Arrival, Spread, and Early Dynamics of a Zebra Mussel (Dreissena polymorpha) Population in the Hudson River Estuary

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Arrival, spread, and early dynamics of a zebra mussel (Dreissena polymorpha) population in the Hudson River estuary

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Abstract: The zebra mussel *(Dreissena polymorpha)* population of the Hudson River estuary grew and spread rapidly following its first detection in May 1991. The population reached 550 billion animals ($4000/m^2$, mean over the freshwater tidal river) by the end of 1992, constituting >70% of zoobenthic biomass, and filtered a volume equivalent to the entire water column in 1 day. Over 95% of the population lived on subtidal rocks. Following the period of rapid population growth in 1991-1992, reproductive success (young of the year per adult) fell by four orders of magnitude in 1993-1994. Furthermore, at the end of the 1993-1994 growing seasons, young of the year were only 20-30% as large as in 1991. Adult zebra mussels may have been outcompeting the larvae for food. We propose that such food-limited zebra mussel populations may be especially frequent in rivers and estuaries, where the ratio of food supply to available substratum is small.

Résumé : Les effectifs de la moule zébrée *(Dreissena polymorpha)* dans l'estuaire de l'Hudson ont augmenté et se sont propagés rapidement depuis la découverte des premiers individus en mai 1991. La population s'établissait à 550 milliards de moules ($4000 moules/m^2$, moyenne établie pour la portion dulcicole de la rivière qui est soumise aux marées) à la fin de 1992. Elle formait alors plus de 70% de la biomasse zoobenthique et filtrait quotidiennement un volume équivalent à toute la colonne d'eau. Plus de 95% des moules vivaient fixées aux pierres de la zone subtidale. Par suite de l'explosion démographique enregistrée en 1991–1992, le succès de la reproduction (nombre de jeunes de l'année par adulte) a chuté de quatre ordres de grandeur en 1993–1994. En outre, la taille des jeunes de l'année à la fin de la saison de développement de 1993–1994 atteignait seulement 20 à 30% de celle des jeunes de l'année de 1991. L'incapacité des larves de résister à la forte compétition pour la nourriture exercée par les adultes pourrait avoir été la cause de ce phénomène. Les auteurs estiment que de telles populations limitées par la nourriture pourraient être particulièrement fréquentes dans les rivières et les estuaires, où la quantité de nourriture par rapport à la surface des supports est faible.

[Traduit par la Rédaction]

Introduction

Despite a long history of European research (summarized by Stanczykowska 1977; Mackie et al. 1988) and recent North American studies (e.g., Haag et al. 1993; Nalepa and Schloesser 1993; Nicholls and Hopkins 1993; Mellina and Rasmussen 1994; Ricciardi et al. 1995), many critical questions remain about the dynamics, control, and ecological effects of zebra mussel *(Dreissena polymorpha)* populations. Specifically, little is known about the dynamics and ecological effects of zebra mussel populations in habitats other than lakes or about the ecology of zebra mussels over long time scales or large spatial scales. Here, we describe the invasion and early population dynamics of the zebra mussel in the Hudson River estuary, as part of a comprehensive assessment of the ecological effects of the zebra mussel on this ecosystem. As we will

show below, the zebra mussel population expanded very rapidly in the Hudson and has now apparently reached a self-limiting phase in which larvae are strongly suppressed by the adults. A companion paper (Caraco et al. 1996) shows that the zebra mussel has had enormous impacts on the Hudson's phytoplankton that differ in important ways from what has been described for lakes.

Our study focused on the freshwater part of the Hudson River estuary, extending from the dam at Troy, New York, (river kilometre (RKM) 248; i.e., 248 km upriver from the southern end of Manhattan in New York City) to Newburgh, New York (RKM 99). The study area covers 140 km² and has a mean depth of 8.3 m (Gladden et al. 1988). The entire study reach is subject to tides of 0.8-1.6 m and is well mixed vertically by tidal flows. Water in the Hudson is hard (Ca^{2+} concentration = 22-30 mg/L), nutrient rich (NO_3-N concentration = 0.5-1 mg/L; soluble reactive P concentration = 3-30 µg/L), and moderately turbid (Secchi disk depth = 1-2 m; concentration of suspended solids = ~20 mg/L) (Cole et al. 1991, 1992; Findlay et al. 199 1 a, 1991b). The sediments are dominated by various mixes of sand, silt, and clay, but about 7% of the bottom is rocky (Simpson et al. 1986; D.L. Strayer, J. Powell, P. Ambrose, L.C. Smith, M.L. Pace, and D.T. Fischer, unpublished data). The Mohawk River enters the Hudson just above the head of the estuary. The Mohawk is part of the New York State Barge Canal, which connects the Hudson with lakes Erie

