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The zoobenthos of the freshwater tidal Hudson River and its response to the zebra mussel (*Dreissena polymorpha*) invasion

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with 21 figures, 9 tables and 1 appendix

Abstract: We describe the composition of the zoobenthos of the freshwater, tidal Hudson River, its relationships to environmental variables, and its response to the zebra mussel (*Dreissena polymorpha*) invasion. We collected samples using a petite PONAR grab and a 0.5-mm mesh sieve at 28 sites throughout the freshwater, tidal Hudson in 1990–97. The fauna contained more than 200 species, and was dominated by tubificid oligochaetes, unionid mussels, amphipods, and chironomid midges. Average density and biomass of the zoobenthos were 10,000/m^2 and 7.4 g DM/m^2 (before the zebra mussel invasion). The composition of the fauna was determined chiefly by the presence or absence of rooted vegetation and by salinity. Within the range of sediments sampled (clay to medium sand), sediment grain size and organic content had only a weak influence on the fauna. We discuss the biology, distribution, and response to the zebra mussel invasion for all common zoobenthic species in the Hudson. The zebra mussel invasion caused populations of benthic planktivores (bivalves, tanytarsine midges, and *Chaoborus*) to decline by 35–100%. Populations of other benthic animals typically rose in shallow-water, vegetated sites, and fell in unvegetated, deepwater sites. On a riverwide basis, the zebra mussel invasion caused density and biomass of all other benthic animals to fall by 38% and 57%, respectively. Benthic animals played important roles in the Hudson ecosystem as suspension-feeders, fish food, and sediment mixers. The zebra mussel invasion changed the importance of these roles.

Key words: Invasive species, zoobenthos biomass, zoobenthos diversity, suspension feeders.

Introduction

Large rivers have been important to humans for centuries as sites for settlements, builders of agricultural land, routes for transportation, and sources of fresh water and valuable biological resources such as migratory fish. Because of this intensive human use, many large rivers have been highly modified or severely degraded. Large rivers also support a characteristic and often endemic biota. Despite these compelling reasons for focusing on the ecology of large rivers, these systems are understudied by aquatic ecologists. This relative neglect probably stems from the logistical difficulties of working in large rivers and from an aversion by some ecologists to work in non-pristine ecosystems. Thus, much remains unknown about the structure and function of these important ecosystems.

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The zoobenthos is one of the most important and interesting parts of large river ecosystems. The zoobenthos of large rivers often contains hundreds of species (e. g., Beckett et al. 1983; Caspers 1991; Moog et al. 1995), many of them endemic (e. g., Neves et al. 1997; Dudgeon 2000). Because zooplankton may be sparse as a result of advective losses (e. g., Pace et al. 1992), benthic animals often are the dominant macroconsumers in large rivers, and may play important roles in large-river food webs (e. g., Cohen et al. 1984; Effler et al. 1997; Welker & Walz 1998; Strayer et al. 1999; Malmqvist et al. 2001). Further, the zoobenthos is highly sensitive to human impacts (e. g., Hart & Fuller 1974; Rosenberg & Resh 1993), and so has changed in many rivers as a result of human activities (e. g., Diaz 1989; Fruget 1992; Humpesch 1996). In fact, many large-river benthic animals are now extinct or endangered as a result of human activities (e. g., Neves et al. 1997; Dudgeon 2000; Strayer 2001).

