

## Interactions between alien species and restoration of large-river ecosystems

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With 3 figures and 1 table in the text

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**Abstract:** The large-river ecosystems that are the subject of restoration efforts also typically are heavily invaded by alien species. We use our experience on the Hudson River estuary, New York (USA), to illustrate some important interactions that link alien species and river restoration. Most obviously, restoration may be aimed at controlling populations of undesirable alien species. Alien species like common reed (*Phragmites communis*), water-chestnut (*Trapa natans*), and purple loosestrife (*Lythrum salicaria*) have been the targets of eradication programs in the Hudson. Such eradication efforts sometimes are poorly motivated, have non-target effects, have had mixed success in controlling the target species, or are entirely infeasible. Second, the presence of alien species may complicate restoration programs designed to address other goals. The presence of alien species may limit the range of available options, make the results of restoration activities more difficult to predict, and make it difficult to define or reach reference conditions. Finally, restoration programs may bring in or favor alien species. For example, materials used in restoration projects may be contaminated with the propagules of alien species. Consequently, restoration projects in large rivers often are intertwined with alien species in one way or another.

### Introduction

Like many large rivers in the developed world, the Hudson River has been deeply affected by human activities such as toxic pollution (BOPP & CHILLRUD 2005), destruction of shallow-water habitats (JACKSON et al. 2005), hydrologic alterations, land-use change in the watershed (SWANEY et al. 1996), and overharvesting of valuable species (WALDMAN & WIRGIN 1998). Consequently, the Hudson is the subject of planned and ongoing restoration efforts in attempts to reverse or reduce the undesirable effects of past human activities. Also like many large rivers, the Hudson has been heavily invaded by alien species (MILLS et al. 1996; STRAYER

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2005). Here, we describe how these two issues – alien species and river restoration – interact with one another, using the Hudson River as a case study. Although our focus is on the Hudson River, we believe that the interactions we describe between alien species and restoration affect many ecosystems around the world, including most large-river ecosystems.

## Large rivers as foci of species invasions

The main vectors that carry alien species between aquatic ecosystems are (1) ballast (both solid ballast and ballast water), (2) canals, (3) fouled ship hulls, (4) deliberate introductions of “desirable” species, (5) deliberate releases of organisms not intended to form sustaining populations (e.g., release of unwanted pets or bait), and (6) inadvertent releases of organisms (e.g., escapes from aquaculture or agriculture, contaminants of deliberate releases) (MILLS et al. 1996, 1997). Large rivers are heavily invaded by alien species because they are subject to high rates of input from most of these vectors. Because large rivers often are used for navigation, vectors 1–3 typically carry many alien species into large rivers. Vectors 4–6 are associated with general human use, and because large rivers often serve as foci for human habitation, these vectors probably also carry many alien species into large rivers. In addition, habitats in large rivers often are disturbed by activities like dredging and filling, which may favor the establishment of alien species (e.g., MACK et al. 2000).

Ecologically and economically important invaders have appeared in large rivers around the world (e.g., DARRIGRAN & DE GRAGO 2000; JANG et al. 2002; FEYRER & HEALEY 2003; KHARAT et al. 2003; MINCKLEY et al. 2003), but only a few comprehensive inventories of the extent of species invasions in large rivers have appeared (e.g., MILLS et al. 1996; LAVOIE et al. 2003). The fresh waters of the Hudson basin contain >100 species of alien fish, vascular plants, and large invertebrates, many of them in large-river habitats (MILLS et al. 1996, 1997). Large rivers in developed regions probably usually contain dozens to hundreds of alien species, perhaps 10–20 % of which are ecologically important (MILLS et al. 1996; Table 1).

The widespread importance of alien species has several consequences for large-river restoration. In brief, restoration programs may aim to control alien species, they may be complicated by the occurrence of alien species, and they may promote the arrival and spread of alien species (Fig. 1).