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and Ontario and has been seen as a potential invasion route for the zebra mussel (e.g., Griffiths et al. 1991).

Methods

To estimate the size of the zebra mussel population in the Hudson, we subdivided the freshwater estuary into nine sampling strata, representing three habitats (rocks, fine-grained sediments, and unionid clams) in each of three geographic strata (RKM 999151, RKM 151-213, RKM 213-248). We estimated the extent of rocky versus fine-grained (i.e., sand-silt-clay) sediments by taking petite PONAR grabs (15 x 15 cm) at 253 sites throughout the estuary. If we failed to retrieve a sample in repeated (more than five) grabs, we classified the site as rocky; otherwise, we classified the site as fine grained.

Zebra mussel densities on rocks were estimated in two ways. In 1991-1992, we took rock samples using a modified oyster dredge from four (1991) or nine (1992) sites in the infested area of the river. We counted the number of zebra mussels on each rock and estimated rock area by covering rocks with a layer of aluminum foil and weighing the foil. Surface areas measured in this way were converted to square metres of river bottom occupied by the rock by dividing by 3 (cf. Bailey et al. 1995). In 1993-1994, divers collected at least 10 rocks from each of six sites in the river (two in each geographic stratum). We counted the number of zebra mussels per rock and estimated the area of the river bottom occupied by the rock as the maximal projected area of the rock. In 1992-1994, we measured the shell lengths (and dry masses, see below) of subsamples of zebra mussels from each rock.

To estimate the number of zebra mussels on fine-grained sediments and unionids, we took samples from 16 sites in each of the three geographic strata. Five samples were collected from each site with a standard (22.9 X 22.9 cm) PONAR grab and sieved in the field through a 2.8-mm mesh. Each unionid in the sample was bagged separately and the sieve residue frozen. Zebra mussels and unionids were removed from thawed samples in the laboratory and counted.

To follow dynamics of zebra mussel populations on rocky shorelines, we took monthly samples from a rocky beach on Cruger Island (RKM 158). Five or 10 rocks were taken from each of three elevations: 34 cm above mean low tide, mean low tide, and 34 cm below mean low tide. The maximal projected area and the number of zebra mussels on each rock were recorded.

We estimated the numbers and size of young-of-the-year (YOY) zebra mussels by sampling navigation buoys in 1991-1994. In December or January, the U.S. Coast Guard replaces summer navigation buoys in the Hudson with winter buoys. About 40 of these buoys are changed in the freshwater tidal reach of the Hudson. Because these buoys are stored in a yard over the winter, there is no carry-over of mussels from year to year. We estimated the number of YOY per metre circumference of the buoy (we used circumference rather than area because most zebra mussels settled in a band along a seam near the base of the buoys) as an index of year-class strength and removed a sample of 10 mussels from each buoy for later measurement of shell length.

Veligers were sampled biweekly during the ice-free season at Kingston, New York, by pumping 42 L of surface water through a 73-μm mesh plankton net. In 1992-1993, samples were counted live upon arrival in the laboratory. In 1994, samples were preserved in buffered formalin and counted using cross-polarized light (Marsden 1992). All counts were made with a stereomicroscope at magnifications of 25x or greater.

To estimate the biomass of the zebra mussel population, we regressed dry body mass (dried overnight at 60°C) on shell length and applied these equations to shell lengths and densities observed in the field.

To estimate zebra mussel filtration rates in the field, we applied the regression of Kryger and Riisgard (1988) to observed numbers and sizes of zebra mussels in the Hudson River. Our own estimates

of filtration rates of zebra mussels on natural Hudson River water agree closely with Kryger and Riisgard's results (Roditi et al. 1996). (We did not use the results of Roditi et al. here because they are not normalized for body size of zebra mussels.) All estimates of filtration rates presented here are based on 20°C.