Large rivers also have been foci for invasions of exotic species. Major vectors for movement of exotic freshwater species include shipping, deliberate stocking of sport fish and other "useful" plants and animals, and inadvertent escapes of plants and animals from agriculture, aquaculture, and the pet trade (Mills et al. 1993, 1997). Many large rivers are centers of intensive human activity and thus have been subjected to many introductions from these vectors. As a result, many large rivers contain a large and growing number of exotic species. For example, the fresh waters of the Hudson River basin contain at least 113 exotic species of macroscopic plants and animals, and new invasions occur at the rate of about 6 species/decade (Mills et al. 1996, 1997). One of the most prominent recent invaders is the zebra mussel (*Dreissena polymorpha*), which first appeared in the Hudson in 1991, and has been abundant since late 1992 (Strayer et al. 1996). Zebra mussels may have large effects on freshwater ecosystems (MacIsaac 1996; Karatayev et al. 1997; Strayer et al. 1999). Although several studies have shown that zebra mussels have strong local effects on the zoobenthos (Stewart & Haynes 1994; Botts et al. 1996; Ricciardi et al. 1997; Stewart et al. 1998a; Horvath et al. 1999; Kuhns & Berg 1999), ecologists have not often looked beyond these local effects to assess the effects of zebra mussels on benthic animals at the scale of whole ecosystems (but see Dermott & Kerec 1997; Nalepa et al. 1998).

Our goals were to (1) describe the composition and abundance of the zoobenthos in the freshwater tidal Hudson River; (2) to investigate how community composition varied with environmental factors such as water depth, sediment characteristics, the presence of rooted plants, and geographical position along the river; (3) to describe how the zebra mussel invasion affected the zoobenthos; and (4) to make a preliminary assessment of the roles that benthic animals played in the Hudson River ecosystem. Impacts of zebra mussels on the zoobenthos were described in a preliminary paper based on taxonomically aggregated data from 1990–95 (Strayer et al. 1998). Here, we use a longer run of data (1990–97) at the species or genus level to analyse in detail zebra mussel impacts on the zoobenthos.

The study area

The study area was the freshwater tidal Hudson River (Fig. 1), which extends from the dam at Troy (RKM 248 = river kilometers north of the mouth of the Hudson at Battery Park in New York City) to approximately Newburgh (RKM 99), where seawater salinity often is detectable during late summer. The water in the Hudson is warm, alkaline, and nutrient-rich (Table 1). Except below RKM 120, where salinity sometimes reaches 1–2 psu (~ ppt) during times of low freshwater flow, the water in

