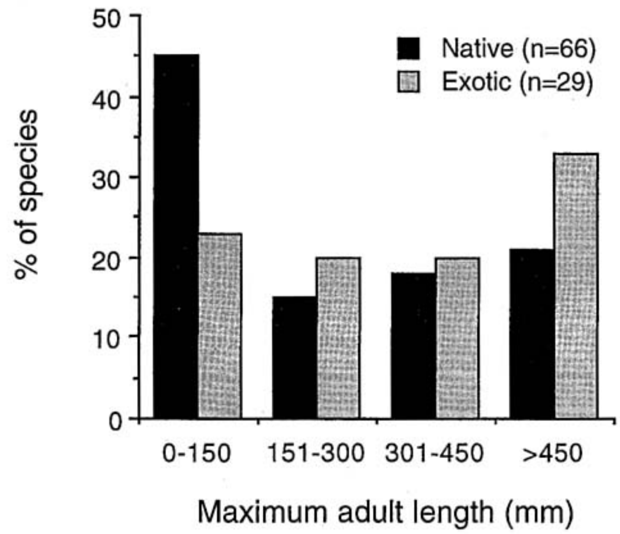

Fig. 2. Size structure (expressed as the maximum adult length of each species) of the native and exotic freshwater fish assemblages of the Hudson River basin. The two distributions are not significantly different ($\chi^2 = 4.86$, $p > 0.10$). Data from Smith (1985) and Smith and Lake (1990).

subject to an unusually large number of species invasions. The high number of exotics in the Hudson probably is due in part to the long history of human commerce through the region, but it also is possible that the relatively depauperate native biota of the region made it especially vulnerable to invasion (cf. Mooney and Drake 1986; Drake et al. 1989). In comparison with other east coast and North American coastal drainages, however, the high rate of invaders is probably not unique to the Hudson River drainage as human intervention and ecosystem disturbance has increased (Elton 1958).

In a study of natural invasions and deliberate introductions in the United Kingdom over the past century, Williamson and Brown (1986) found that about 10% of exotic species had become established. Similarly, Groves and Burdon (1986) estimated that about 10% of plant introductions to Australia became established. If the 10% rule also applies in North America, then perhaps some 1130 nonindigenous species have attempted colonization in the Hudson River basin.

Species invasions have not only simply increased the size of the local flora and fauna but also qualitatively and selectively altered its composition. For example, among the vertebrates only the fish fauna has been substantially enriched through species invasions, even though the Hudson basin contains many native freshwater species from other vertebrate groups (Table 3). Likewise, species invasions have changed the specific taxonomic and ecological character of the fish community. For example, the pre-Columbian fauna of the basin contained five catostomids and only four centrarchids. Human activities have brought in seven additional centrarchids but no catostomids. As a whole, the exotic fish are more likely to be piscivorous than the native fish of the basin; only 14% of the native fish are substantially piscivorous as adults (dietary information from Smith 1985), while 38% of the exotics are piscivorous ($\chi^2 = 7.2$; $p < 0.01$; df = 1). Interestingly, this does not appear to be a result of the exotics being larger than the native fish. Although exotic fish are slightly larger than natives (Fig. 2), this difference is small and not statistically significant (χ^2; $p < 0.05$; df = 1). Similarly, species invasions have selectively enriched the freshwater mollusk fauna of the basin in dreissenid and unionid bivalves and prosobranch snails, which together constitute 75% of the exotic mollusks but only 36% of the native mollusks. In addition, establishment of non-native piscivorous fish, such as walleye and bass, has enhanced angling opportunities. Thus, human activity has both increased the number of species in the Hudson River basin and strongly influenced the kinds of species that are present.

Origins and Vectors of the Invaders

Freshwater species have invaded the Hudson River from throughout North America, Europe, and Asia. None of the exotics in the Hudson basin are thought to have originated from the Southern Hemisphere. About 85% of the exotics in the Hudson basin came from Eurasia or the American Interior Basin (i.e., the Mississippi-Great Lakes basin). There are striking differences in origin among the different taxonomic groups: 80% of the exotic vascular plants came from Europe, while most of the animals came from the American Interior Basin (Table 4).