## Restoration programs may aim to control or eradicate alien species

Restoration programs often aim to control or eradicate alien species that have undesirable effects (Table 1). Nevertheless, such restoration efforts may be hard

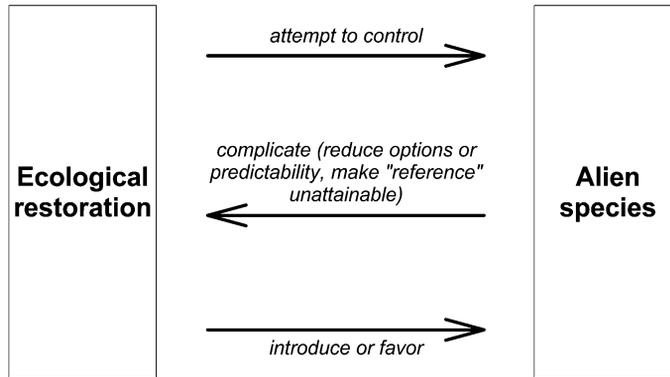


Fig. 1. Interactions that link alien species to ecological restoration.

to justify to the public, be difficult and costly, have undesirable impacts, and ultimately be futile. We illustrate these points with brief histories of some alien species in the Hudson.

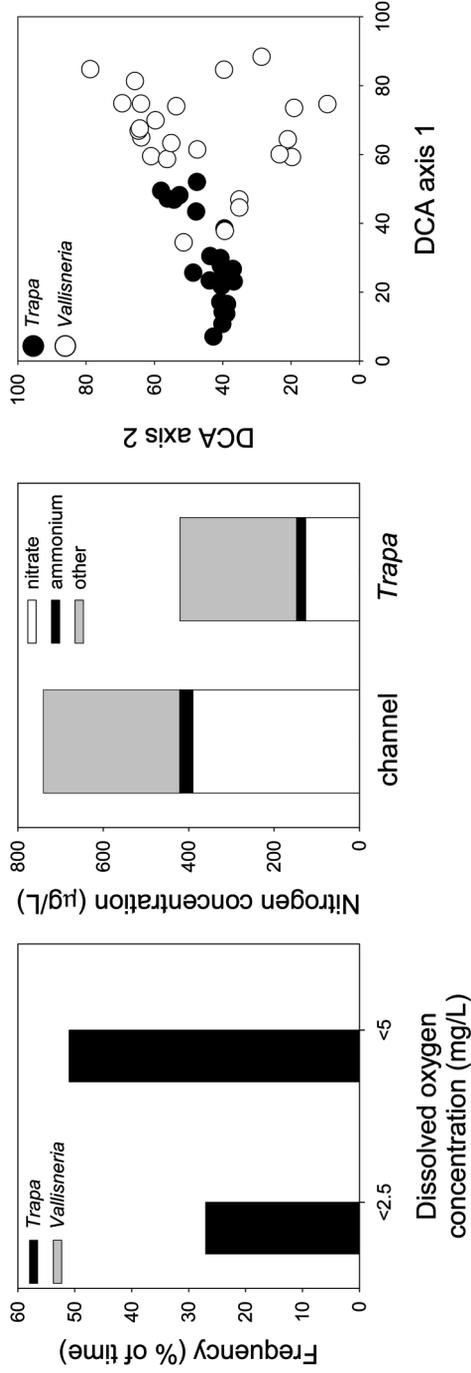
### Water-chestnut (*Trapa natans*)

Water-chestnut was deliberately introduced into the Hudson basin as an ornamental plant in 1884 (KIVIAT 1993). It is now widely distributed in shallow, quiet waters in lakes and large rivers in the basin, forming dense ( $>1$  kg dry matter/m<sup>2</sup>) monospecific stands that may cover  $>100$  ha. Water-chestnut beds are so dense that boats, swimmers, and anglers cannot penetrate them, greatly diminishing the recreational value of shallow-water habitats. In addition, because water-chestnut has floating leaves that release photosynthetic oxygen into the air while shading out and preventing photosynthesis in the underlying water, dissolved oxygen concentrations can fall to zero in large, dense beds (CARACO & COLE 2002). Water-chestnut supports a distinctive invertebrate community, including species that are rare or absent in the native plants that water-chestnut presumably displaced (Fig. 2). It may support different fish and wildlife than native plants, but this has not been well documented (STRAYER 2005). Finally, water-chestnut beds remove much of the inorganic nitrogen from water that passes through them (Fig. 2).