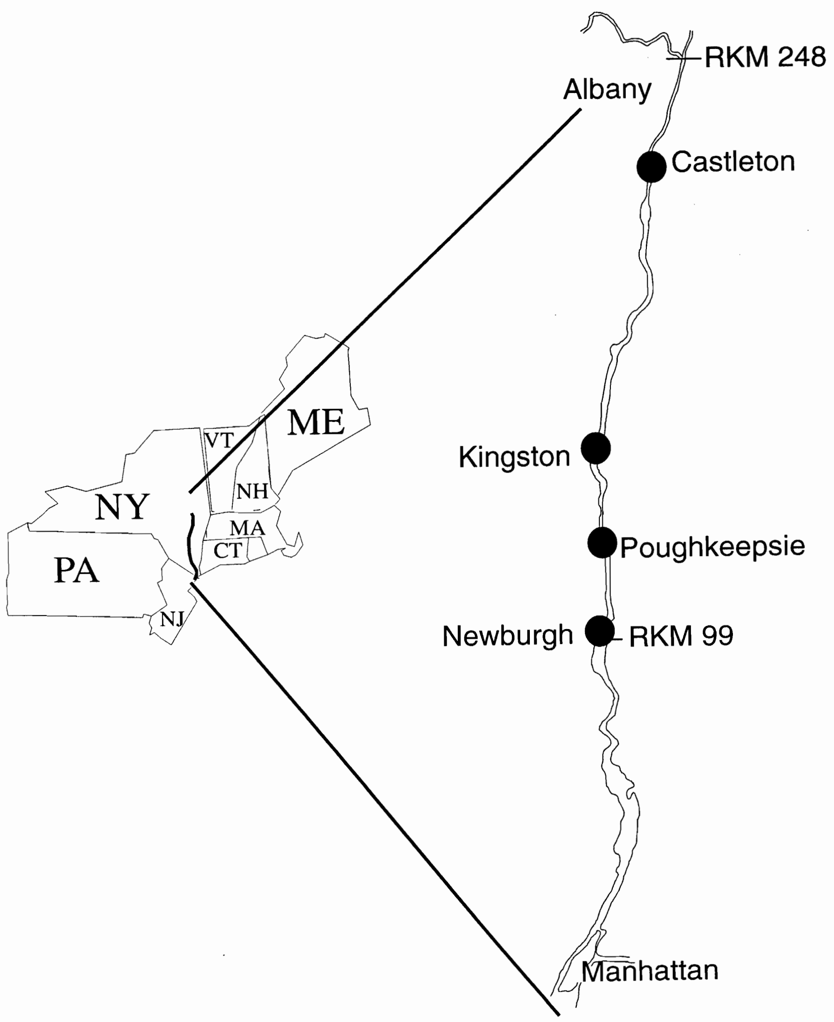

Fig. 1. Map of the study area showing the main study sites near Newburgh (RKM 100), Poughkeepsie (RKM 122), Kingston (RKM 146), and Castleton (RKM 216). The freshwater tidal section of the Hudson River extends roughly from RKM 99 to RKM 248.

Table 1. Selected physiochemical characteristics of the freshwater tidal Hudson River before the zebra mussel invasion, summarized from Cooper et al. (1988), Gladden et al. (1988), Findlay et al. (1991), Abood et al. (1992), Mancroni et al. (1992), Ashizawa & Cole (1994), and Caraco et al. (1997).

Variable	Mean (range)
Area	140 km^2
Width	0.9 km
Depth	8.3 m (0–30)
Temperature	12.2°C (0–30)
Mean annual discharge	384–533 m^3/s
pH	7.6
Calcium	27 mg/l
NO_3–N	0.5 mg/l
PO_4–P	11 μg/l
Suspended solids	20 mg/l

Table 2. Characteristics of the 28 stations sampled in 1990–92.

Variable	Mean (range)
Water depth (m)	9.2 (1.1–18.7)
Median phi	5.3 (2.2–7.8)
% clay	18.8 (2.6–42.1)
% silt	38.1 (4.0–72.0)
% 63–250 μm sand	28.8 (0–87.3)
% 250–1000 μm sand	6.8 (0.9–56.1)
% >1000 μm sand	6.8 (0–62.5)
% loss on ignition	5.6 (1.7–17.8)

the study area is fresh. Twice-daily tides of 0.8–1.6 m amplitude occur throughout the entire study area. Net movement of water downriver is dwarfed by tidal flows, which keep the water column well mixed vertically (Limburg et al. 1986; Findlay et al. 1991). Although parts of the Hudson were badly polluted by industrial and municipal waste (e.g., Boyle 1979; Rohmann 1985; Limburg et al. 1986; Rohmann & Lilienthal 1987), and significant contamination remains in places, overall water quality in the study area is good, and the freshwater tidal Hudson is used for recreation and drinking water. Simpson et al. (1986) concluded that pollution was not a primary determinant of benthic community structure in the study area.

The mean depth of water in the study reach is 8.3 m (Table 1), but ~ 15% of the study area is less than 3 m deep at low tide and supports rooted vegetation (chiefly *Vallisneria americana, Trapa natans, Potamogeton* spp., and *Myriophyllum spicatum*) (Harley & Findlay 1994; Caraco et al. 2000). About 7% of the river bottom is stony, with the remainder being composed of various combinations of sand, silt, and clay with a high organic content (cf. Table 2).