The apparent chronology of introductions, to the extent they are known, differ markedly between plants and animals (Fig. 3). However, there

TABLE 4. Origin of freshwater exotic species in the Hudson River basin, by taxonomic group.

Taxonomic Group	Eurasia	Interior Basin	Other[a]
Vertebrates	5	19	6
Mollusks	6	10	4
Crayfish	0	4	1
Vascular plants	90	1	5

[a] Includes Asia (n = 7), Pacific Coast basin of North America (n = 3), Atlantic Coast basin of North America (n = 3), southern United States (n = 2), and hatchery origin (n = 1).

TABLE 5. The number of exotic freshwater species in the Hudson River basin, according to taxonomic group and entry vector.

Vector	Taxon: Plants	Vertebrates	Invertebrates
Unintentional releases	38	3	11
Shipping	17	0	4
Canals	0	11	13
Intentional release	1	10	3
Multiple vectors	9	6	10
Vector unknown	31	0	1

is an historical bias in biological investigations, with botanical research in the Hudson River system well preceding fish research. Most exotic plants were first reported from the Hudson basin in the nineteenth century, and the current rate of new plant introductions appears to be relatively low. In contrast, rates of appearance of new exotic fish and invertebrates are rising. The overall rate of establishment of new exotic species of vascular plants, fish, and large invertebrates in the Hudson basin has been high (ca. one species yr^{-1}) since at least 1840, and continues to be high.

Several vectors have brought large numbers of exotic species into the Hudson basin (Table 5). Again, there are large differences across taxa in the importance of various vectors. Exotic plants have originated chiefly as escapees from cultivation or in the solid ballast of ships. Exotic fish came into the basin mainly through canals and intentional releases, while invertebrates have arrived through a variety of vectors. The importance of the major classes of vectors shows the importance of canals over the last 30 yr and shifts within classes (e.g., from solid ballast to ballast water as a vector within ships) (Fig. 4). All four of the major classes of vectors are still supplying significant numbers of exotic species to the Hudson basin.

Finally, it should be apparent that the movement of exotic species into the Hudson basin has been highly selective. The list of species that have moved into the Hudson basin is strikingly different from that of the source regions and that present in the basin in pre-Columbian times, and reflects the ability of specific human activities to break down barriers to dispersal for various specific kinds of organisms. Thus, the breaching of the Allegheny Divide by the Erie Canal brought in a large number of new fishes and mollusks, but not plants or vertebrates other than fish, for which the Divide had never represented a barrier. When ships stopped carrying solid ballast and began to use fresh water for ballast, it closed a door for plants and opened a door for aquatic invertebrates. This change in practice has contributed to the declining rate of plant invasions into the fresh waters of the Hudson basin (Fig. 3).

Impacts of the Invaders

Because exotic species are so numerous in the Hudson River basin, and many of these species are abundant, it is natural to ask what effects these exotic species have had on the structure and function

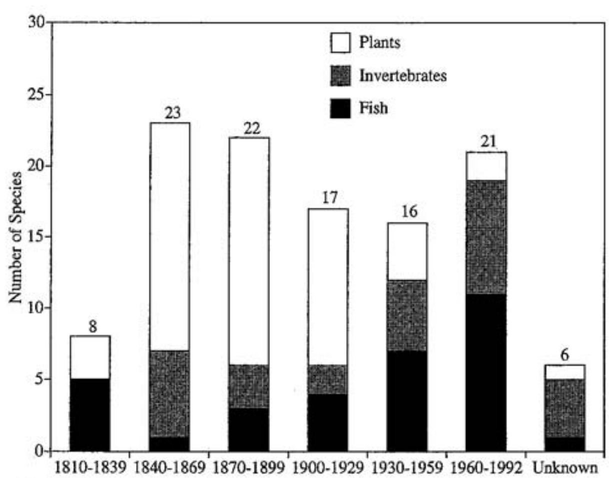

Fig. 3. Time-course of exotic freshwater vascular plants, invertebrates, and fish in the Hudson River basin. An unknown category is included for organisms whose time of establishment is not known.