Largely because of recreational problems, New York State mounted an aggressive effort to eradicate water-chestnut in the Hudson and Mohawk Rivers in 1961–1976. The herbicide 2,4-D (dichlorophenoxyacetic acid) was sprayed at a rate of 19 l (3.6 kg acid equivalent)/ha by air boat in dense stands and by hand in less dense stands. At low densities, *Trapa* was pulled by hand. Die-off varied from 80–100%. Although *Trapa* coverage was reduced by 60% in the Hudson and Mohawk

**Table 1.** Alien species in the Hudson River that are abundant enough and have enough undesirable traits that they might be the objects of control efforts.

Species	Undesirable traits	History of control efforts in Hudson
<i>Myriophyllum spicatum</i> (Eurasian water-milfoil)	Interference with recreation; competition with native plants; alteration of animal habitat	None; currently not dominant in the Hudson, although formerly abundant (E. KIVIAI, pers. comm.)
<i>Lythrum salicaria</i> (purple loosestrife)	Competition with native plants; alteration of animal habitat	Biological controls agents (Coleoptera) have been released regionally
<i>Trapa natans</i> (water-chestnut)	Interference with recreation; creation of extensive hypoxia; competition with native plants; alteration of animal habitat	Extensive herbiciding in 1961–76; limited mechanical removal to provide recreational access
<i>Potamogeton crispus</i> (curly pondweed)	Competition with native plants; alteration of animal habitat	None
<i>Phragmites australis</i> (common reed)	Competition with native plants; alteration of animal habitat	Pilot studies using geotextiles; more extensive control often discussed
<i>Bithynia tentaculata</i> (mud bithynia)	Competition with native gastropods	None
<i>Dreissena polymorpha</i> (zebra mussel)	Competition with native animals; fouling of boats and water intakes	Local chemical and mechanical control for boats and water intakes
<i>Rangia cuneata</i> (Atlantic rangia)	Competition with native animals	None
<i>Cyprinus carpio</i> (common carp)	Destruction of aquatic vegetation; competition with native fishes	None



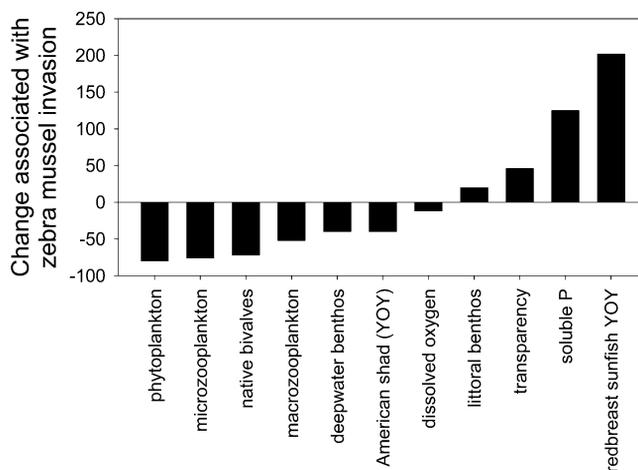
**Fig. 2.** Selected ecological impacts of water-chestnut in the Hudson River. Left: Low oxygen concentrations often occur in July–August in *Trapa* but not in nearby *Vallisneria*. Center: Concentrations of inorganic nitrogen are much lower in beds of *Trapa* than in the nearby unvegetated channel during the summer. Right: Ordination results showing that communities of plant-dwelling invertebrates living on *Trapa* are different from those living nearby on *Vallisneria*. Modified from CARACO & COLE (2002) and STRAYER et al. (2003).

rivers, from 1376 ha in 1965 to 546 ha in 1976, the program was abandoned in 1977 as a result of changing herbicide regulations, high costs relative to perceived benefits, and shifting state priorities. Currently, water-chestnut is mechanically harvested from small areas of the Hudson to provide passage for recreational boats. There has been interest in biological control, but no promising biological control agents have been found (PEMBERTON 1999).