We roughly estimated the food demands (assimilation) of the zebra mussel population by summing estimates of respiration and production. To estimate respiration, we fitted a regression through the laboratory data of Dorgelo and Smeenk (1988), Sprung and Borcherding (1991, day 2 data), and Quigley et al. (1993), producing the following general equation:

$$R = 61.9 \text{DM}^{-0.4653} \times 10^{0.01208\,T}$$

where R is respiration (milligrams O_2 per gram dry matter per day), DM is dry body mass (milligrams), and T is water temperature (°C) (for the log-log regression, adjusted $r^2 = 0.92$, n = 11, p < 0.0001). We estimated respiration from this equation using observed body sizes and water temperatures from the Hudson River, assuming respiration was negligible before 3 April and after 2 December, when water temperatures were low (<4°C). We estimated production in two ways: from respiration, assuming a net growth efficiency of 30% (cf. Valiela 1984), and from biomass, assuming an annual production to biomass ratio of 1 (Stanczykowska 1976; Waters 1977; Cleven and Frenzel 1993).

Some of the confidence intervals we present would have been difficult or impossible to calculate using conventional statistical methods and were estimated instead by bootstrap methods using Resampling Stats (Bruce 1993) with 1000 runs.

Results and discussion

Chronology of the invasion

Zebra mussels were first seen in the Hudson near Catskill in May 1991 (Fig. 1). By the end of 1991, zebra mussels had spread downriver 80 km to Newburgh, but just one animal was seen more than 5 km upriver of Catskill, despite extensive searches of the upper estuary (Fig. 1). Only 1 year later, zebra mussels were found everywhere that we sampled in the freshwater and oligohaline parts of the estuary (Fig. 1), reaching as far downriver as northern Haverstraw Bay, where salinity during the settling season was 3-5 ppt (Walton 1993). The range in the estuary has not expanded since 1992 and presumably now is limited by salinity.

The pattern of spread shows that the Hudson received two distinct invasions. The first invasion came near Catskill from some unknown human vector (e.g., barges, boat trailers) and an unknown source, probably in 1989 or 1990. The population must have been large by the end of 1990 (at least ~10^6 animals; cf. Fig. 2), so the initial inoculum would have had to have been very large if it came in 1990. Alternatively, the population may have been building from a small inoculum that came no later than 1989. The initial invasion of the Hudson represented a large jump across country by the zebra mussel, as the nearest potential source populations were in Lake Erie in 1989 and Lake Ontario and the western part of the Erie Canal in 1990 (O'Neill and Dextrase 1994). A second invasion occurred in 1992, when zebra mussels were carried into the head of the estuary by fluvial transport from the Mohawk River. (The Mohawk itself was not infested until 1991 (O'Neill and Dextrase 1994).) The two populations merged in 1992.