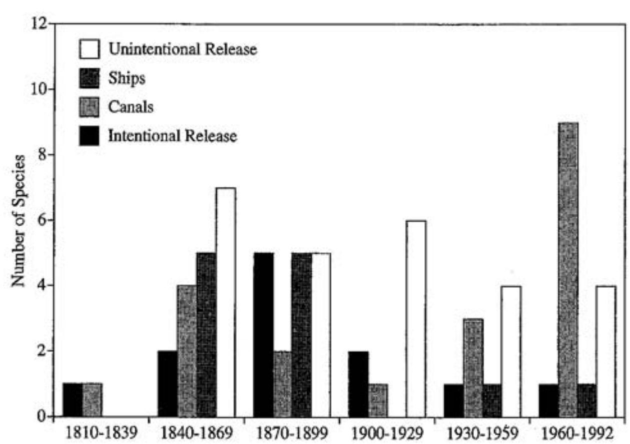

Fig. 4. Time course of entry mechanisms for exotic species in the Hudson River basin.

TABLE 6. Exotic freshwater species considered to have had significant ecological impacts in the Hudson River basin.

Taxonomic Group	Species
Plants	*Potamogeton crispus* (curly pondweed)
	Rorippa nasturtium (watercress)
	Trapa natans (water chestnut)
	Myriophyllum spicatum (Eurasian water-milfoil)
	Lythrum salicaria (purple loosestrife)
Fish	*Cyprinus carpio* (carp)
	Salmo trutta (brown trout)
	Esox lucius (northern pike)
	Ambloplites rupestris (rock bass)
	Micropterus dolomieui (smallmouth bass)
	Micropterus salmoides (largemouth bass)
	Pomoxis nigromaculatus (black crappie)
Invertebrates	*Bithynia tentaculata* (mud bithynia)
	Dreissena polymorpha (zebra mussel)
	Orconectes spp. (crayfish)

of freshwater communities and ecosystems in the basin. Despite the importance of this question, a paucity of site-specific information exists on the impact of exotics for the Hudson River. The mechanisms for damage to ecosystems by colonizing species are many and include habitat modifications, competition, predation, associated pathogens and parasites, and genetic effects (Krueger and May 1991; Li and Moyle 1993). All have been implicated in impacts for large ecosystems such as the Great Lakes (Leach 1995) and can be implicated for the Hudson River ecosystem as well.

Nevertheless, many of the exotic species in the Hudson basin have probably had ecological impacts, and several of these species have certainly had major impacts. Table 6 contains a list of the exotics we believe to have had relatively large ecological impacts over extensive areas in the Hudson. All of the plants listed in this table form dense stands in appropriate habitats in the basin: *P. crispus* (curly pondweed) in lakes and streams, *R. nasturtium* (watercress) in springs and spring brooks, *T. natans* (water chestnut) in low energy environments in lakes and rivers (especially the freshwater tidal Hudson River), *M. spicatum* (Eurasian watermilfoil) throughout the Hudson River basin, and *L. salicaria* (purple loosestrife) in wetlands. Several local studies (Kiviat 1987; Malecki 1987; Schmidt et al. 1992) have demonstrated that these plants have displaced native species and markedly altered the food and habitat resources available to microbes and animals. These plants are so abundant, however, that their effects are likely to have been basinwide. In some regions, alterations of the environment (cultural eutrophication, siltation, hydrological modifications, etc.) contributed more to the success of *Trapa, Myriophyllum spicatum, Lythrum salicaria* and possibly others than did extirpation of native plants.

Most of the fish in Table 6 are piscivores that are now abundant in lakes, creeks, and rivers throughout the Hudson basin. Piscivore introductions have been widely recognized throughout the invasions literature as having critical and broad impacts on the abundance and composition of fish and invertebrate communities. We assume that such impacts have taken place in the Hudson River system, although we have found no studies on the ecological impacts of exotic fish in the basin. The lone nonpiscivorous fish in Table 6 is the carp, which has frequently been thought to destroy aquatic plants and increase the turbidity of the water through its feeding activities (e.g., Smith 1985). These effects presumably occur in waters of the Hudson basin where carp are abundant (e.g., wetlands and low-gradient streams and rivers). On the other hand, some of the fish species such as largemouth and smallmouth bass have provided unique angling opportunities (Stang et al. 1995) and important economic benefits. The Hudson River has supported a growing largemouth bass fishery since the 1970s (Nack et al. 1993), and much economic benefit to local communities from this activity has been derived from both tournament and recreational fishing. In 1986, for example, Hudson River bass tournaments generated 2–2.25 million dollars to one locality alone (Green et al. 1989).