Despite strong support for control and a long history of control efforts, water-chestnut has not been eradicated from the Hudson; in fact, it appears that it is as abundant as it ever has been. Herbicides and harvesting provided control for the limited times and places where they were used. Non-target impacts of herbicide treatments and mechanical harvesting were not studied, but presumably were large. Further, as the roles of water-chestnut are better studied, it appears that the species may play important (even positive?) roles in the ecosystem, e.g., removing nutrients and providing invertebrate habitat.

### Zebra mussel (*Dreissena polymorpha*)

Zebra mussels were introduced into the Great Lakes in European ballast water and spread rapidly through eastern North America, appearing in the Hudson in 1991. They have been abundant in the Hudson since autumn 1992, and constitute more than half of the heterotrophic biomass in the freshwater tidal Hudson (STRAYER 2005). Consequently, the entire character of the Hudson's ecosystem changed



**Fig. 3.** Summary of some of the ecological changes associated with the zebra mussel invasion of the Hudson River. Summarized from CARACO et al. (1997, 2000), STRAYER & SMITH (1996, 2001), PACE et al. (1998), and STRAYER et al. (2004).

(Fig. 3). Many ecological changes that occurred (e.g., dwindling of the planktonic food web, decline in dissolved oxygen, decline of fish and native bivalves, increase in dissolved phosphorus) could be considered undesirable. In addition, zebra mussels foul boat hulls, water intake pipes, and other underwater structures in the Hudson.

Zebra mussels are controlled in industrial and municipal water intakes on the Hudson River estuary through chemical treatment (chlorine, potassium permanganate, and polyquaternary ammonium compounds) and mechanical cleaning, at a cost of perhaps \$ 100,000–1,000,000/year. Despite their widespread and severe ecological effects, control of zebra mussels in the open waters of the Hudson has not been seriously contemplated, because of the absence of any feasible control measures at this scale.

### **Common reed (*Phragmites australis*)**

Although common reed is native to North America, highly invasive alien genotypes have spread over much of the continent (SALTONSTALL 2002). These alien genotypes often form dense, monospecific stands. On the Hudson, invasive genotypes of common reed probably appeared in the late 19<sup>th</sup> or early 20<sup>th</sup> century, displaced large areas of native vegetation (chiefly cattail, *Typha angustifolia*), especially in mesohaline areas, and continue to spread (WINOGROND & KIVIAT 1997). Largely because of concern about negative impacts on native plants and wildlife, many wetlands managers have tried to eradicate or control common reed in freshwater wetlands using herbicides, fire, or mowing. Such control measures need to be repeated periodically if more than temporary control is desired (e.g., AILSTOCK et al. 2001; WARREN et al. 2001). However, recent studies show that stands of common reed support animal communities, productivity, and nutrient cycling (although not plant diversity – AILSTOCK et al. 2001) as good or better than native freshwater plants and question the need for aggressive control programs (e.g., WARREN et al. 2001; HANSON et al. 2002; FINDLAY et al. 2003; WEINSTEIN et al. 2003).

In the case of common reed, we have an example of an aggressive alien that is still spreading along the Hudson and in many other habitats and has some undoubted troubling effects (displacement of native vegetation). Control of common reed is possible, but requires sustained effort (although research on biological control is proceeding – TEWKSBURY et al. 2002). Further, the overall ecological value of common reed in American wetlands has become less rather than more clear as more research has been done, so the species looks less like a pure pest than it did 20 years ago. A similar controversy has arisen about the need for control of purple loosestrife, another alien wetland plant in North America, again after aggressive control programs already began (ANDERSON 1995; HAGER & MCCOY 1998; BLOSSEY et al. 2001; FARNSWORTH & ELLIS 2001).