The zoobenthos of the freshwater tidal Hudson River was described by Townes (1937), Hirschfield et al. (1966), and Howells et al. (1969), as well as in scattered papers dealing with selected taxonomic groups (e.g., the mollusk surveys summarized by Strayer 1987). These early surveys presented few quantitative data and examined few sites, and so offered limited insight into the zoobenthic community. A more comprehensive survey of zoobenthos by the Boyce Thompson Institute (Ristich et al. 1977; Weinstein 1977) focused on the lower river, and barely reached up into the freshwater section of the river. Further, they identified oligochaetes and chironomids only to family. Thus, very little information on the zoobenthos of the freshwater tidal Hudson was available until the surveys of SIMPSON et al. (1984, 1986) and BODE et al. (1986) in 1983 and 1984. These surveys extended over the length of the freshwater tidal Hudson, and used quantitative methods and a fine level of taxonomic detail. We include some of the data from SIMPSON et al.'s and BODE et al.'s surveys, and present more details about their methods below. Also in the 1980s, FINDLAY et al. (1989) described the macroinvertebrate communities living among beds of water chestnut (*Trapa natans*) in the mid-Hudson River.

Materials and methods

The results we present here came from several more or less discrete studies. Most of the data came from an annual survey of the macrozoobenthos from 1990–97 that was specifically designed to assess the impacts of the zebra mussel invasion. We sampled zoobenthos along four transects (Castleton = RKM 216, Kingston = RKM 146, Poughkeepsie = RKM 122, Newburgh = RKM 100; Fig. 1). In 1990–92, we sampled each transect at eight stations evenly spaced across the river, except at Castleton where we sampled only four stations across the narrow channel. In 1993–97, we reduced the number of stations to two per transect: one in shallow water and the other in deep water, if possible. All of the shallow-water sites (< 1 m deep at low tide) were heavily vegetated, while none of the deepwater sites (> 5 m deep at low tide) supported rooted vegetation. Samples were taken in September–October. Sampling stations were relocated by using loran, which has a precision of approximately 35 m. Because these stations all were on soft sediments, where zebra mussels were uncommon (mean soft-sediment density in 1993–97 was 143/m^2), they were largely outside the zone of direct influence of zebra mussel beds (i. e., the local increases in biodeposition and shelter described by BOTTS et al. (1996), RICCIARDI et al. (1997), STEWART et al. (1998a), HORVATH et al. (1999), and KUHNS & BERG (1999)).

We used a petite PONAR grab (15 × 15 cm) to take five replicate samples at each station. We lowered the PONAR slowly (< 1 m/s) to the sediment surface to avoid creating a pressure wave. We sieved samples in the field through a 0.5-mm mesh sieve and preserved them in 10% formalin. Before sieving the sample, we removed a small subsample (approximately 10 ml) for sediment analyses. This subsample was refrigerated immediately, and frozen upon return to the laboratory.

In the laboratory, faunal samples were stained overnight with rose bengal, then sorted under 6 × magnification. Animals were counted, removed from the samples, and placed into 10% formalin, 70% ethanol, or Koenike's fluid for long-term storage. At least 20% of the samples were picked twice to allow for calculation of sorting efficiency using the removal method (ZIPPIN 1958). Subsamples of preserved animals (1–20 animals per replicate sample for chironomids and oligochaetes) were identified to genus or species, following slide-mounting where necessary. To account for fragmentation of oligochaetes, we counted only specimens that had a head. Sources used for identification and nomenclature include THORNE & SWANGER (1936), HYMAN (1959), GOSNER (1971), BOUSFIELD (1973), ANDRASSY (1981, 1988), EBSARY (1982), WIEDERHOLM (1983), BRINKHURST (1986), PENNAK (1989), OLIVER et al. (1990), PECKARSKY et al. (1990), THORP & COVICH (1991), SMITH (1995), MERRITT & CUMMINS (1996), and WIGGINS (1996). Voucher specimens from this survey were deposited in the American Museum of Natural History, New York. Sediment samples were thawed, then analysed for grain size distribution by the hydrometer method, followed by dry-sieving of the sand fraction (GEE & BAUDER 1986). Organic content was estimated by loss on ignition after 16 hours at 500 °C. Biomass of animals other than bivalves was measured on preserved animals that were dried overnight at 60 °C. To account for mass loss in preservative, we adjusted the biomass of animals other than bivalves up by 10% (LEUVEN et al. 1985). Bivalve biomasses were estimated by weighing the bodies of animals dried for 24 hours at 60 °C (STRAYER & SMITH 1996; STRAYER et al. 1996).