The invertebrates listed in Table 6 have highly varied effects. The snail *B. tentaculata* is the dominant invertebrate along stony shores in the tidal freshwater Hudson River (Strayer 1987, and unpublished data). Its effects on other invertebrates are unstudied, although it has been thought to outcompete some native snails (Harman 1968, 1969). The zebra mussel, *Dreissena polymorpha,* is an extremely abundant filter-feeder that is considered to have large and wide-reaching effects on aquatic ecosystems (e.g., Mackie et al. 1989; Nalepa and Schloesser 1993). It is one of the few exotics in the Hudson basin whose effects have been well-documented; early data show that it has had strong effects on the phytoplankton and zooplankton in the freshwater tidal Hudson River (Caraco et al. in press). The introduced crayfish are omnivores that are now abundant at many places in the Hudson basin. Based on studies done elsewhere (e.g., Pickett and Sloan 1985; Lodge and Lorman 1987; Olsen et al. 1991; Lodge et al. 1994), we expect that these crayfish have had strong effects on communities of plants and invertebrates, including native crayfish. In all cases, the impacts of these invertebrates has been largely negative, outweighing any benefits they may have provided as food for other fauna.

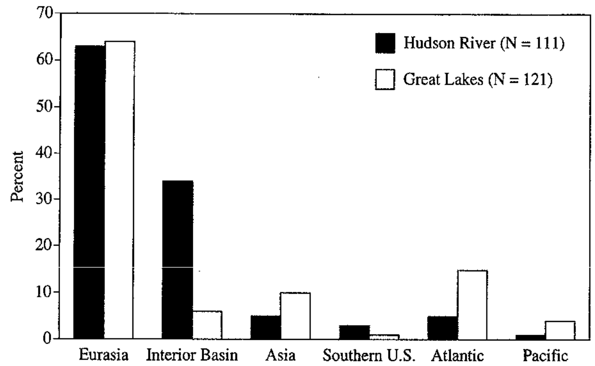

Fig. 5. Origins of exotic freshwater fish, invertebrates, and vascular plants to the Great Lakes and the Hudson River basin. Compiled from Mills et al. (1993, in press).

Because about 10% of the exotic species in the basin probably have major ecological impacts, and the long-term average rate of introduction to the basin is about one species yr^{-1}, a species capable of making large ecological changes arrives about once a decade. This is frequent enough that species introductions must be one of the human activities that have had the most profound ecological impacts on the fresh waters of the Hudson River basin.

Comparisons With the Laurentian Great Lakes

In most respects, the invasion history of the Hudson basin is similar to that of the nearby Great Lakes, which was recently documented by Mills et al. (1993). Both regions have received a large number of exotic vascular plants, fish, and large invertebrates (ca. one species yr^{-1}), chiefly from Eurasia (Fig. 5). In both areas, unintentional and deliberate releases and shipping have contributed most of the exotic species (Fig. 6). Both regions have received a large number of species (about 10% of the exotics, in both cases) that are thought to have had strong ecological impacts. There are several interesting differences between the regions, though. The Hudson received much higher numbers of exotics in the nineteenth century compared to twentieth century introductions, which have been higher for the Great Lakes (Fig. 7). This difference presumably reflects an earlier history of commerce and agriculture in the Hudson basin. Canals were a major source of exotics to the Hudson but not to the Great Lakes (Fig. 6). Furthermore, the exchange between the Hudson and the Great Lakes was not symmetrical; the Hudson received many more species from the American Interior Basin than the Great Lakes did from the Atlantic Slope. These last two differences probably occurred because the freshwater biota of the Atlantic Slope is much poorer than that of the American Interior Basin (Ortmann 1913; Hocutt and Wiley 1986), so when these two regions were connected by the Erie Canal and other human activities, the net movement of species was from the species-rich west to the species-poor east.