Growth of the population and its activity

The spread of zebra mussels in the Hudson was accompanied

Fig. 1. Spread of zebra mussels through the Hudson River estuary, 1991-1992. Solid circles show sites where zebra mussels were found, and open circles show sites where zebra mussels were sought but not found. From left to right: September 1990 through June 1991, September through December 1991, and September through December 1992.
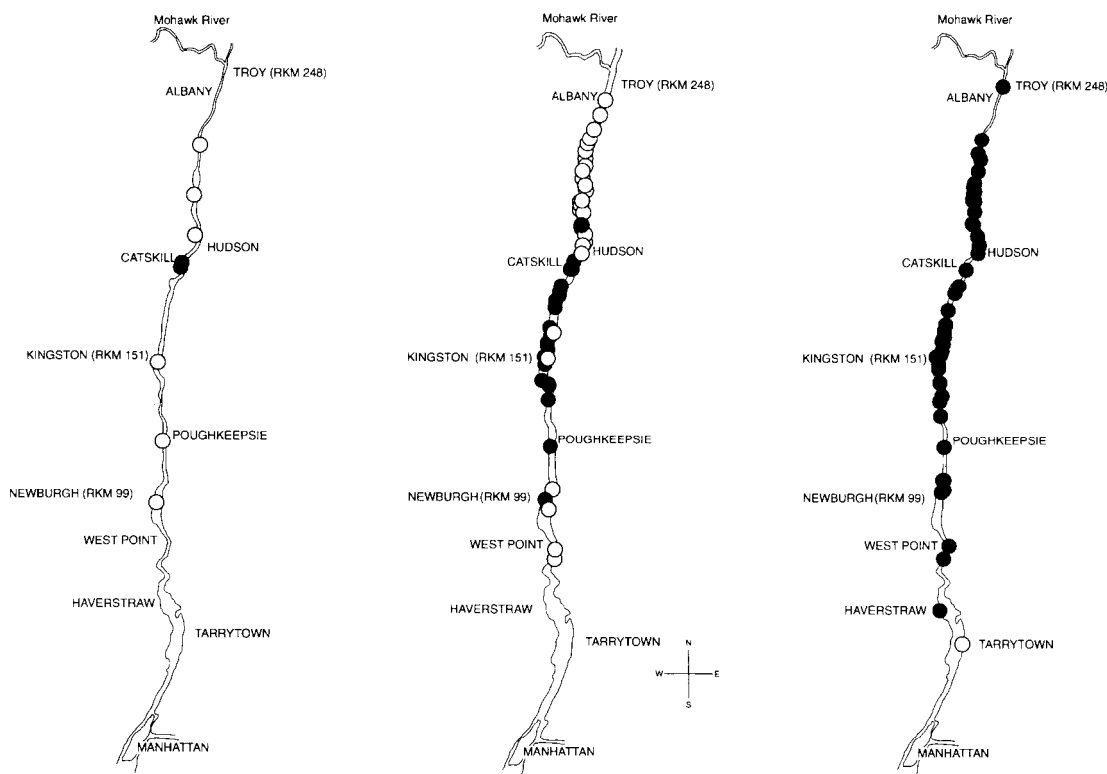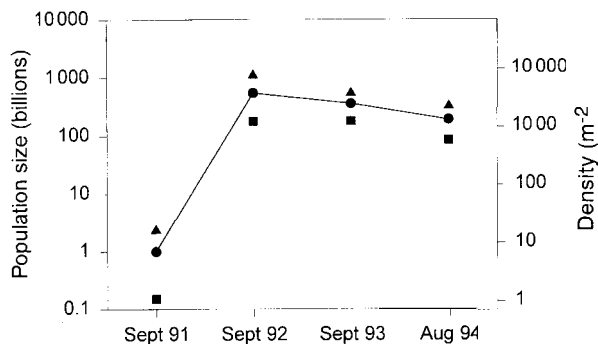

Fig. 2. Growth of the zebra mussel population in the Hudson River estuary, 1991-1994, expressed both as total population size and as mean density over the entire study area (RKM 999248). Shown are the means (line) and 95% confidence limits (squares and triangles), as estimated by bootstrap methods.

Table 1. Importance of the zebra mussel population in the freshwater, tidal Hudson River.

	Zebra mussels	All zoobenthos	All heterotrophs
Biomass (g DM·m^{-2})	21	11	15
Filtration rate (m^3·m^{-2}·day^{-1})	6	0.1	~0.25
Respiration (g C·m^{-2}·year^{-1})	105	—	570

Note: Zebra mussel data are means from 1993–1994; other data are from the preinvasion period (1986-1991). Data are from Lints et al. (1992), Howarth et al. (1992), Limburg (1993), Strayer et al. (1994), and M.L. Pace (unpublished data).

During 1993, assimilation by the zebra mussel population was estimated to be about 120–150 g C·m^{-2}·year^{-1}. Because this is somewhat larger than current rates of phytoplankton production in the Hudson (estimated to be about 50 g C·m^{-2}·year^{-1}; N. Caraco, Institute of Ecosystem Studies, personal communication), zebra mussels may have fed on bacteria and detritus as well as phytoplankton. The demands of the zebra mussel population are large compared either with summed inputs of organic carbon to the freshwater tidal Hudson (~820 g C·m^{-2}·year^{-1}; Howarth et al. 1992) or with total heterotrophic respiration in the system (Table 1).