We will refer to data from several other studies conducted in 1990–97 as well. Data on zebra mussels were taken from a study that began with the appearance of this species in the Hudson in

1991. Samples were taken once or twice a year by diver (rocks) or standard (23 cm × 23 cm) PONAR at 54 sites arrayed in a stratified random design throughout the freshwater tidal Hudson. From these samples, we estimated the abundance, shell length, and body condition of zebra mussels. Results of this study through 1995 were published by Strayer et al. (1996).

Data on unionid mussels were taken from annual measurements of the abundance, species composition, fouling by zebra mussels, and body condition of unionid mussels in the freshwater tidal Hudson begun in 1991. This study was based on five replicate samples taken at 48 sites with a standard PONAR grab and sieved through a 2.8-mm mesh. The results of this survey through 1995 have been published (Strayer et al. 1994; Strayer & Smith 1996).

We conduced a supplementary study of the zoobenthos of a rocky shoreline at RKM 158 in 1992–94 (Strayer & Smith 2000). This study encompassed the intertidal zone as well as the upper subtidal, and was designed to estimate the abundance and taxonomic composition of benthic animals, including zebra mussels. Rocks were collected and scrubbed by hand, and the sample was collected on a 0.5-mm mesh screen.

In addition to the work done in 1990–97, we present data from Simpson et al.'s survey of the river in 1983 (Simpson et al. 1984, 1986). In this survey, samples were taken at 16 sites in the navigation channel (i. e., in deep water, near the center of the river) between RKM 108 and 227. Simpson et al. took three replicate samples at each station monthly in June–September using a petite PONAR grab and a 0.59-mm mesh sieve. They also collected samples for grain size and carbon analysis of the sediments. A summary of this survey was published (Simpson et al. 1986), with many additional data given in a report (Simpson et al. 1984). This survey was extended by samples taken in the upper estuary (RKM 227–247) twice in 1984 using both petite PONAR and modified Hess samplers (Bode et al. 1986).

The 1983–84 and 1990–97 surveys both were quantitative and taxonomically detailed, and complement one another. The 1983–84 surveys describe the longitudinal distribution of the zoobenthos in detail, and included seasonal variation. They were based on one year's data and provided limited information on the zoobenthos away from the navigation channel. The 1990–97 surveys were designed to describe lateral and interannual variation in the zoobenthos, and much less detail on longitudinal or seasonal variation in the zoobenthos. Because of the different coverage of the two surveys, they produced very different estimates of zoobenthic abundance and community structure in the Hudson. Taken together, though, these two surveys provide a fairly complete picture of the zoobenthos in the freshwater tidal Hudson.

We performed several kinds of statistical analyses to describe the Hudson's zoobenthos and its response to the zebra mussel invasion. We described overall community composition and its relationships to environmental variables by using canonical correspondence analysis. We used simple and multiple regressions to correlate the abundance of benthic animals with environmental variables. To test for differences in animal abundance between deepwater, unvegetated sites and shallow-water, vegetated sites, we performed unpaired, two-tailed t-tests. These descriptions of community composition are based on samples taken before the zebra mussel invasion, in 1990–92, and include 84 samples (28 sites times 3 years).

We tested the hypothesis that the zebra mussel invasion caused a simple temporal change in macrozoobenthic densities by performing a paired, two-tailed t-test on mean densities at each sampling site before (1990–92) and after (1993–97) the invasion. To test whether the impacts of the zebra mussel invasion were different in shallow-water sediments than in deep-water sediments, we tested for a depth × time interaction as follows. We separated our stations into shallow-water stations (low-water depth < 1 m, $n = 3$) and deep-water stations (low-water depth > 5 m, $n = 5$), then calculated a mean change in density at each of these groups of stations between 1990–92 and 1993–97. We then calculated the difference between the mean change at shallow-water stations and the mean change at deep-water stations. If zebra mussel effects did not differ between shallow-water and deep-water stations, then this difference would have a mean of 0 and a variance equal to variance in the mean change at the shallow-water stations plus the variance in the mean change at the deep-water stations. We used a one-tailed t-test with six degrees of freedom to test whether densities at shallow-water sites declined less than those at deep-water sites following the zebra mussel invasion (Strayer et al. 1998).