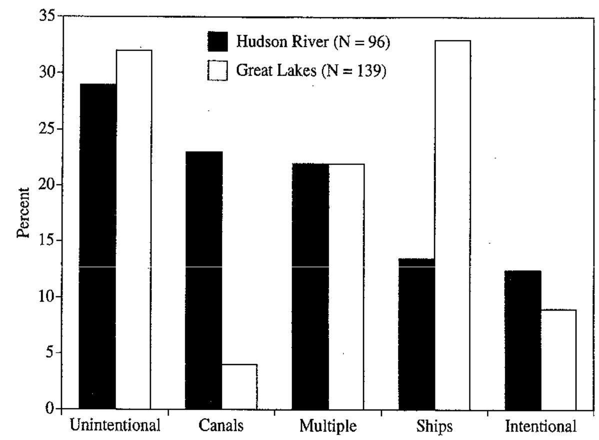

Fig. 6. Comparison of major vectors responsible for the entry of exotic freshwater fish, invertebrates, and vascular plants into the Great Lakes and the Hudson River basin. Compiled from Mills et al. (1993, in press).

Conclusions

Gross (1982) reviewed the human impacts on the Hudson River basin without mentioning exotic species. It is now clear that biological invasions can confidently be added to the list of major human-influenced alterations to the river. Human activities have brought (and continue to bring) many exotic freshwater species into the Hudson River basin. Within the groups traditionally thought to constitute the macroscopic freshwater biota (vascular plants, fish, mollusks, and crustaceans [here fo-

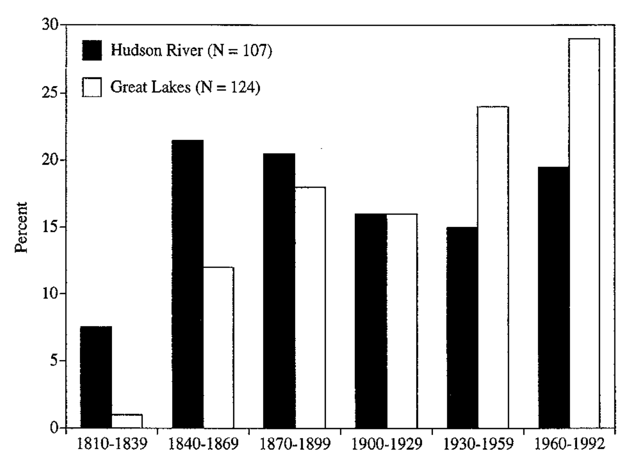

Fig. 7. Time course of the entry of established exotic freshwater species (fish, invertebrates, and vascular plants) into the Hudson River basin and the Laurentian Great Lakes. Great Lakes data from Mills et al. (1993).

cused on crayfish]) nearly 20% to 60% of the species now in the Hudson basin are exotics. Included in this range are some of the most abundant and conspicuous organisms in the basin. Even though the ecological effects of exotic species in the Hudson basin have not been well-studied, they must be widespread, profound, and diverse.

The invasion history of the Hudson basin is thus highly idiosyncratic, and reflects the history, location, and nature of human activities in and around the basin. Our analysis understates the extent to which anthropogenic species introductions have altered freshwater communities in the Hudson basin. Severe limitations on our data make us blind to invasions by microscopic organisms, which may have been numerous (cf. Mills et al. 1993). In addition, by adopting the drainage basin as our unit of study, we neglect movements of species within the basin. Certainly human activities have greatly expanded the distributions of both exotic (black bass) and native (lake trout) species within the basin, in addition to bringing new species into the basin.

Epilogue

In 1992, the United States Congress passed an amendment to Public Law 101-646, the "Nonindigenous Aquatic Nuisance Species Act," extending some of the Great Lakes-oriented provisions of that Act and the regulations that followed from it to the Hudson River. In particular, as of late 1994, vessels entering the Hudson River with foreign ballast water must have exchanged that water in mid-ocean and must arrive with water of a salinity not less than 30‰. Similar regulations have been in place for the Great Lakes since May 1993. If the 1994 regulations are effective, fewer direct ballast water invasions may occur in the Hudson River. However, ships will be able to continue to release ballast water in United States freshwater ports—such as the Delaware and Chesapeake Bay systems—from which invasions could be transferred by coastal vessel traffic into the Hudson. But, by 1995, at least, one major door for invasions should swing shut.

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