Reproduction, survival, and growth

Survival and growth rates of zebra mussels in the Hudson have varied greatly among years. Although veligers were abundant throughout much of the summers of 1992-1994 (Fig. 4), year-class strength varied dramatically over this period, especially

by rapid growth in the size and activity of the population (Fig. 2, Table 1). By the end of 1992, the population had reached 550 billion individuals and a biomass of 28 g DM/m^2 (shell free), averaged over the entire freshwater estuary. The estimated filtration rate (normalized to 20°C) of the zebra mussel population was almost 8 m^3·m^{-2}·day^{-1} in October 1992. The density, biomass, and filtration rate of the population all declined from 1992 to 1994, but remained high. Because of the uneven distribution of suitable substrata in the estuary (see below), the numbers and activity of zebra mussels were likewise distributed unevenly in the estuary (Fig. 3).

Fig. 3. Development of the zebra mussel population in different sections of the Hudson estuary: upper (RKM 213-248), middle (RKM 151-213), and lower (RKM 99-151), 1991-1994.
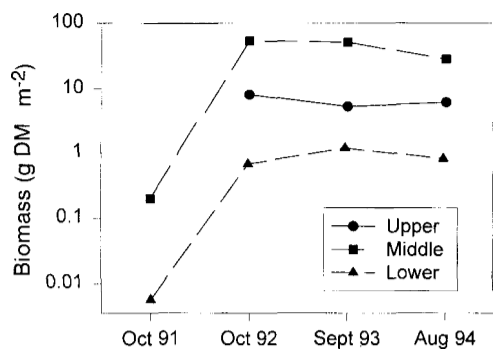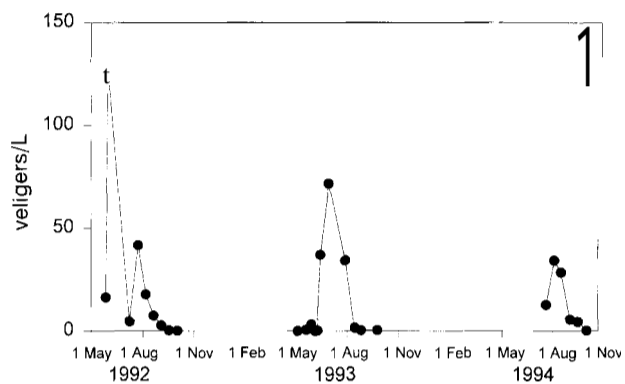
Fig. 4. Density of veligers in the Hudson River at Kingston (RKM 151), 1992-1994.

Fig. 5. Numbers and growth of young-of-the-year (YOY) zebra mussels in the Hudson estuary, 1991-1994. (a) YOY index (i.e., average number of YOY on navigation buoys per metre circumference). Line shows means and other symbols show 95% confidence limits, as estimated by bootstrap methods. Note logarithmic scale. (b) YOY index normalized for the estimated number of adult spawners in the estuary. Note logarithmic scale. (c) Mean body mass (mg DM, shell free) of YOY (n = 1666485) taken from navigation buoys at the close of the growing season. Vertical lines show 95% confidence interval around the means, estimated by conventional statistical methods.
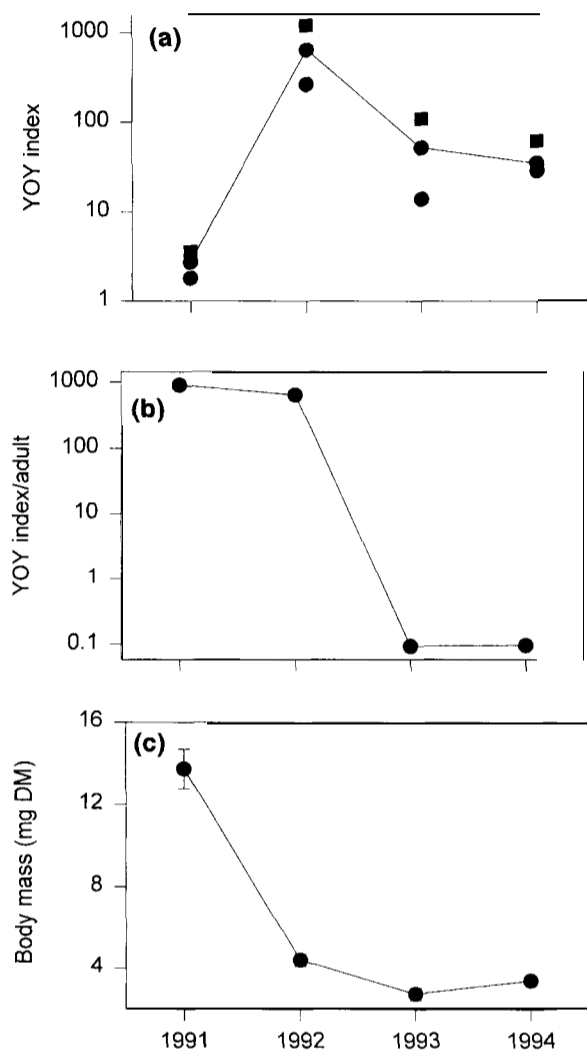
when normalized for the number of adult spawners (Fig. 5). The 1993 and 1994 year-classes were so small that they scarcely were detectable in benthic samples (Fig. 6). Growth of YOY zebra mussels likewise varied from year to year, declining sharply from the early stages of colonization (Fig. 5).