Although zebra mussels were first seen in the Hudson in May 1991, we treated 1991 and 1992 as pre-impact years, because zebra mussel biomass and filtration activity were low before September 1992 (Strayer et al. 1996; Caraco et al. 1997), the month in which our 1992 samples were taken.

Following the recommendation of Downing (1979), all zoobenthic data were fourth-root transformed prior to analysis. Although statistical tests were based on fourth-root transformed data, we show untransformed data in some of the figures to more clearly show the magnitude of differences between groups of samples.

Results and discussion

Composition and distribution of the fauna

Approximately 200 species of macrobenthic animals have been identified from the freshwater tidal Hudson River (Appendix 1). The fauna was numerically dominated by tubificid oligochaetes, amphipods, chironomid midges, sphaeriid clams, flatworms, nematodes, isopods, and gastropods (Appendix 1, Table 3). The Hudson's fauna closely resembled that of other freshwater tidal rivers in northeastern North America, from the James to the St. Lawrence (Massengill 1976; Crumb 1977; Vincent 1979; Ettinger 1982; Diaz 1989). The macrozoobenthos of these rivers

Table 3. Summary of the composition of the macrozoobenthos of the freshwater tidal Hudson River.

Taxon	No. species known from river	No. species known from soft sediments
Cnidaria	2	2
Turbellaria	2	2
Nemertea	1	1
Nematoda	6	6
Polychaeta	2	2
Oligochaeta	27	26
Hirudinea	10	6
Entoprocta	1	1
Ectoprocta	1	0
Cumacea	1	1
Isopoda	3	3
Amphipoda	3	3
Decapoda	3	3
Acari	5	3
Ephemeroptera	6	2
Trichoptera	12	3
Coleoptera	8	2
Chironomidae	71	47
Ceratopogonidae	6	5
Chaoboridae	1	1
Other Insecta	12	6
Gastropoda	24	10
Bivalvia	11	11
Total	218	146