Thus, while alien species have had enormous impacts on the Hudson, it is difficult to classify those effects as unambiguously negative. Activities designed to control or eliminate these aliens may have negative as well as positive effects, resulting in scientific and public controversy about the desirability of control. Restoration programs to control aliens often require costly, sustained efforts (water-chestnut, common reed) or are infeasible (zebra mussel). Further, although non-target effects of restoration programs have not been well studied in the Hudson, these programs may have unintended negative effects (e.g., nutrient leakage from control of common reed – FINDLAY et al. 2003). These problems are by no means restricted to the Hudson, but will occur wherever an alien species is abundant, widespread, and has strong ecological or economic effects.

### **Restoration programs may be complicated by alien species**

Even where alien species are not the target of restoration activities, their presence can complicate restoration programs, especially in the many cases in which the alien population cannot be controlled. First, the presence of alien species can limit the range of feasible restoration options. For example, one of the biggest human impacts on the Hudson River was the widespread elimination of shallow-water habitats, with their many valuable ecological functions (LADD, in JACKSON et al. 2005). A reasonable goal for restoration might be to restore shallow-water areas to the Hudson, but it is likely that many such habitats would be monopolized by water-chestnut rather than the native vegetation that originally occupied these habitats. Such recreated shallow-water habitats would have neither the ecological functions nor support the same species as the original habitats they are intended to replace. Likewise, the zebra mussel's major impact is on the planktonic food web that supports open-water fish; this limits management options to maintain a sustainable fishery of American shad (*Alosa sapidissima*) (STRAYER et al. 2004).

Second, alien species can make the response of the system to restoration unpredictable. If the alien species arrived recently, managers may simply not have enough experience with the newly altered system to predict its response to restoration or other management activities (STRAYER et al. 2004). Further, arrival of additional alien species in the future can make future states of the ecosystem impossible to predict. This latter problem is important because current establishment rates of alien species are so high (0.1–1 species/year) in many aquatic ecosystems in developed regions (MILLS et al. 1993, 1996; COHEN & CARLTON 1998; RUIZ et al. 1999) that it is almost certain that new alien species will strongly affect system function in the coming decades.

Finally, aliens can make the reference conditions of the ecosystem difficult to define or reach. Many alien species arrived before detailed scientific studies of the ecosystem were done, so it is difficult even to describe the “reference” ecosystem.

For instance 86 of the 113 alien species known from the fresh waters of the Hudson basin were established prior to 1960 (MILLS et al. 1997), well before most scientific studies of the river began. Alternatively, alien species may be so deeply embedded that there is little prospect for removing them. It is difficult to imagine how zebra mussels could be removed from the Hudson, or how the Hudson could be restored to anything resembling its pre-1992 state without effective control of zebra mussels.

### **Restoration programs may introduce or favor alien species**

Restoration programs may encourage the development of alien species in three ways, possibly creating future problems for the management of large rivers. First, managers may deliberately bring in alien species to aid in ecological restoration. The invasive species literature is filled with examples of species (the terrestrial plants crown vetch, multiflora rose, and kudzu in North America, for example) that were introduced to aid in ecological restoration, but which led to subsequent ecological problems. An example in large rivers is the grass carp (*Ctenopharyngodon idella*), which was brought to North America to control aquatic macrophytes and is now established in large rivers in central North America.

Second, alien species may be inadvertently introduced with desirable plants or animals as part of restoration programs. The best-known example in aquatic ecosystems probably is the unintended transport of alien species on shells and living animals used in oyster restoration (CARLTON 1992; RUIZ et al. 2000; WOLFF & REISE 2002), but there are many other situations in which aliens may arrive as contaminants in shipments of plants, fish, or soils used in restoration projects.