Circumstantial evidence strongly suggests that the poor growth and recruitment of YOY in 1993 and 1994 were caused by inadequate food supply. Filtration by zebra mussels reduced phytoplankton biomass in September 1992 through 1994 to 10-20% of preinvasion levels (Caraco et al. 1996). The hypothesis that an inadequate food supply limited zebra mussel growth and recruitment is consistent with the observations that both growth and recruitment were reduced after the phytoplankton crash and that recruitment was high in 1992, but postrecruitment growth was poor. (The phytoplankton crash occurred in August-September, after much settling could have occurred but before most postsettling growth.)
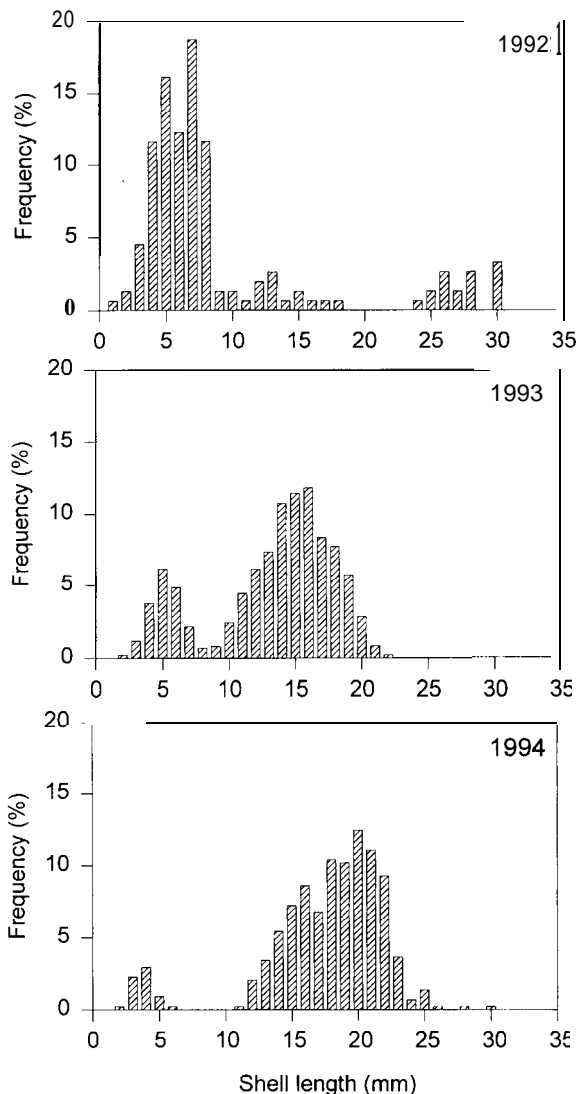
We doubt that environmental conditions, inadequate space for larval settlement, cannibalism of larvae by adult zebra mussels, or predation by other species could have been responsible for fluctuations in YOY recruitment and growth. In 1993-1994, important environmental variables such as temperature, freshwater flow, nutrients (N, P), and calcium were well within the ranges observed in previous years. As for local competition for space, even substrata that lacked adults during the settling season (e.g., navigation buoys, docks, boat hulls) were not heavily colonized in 1993-1994 (Fig. 5 and unpub-