Finally, restoration activities may create habitats that favor alien species. For instance, creation of sheltered, shallow-water habitats in the Hudson is likely to favor water-chestnut. More generally, because disturbance is thought to favor alien species (e.g., MACK et al. 2000), restoration activities may allow the establishment or spread of a wide range of alien species.

### **Conclusions**

Our long-term ability to maintain and restore large-river ecosystems is linked in several ways to alien species. Because alien species often cause ecological and economic problems, they may be targets of restoration programs. However, alien species are difficult to control or eradicate, particularly in large rivers, which are open systems connected not only to upstream lakes and rivers but also to other waterways through human commerce. Biological controls have been effective with some aquatic plants, but are not available for many pest species, and have their own risks (e.g., STRONG & PEMBERTON 2000; PEARSON & CALLAWAY 2003).

Because control or eradication of existing aliens in large rivers often is infeasible, restoration programs may simply have to work around these species.

Because undesirable alien species can complicate or even undo efforts to restore and manage large rivers, it is important for restoration programs in large rivers to explicitly consider alien species. Restoration programs should be planned to minimize the potential for problems with undesirable aliens. Careless restoration programs may also worsen alien species problems by bringing in new aliens, either deliberately or inadvertently, or by creating habitat that favors alien species. Restoration of large rivers should be coordinated with international efforts to reduce the arrival and establishment of alien species, which will ultimately reduce future problems associated with alien species.

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### References

- AILSTOCK, M.S., NORMAN, C.M. & BUSHMANN, P.J. (2001): Common reed *Phragmites australis*: control and effects on biodiversity in freshwater nontidal wetlands. – *Restor. Ecol.* **9**: 49–59.
- ANDERSON, M.G. (1995): Interactions between *Lythrum salicaria* and native organisms – a critical review. – *Environ. Mgmt.* **19**: 225–231.
- BLOSSEY, B., SKINNER, L.C. & TAYLOR, J. (2001): Impact and management of purple loosestrife (*Lythrum salicaria*) in North America. – *Biodiversity and Conservation* **10**: 1787–1807.
- BOPP, R. & CHILLRUD, S. (2005): Contaminant histories in the Hudson estuary. – In: LEVINTON, J.S. & WALDMAN, J.R. (eds.): *The Hudson River ecosystem*. Cambridge Univ. Press. (in press).
- CARACO, N.F. & COLE, J.J. (2002): Contrasting impacts of a native and alien macrophyte on dissolved oxygen in a large river. – *Ecol. Appl.* **12**: 1496–1509.
- CARACO, N.F., COLE, J.J., FINDLAY, S.E.G., FISCHER, D.T., LAMPMAN, G.G., PACE, M.L. & STRAYER, D.L. (2000): Dissolved oxygen declines in the Hudson River associated with the invasion of the zebra mussel (*Dreissena polymorpha*). – *Environ. Sci. Technol.* **34**: 1204–1210.
- CARACO, N.F., COLE, J.J., RAYMOND, P.A., STRAYER, D.L., PACE, M.L., FINDLAY, S.E.G. & FISCHER, D.T. (1997): Zebra mussel invasion in a large, turbid river: phytoplankton response to increased grazing. – *Ecology* **78**: 588–602.
- CARLTON, J.T. (1992): Introduced marine and estuarine mollusks of North America: an end-of-the-20<sup>th</sup>-century perspective. – *J. Shellfish Res.* **11**: 489–505.

- COHEN, A.N. & CARLTON, J.T. (1998): Accelerating invasion rate in a highly invaded estuary. – *Science* **279**: 555–558.
- DARRIGRAN, G. & DE GRAGO, I.E. (2000): Invasion of the exotic freshwater mussel *Limnoperna fortunei* (DUNKER, 1857) (Bivalvia: Mytilidae) in South America. – *Nautilus* **114**: 69–73.
- FARNSWORTH, E.J. & ELLIS, D.R. (2001): Is purple loosestrife (*Lythrum salicaria*) an invasive threat to freshwater wetlands? Conflicting evidence from several ecological metrics. – *Wetlands* **21**: 199–209.
- FEYRER, F. & HEALEY, M.P. (2003): Fish community structure and environmental correlates in the highly altered southern Sacramento-San Joaquin Delta. – *Env. Biol. Fishes* **66**: 123–132.
- FINDLAY, S., GROFFMAN, P. & DYE, S. (2003): Effects of *Phragmites australis* removal on marsh nutrient cycling. – *Wetlands Ecol. Mgmt.* **11**: 157–165.
- HAGER, H.A. & MCCOY, K.D. (1998): The implications of accepting untested hypotheses: a review of the effects of purple loosestrife (*Lythrum salicaria*) in North America. – *Biodiversity and Conservation* **7**: 1069–1079.
- HANSON, S.R., OSGOOD, D.T. & YOZZO, D.J. (2002): Nekton use of a *Phragmites australis* marsh on the Hudson River, New York, USA. – *Wetlands* **22**: 326–337.
- JACKSON, J.K., HURYN, A.D., STRAYER, D.L., COURTEMANCH, D. & SWEENEY, B.W. (2005): Atlantic rivers – Northeastern states. – In: BENKE, A.C. & CUSHING, C.E. (eds.): *Rivers of North America*. Academic Press. (in press).
- JANG, M.H., KIM, J.G., PARK, S.B., JEONG, K.S., CHO, G.I. & JOO, G.J. (2002): The current status of the distribution of introduced fish in large river systems of South Korea. – *Int. Rev. Hydrobiol.* **87**: 319–328.
- KHARAT, S., DAHANUKAR, N., RAUT, R. & MAHABALESHWARKAR, M. (2003): Long-term changes in freshwater fish species composition in northwestern Ghats, Pune District. – *Curr. Sci.* **84**: 816–820.
- KIVIAT, E. (1993): Under the spreading water-chestnut. – *News from Hudsonia* **9** (1): 1–6.
- LAVOIE, C., JEAN, M., DELISLE, F. & LETOURNEAU, G. (2003): Exotic plant species of the St. Lawrence River wetlands: a spatial and historical analysis. – *J. Biogeogr.* **30**: 537–549.
- MACK, R.N., SIMBERLOFF, D., LONSDALE, W.M., EVANS, H., CLOUT, M. & BAZZAZ, F.A. (2000): Biotic invasions: causes, epidemiology, global consequences, and control. – *Ecol. Appl.* **10**: 689–710.
- MILLS, E.L., LEACH, J.H., CARLTON, J.T. & SECOR, C.L. (1993): Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. – *J. Great Lakes Res.* **19**: 1–54.
- MILLS, E.L., SCHEUERELL, M.D., CARLTON, J.T. & STRAYER, D.L. (1997): Biological invasions in the Hudson River basin: an inventory and historical analysis. – *N. Y. St. Mus. Circ.* **57**: 1–51.
- MILLS, E.L., STRAYER, D.L., SCHEUERELL, M.D. & CARLTON, J.T. (1996): Exotic species in the Hudson River basin – a history of invasions and introductions. – *Estuaries* **19**: 814–823.
- MINCKLEY, W.L., MARSH, P.C., DEACON, J.E., DOWLING, T.E., HEDRICK, P.W., MATTHEWS, W.J. & MUELLER, G. (2003): A conservation plan for native fishes of the lower Colorado River. – *BioScience* **53**: 219–234.