lished observations). Adult zebra mussels can consume their own larvae (MacIsaac et al. 1991), and filtration rates of zebra mussels in the Hudson were high (Table 1), so cannibalism may have been partly responsible for the poor recruitment in 1993-1994. Cannibalism cannot be the only important mechanism, though; it is hard to see how cannibalism by itself could have reduced the size as well as the number of YOY. Although predators (e.g., fish, blue crabs (Callinectes sapidus)) in the Hudson eat zebra mussels (Molloy et al. 1994; Limburg and Ahrend 1995; Chandler and Schmidt 1995) we do not think they were responsible for the poor growth and recruitment of zebra mussels in 1993-1994. Unless the controlling predator

Fig. 6. Size distribution of zebra mussels in the Hudson River in September, 1992-1994.

Table 2. Average densities of zebra mussels on various substrata in the Hudson River estuary, September-October 1993.

Substratum	Density (no./m^2)
Rocks in deep (>5 m) water	17000
Soft sediments	80
Unionid clams	4.4[a]
Rocky shoreline[b]	50

[a]Equivalent to 0.5 zebra mussels per unionid.
[b]Between 0.3 m above and 0.3 m below mean low tide

Fig. 7. Population density of zebra mussels on a rocky shoreline in the Hudson River, 1992-1993. Data are means of three elevations (see text); vertical bars show 95% confidence intervals around the means, as estimated by conventional statistical methods. Note the winter decline in densities and the absence of a 1993 year-class.

selectively consumed the larger YOY or had a strongly seasonal activity (allowing only the tail end of the year-class to survive), it would not have caused the YOY to be both smaller and fewer in number. We do not know of any abundant predator in the Hudson that meets these requirements. Furthermore, blue crabs were very scarce in the freshwater tidal Hudson in 1993-1994 but abundant in 1992 (J. Powell, unpublished data).

Ecological distribution within the estuary
The distribution of zebra mussels in the Hudson estuary is strongly controlled by the distribution of suitable substrata (Table 2). The highest densities are found on rocks in deep (>5 m) water. Even though such deep-water rocky areas cover only 7% of the estuary, they support >95% of the zebra mussel population. Rocky areas in shallow water occasionally support modest numbers of zebra mussels but are wiped nearly clean in the winter, probably by ice and severe cold (Fig. 7). In shallow waters, zebra mussels are restricted almost entirely to the tops of rocks, in contrast to deep water, where tops, sides,
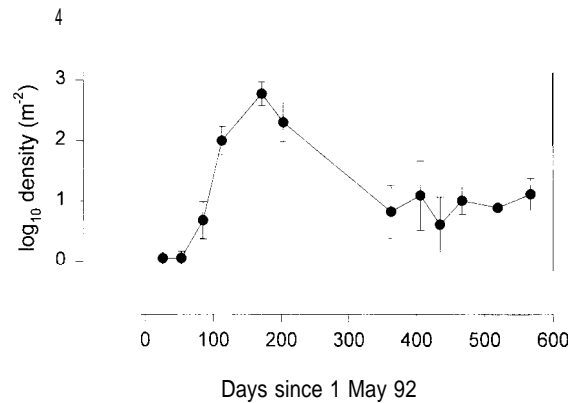
and bottoms are well colonized. Fine-grained sediments (sand, silt, and clay) are populated sparsely by zebra mussels, which live on the numerous objects (e.g., sticks, coal, stones, shells) embedded in such fine sediments. These scattered colonizable objects have not served as nuclei for large zebra mussel colonies in the Hudson, as has been observed in some other rivers and estuaries (Mordukhai-Boltovskoi 1960; Sparks 1994).

Although living unionid clams are heavily infested by zebra mussels in many lakes and rivers (see Ricciardi et al. 1995 for a review) and were predicted to support a large population of zebra mussels in the Hudson (Strayer and Smith 1993; Strayer et al. 1994), they scarcely have been colonized up to 1994. According to the model of Ricciardi et al. (1995), the average infestation in the Hudson should be 53 mussels/unionid, which would translate to 426 mussels/m^2 on unionids. We do not know why unionids are so lightly infested in the Hudson or whether this light infestation is transient or permanent.

In addition to the substrata listed in Table 2, macrophytes (especially *Vallisneria*) in the Hudson support some zebra mussels during the late summer and fall. We have not estimated the size of such plant-supported populations, which are substantial in some systems, at least seasonally (e.g., Lewandowski 1982).

General discussion
The chronology of the zebra mussel invasion of the Hudson confirms two generalizations about zebra mussel populations. First, the appearance of a disjunct population in the middle of the Hudson shows the importance of human vectors in moving

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Fig. 8. Suggested domains of substratum and food limitation of zebra mussel populations.
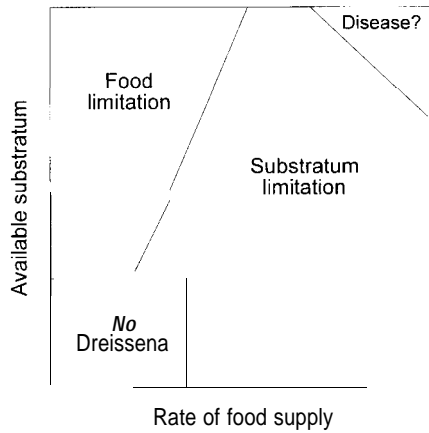
zebra mussels across country, as has been seen elsewhere in North America and Europe. Second, population growth in the Hudson was extremely rapid, providing yet another example of the explosive potential of zebra mussel populations. Only 17 months after their first detection in the Hudson, zebra mussels constituted >70% of zoobenthic biomass and had dramatically altered the pelagic ecosystem (Caraco et al. 1996).

A third generalization, that zebra mussel populations become limited after an initial explosive phase, must of course be true, but has not been described before in detail. In the Hudson, the limitation appears to come not from external factors (predators or pathogens) or from competition among settled animals for space or food, but rather from control of larval survival and growth by competition for food with adults. This probably is not the way that most zebra mussel populations are limited, but may occur where adult impacts on phytoplankton are very severe. Such severe impacts are most likely to occur in systems where there is ample substratum for adult settlement. Furthermore, Caraco et al. (1996) argued that zebra mussels have the most severe impacts on phytoplankton biomass in systems with high concentrations of suspended inorganic particles. Thus, we might expect adult–larval competition for food to limit zebra mussel populations most frequently in turbid systems with ample rocky areas (rivers?) (Fig. 8). In systems with ample food and limited substrata (lakes?), we might expect the population to be substratum limited. In addition, the dynamics of food-limited zebra mussel populations might be erratic, as dominant year-classes develop, monopolize food resources, and then die.

The suggestion that some zebra mussel populations might be limited by food rather than substratum seems to contradict existing models for zebra mussel populations. The only effective model for predicting the population density of zebra mussels (Mellina and Rasmussen 1994) is based on substratum limitation. If the zebra mussel population in the Hudson is not limited by substratum, why does it fall on Mellina and Rasmussen's regression line? (The Hudson was one of the systems studied by these authors.) A possible resolution of this dilemma is to distinguish within-system patterns from among-system patterns of density variation. Even if food rather than substratum is limiting, density within a system should be correlated with substratum particle size. Across systems, substra-

tum-limited populations should fall on a line, with food-limited populations in a cloud below that line. Mellina and Rasmussen's (1994) analysis showed that lakes fall on a well-defined line distinctly above a poorly defined line containing data from rivers. Perhaps this shows that many lacustrine populations are limited by substratum, while most riverine populations are limited by food, as we postulated above. If our speculative analysis is correct, not all zebra mussel populations lie in the domain of substratum-based predictive models (Fig. 8). Therefore, it will be important to determine the number, dynamics, and ecological effects of food-limited zebra mussel populations, such as the one in the Hudson.

Acknowledgements

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