- PACE, M.L., FINDLAY, S.E.G. & FISCHER, D. (1998): Effects of an invasive bivalve on the zooplankton community of the Hudson River. – *Freshwat. Biol.* **39**: 103–116.
- PEARSON, D.E. & CALLAWAY, R.M. (2003): Indirect effects of host-specific biological control agents. – *Trends in Ecology and Evolution* **18**: 456–461.
- PEMBERTON, R.W. (1999): Natural enemies of *Trapa* spp. in northeast Asia and Europe. – *Biol. Control* **14**: 168–180.
- RUIZ, G.M., FOFONOFF, P.W., CARLTON, J.T., WONHAM, M.J. & HINES, A.H. (2000): Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. – *Ann. Rev. Ecol. Syst.* **31**: 481–531.
- RUIZ, G.M., FOFONOFF, P., HINES, A.H. & GROSHOLZ, E.D. (1999): Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. – *Limnol. Oceanogr.* **44**: 950–972.
- SALTONSTALL, K. (2002): Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. – *Proc. Nat. Acad. Sci.* **99**: 2445–2449.
- STRAYER, D.L. (2005): Alien species in the Hudson River. – In: LEVINTON, J.S. & WALDMAN, J.R. (eds.): *The Hudson River ecosystem*. Cambridge Univ. Press. (in press).
- STRAYER, D.L., HATTALA, K.A. & KAHNLE, A. (2004): Effects of an invasive bivalve (*Dreissena polymorpha*) on fish populations in the Hudson River estuary. – *Can. J. Fish. Aquat. Sci.* **61**: 924–941.
- STRAYER, D.L., LUTZ, C., MALCOM, H.M., MUNGER, K. & SHAW, W.H. (2003): Invertebrate communities associated with a native (*Vallisneria americana*) and an alien (*Trapa natans*) macrophyte in a large river. – *Freshwat. Biol.* **48**: 1938–1949.
- STRAYER, D.L. & SMITH, L.C. (1996): Relationships between zebra mussels (*Dreissena polymorpha*) and unionid clams during the early stages of the zebra mussel invasion of the Hudson River. – *Freshwat. Biol.* **36**: 771–779.
- (2001): The zoobenthos of the freshwater tidal Hudson River and its response to the zebra mussel (*Dreissena polymorpha*) invasion. – *Arch. Hydrobiol. Suppl.* **139**: 1–52.
- STRONG, D.R. & PEMBERTON, R.W. (2000): Biological control of invading species – risk and reform. – *Science* **288**: 1969–1970.
- SWANEY, D.P., SHERMAN, D. & HOWARTH, R.W. (1996): Modeling water, sediment and organic carbon discharges in the Hudson-Mohawk basin: coupling to terrestrial sources. – *Estuaries* **19**: 833–847.
- TEWKSBURY, L., CASAGRANDE, R., BLOSSEY, B., HAFLIGER, P. & SCHWARZLANDER, M. (2002): Potential for biological control of *Phragmites australis* in North America. – *Biol. Control* **23**: 191–212.
- WALDMAN, J.R. & WIRGIN, I.I. (1998): Status and restoration options for Atlantic sturgeon in North America. – *Cons. Biol.* **12**: 631–638.
- WARREN, R.S., FELL, P.E., GRIMSBY, J.L., BUCK, E.L., RILLING, G.C. & FERTIK, R.A. (2001): Rates, patterns, and impacts of *Phragmites australis* expansion and effects of experimental *Phragmites* control on vegetation, macroinvertebrates, and fish within the tidelands of the lower Connecticut River. – *Estuaries* **24**: 90–107.
- WEINSTEIN, M.P., KEOUGH, J.R., GUNTENSPERGEN, G.R. & LITVIN, S.Y. (eds.) (2003): *Phragmites australis*: a sheep in wolf's clothing? – *Estuaries* **26**: 397–630.
- WINOGROND, H.G. & KIVIAT, E. (1997): Invasion of *Phragmites australis* in the tidal marshes of the Hudson River. – In: NIEDER, W.C. & WALDMAN, J.R. (eds.): *Final re-*

ports of the Tibor T. Polgar Fellowship Program for 1996: pp. VI-1 to VI-29. Hudson River Foundation, New York.

- WOLFF, W.J. & REISE, K. (2002): Oyster imports as a vector for the introduction of alien species into northern and western European coastal waters. – In: LEPPÄKOSKI, E, GOLLASCH, S. & OLENIN, S. (eds.): Invasive aquatic species of Europe: distribution, impacts, and management: 193–205.

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