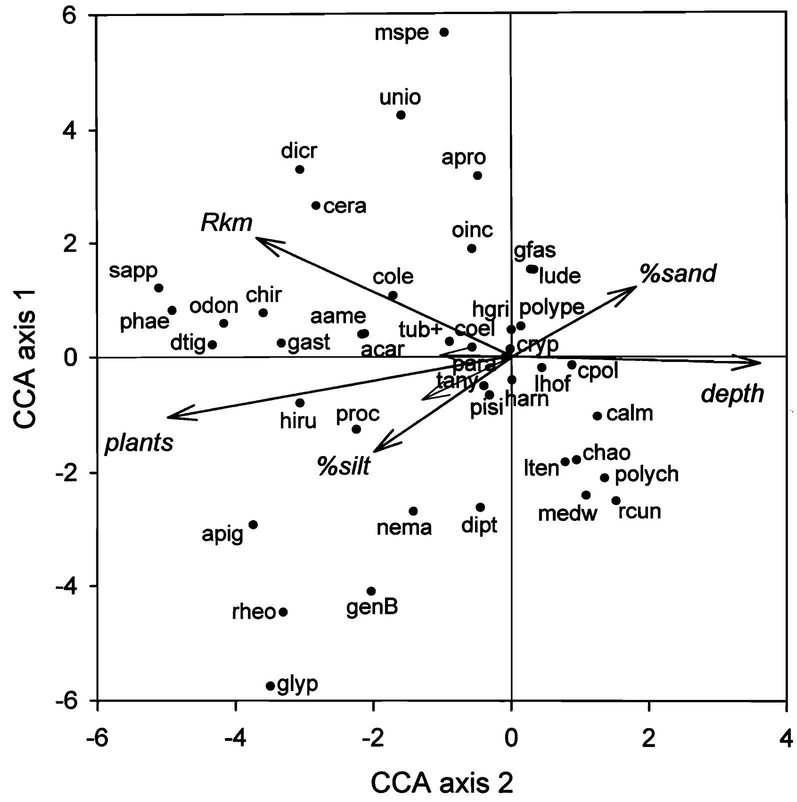

Fig. 2. Results of the canonical correspondence analysis of the Hudson River zoobenthos. Taxa are abbreviated as follows: aame = *Aulodrilus americanus*, acar = Acari, apig = *Aulodrilus pigueti*, apro = *Almyracuma proximoculi*, calm = *Chiridotea almyra*, cera = Ceratopogonidae, chao = *Chaoborus punctipennis*, chir = *Chironomus decorus* group species, coel = *Coelotanypus scapularis*, cole = Coleoptera, cpol = *Cyathura polita*, cryp = *Cryptochironomus* spp., dicr = *Dicrotendipes* spp., dipt = Diptera other than Chironomidae, Chaoboridae, and Ceratopogonidae, dtig = *Dugesia tigrina*, gast = Gastropoda other than *Littoridinops tenuipes*, genB = "genus B" (Chironomidae), gfas = *Gammarus fasciatus*, glyp = *Glyptotendipes lobiferus*, harn = *Harnischia curtilamellata*, hgri = *Hydrolimax grisea*, hiru = Hirudinea, lhof = *Limnodrilus hoffmeisteri*, lten = *Littoridinops tenuipes*, lude = *Limnodrilus udekemianus*, medw = *Monoculodes edwardsi*, mspe = *Manayunkia speciosa*, nema = Nematoda, odon = Odonata, oinc = *Oecetis inconspicua*, para = *Paralauterborniella nigrohalterale*, phae = *Phaenopsectra* sp., pisi = *Pisidium* spp., polych = *Scolecolepides viridis*, polype = *Polypedilum* spp., proc = *Procladius* spp., rheo = *Rheotanytarsus exiguus* group species, rcun = *Rangia cuneata*, sapp = *Slavina appendiculata*, tany = *Tanytarsus guerlus* spp., tub+ = unidentifiable Tubificidae with hair setae, unio = Unionidae. Correlations between ordination axes and environmental factors are shown by the arrows, whose length has been exaggerated 10-fold for clarity. Environmental variables are labeled in italics; arrows for % clay and % loss on ignition both have correlations <0.15 and have been left unlabeled to avoid clutter. The first two CCA axes explained 19% of the variation in community composition.

was almost always strongly dominated by *Limnodrilus hoffmeisteri* and other tubificid oligochaetes, and often contained large populations of predatory chironomids (e.g., *Coelotanypus scapularis, Procladius* spp., *Cryptochironomus* spp.) and sphaeriid clams (usually *Pisidium* spp.). Most of the species in these freshwater tidal rivers in the Northeast are also widely distributed in lakes and lowland rivers, but the fauna was distinctive in two ways. Several species that were common in the Hudson and other freshwater tidal rivers in the region (e.g., *Almyracuma proximoculi, Monoculodes edwardsi, Chiridotea almyra, Cyathura polita, Littoridinops tenuipes*) usually live in oligohaline estuaries and coastal waters, and introduce a distinctively estuarine element to the fauna. Also, net-spinning caddisflies and burrowing mayflies, two groups of suspension-feeding insects that are important in many large rivers worldwide, were very rare in the freshwater tidal rivers of the Northeast, perhaps because rapidly changing tidal currents interfere with the construction and operation of the fixed burrows and nets used in feeding.

The composition of the Hudson's fauna was determined in part by the presence of rooted plants and the salinity regime. The axes of the canonical correspondence analysis (CCA) ordination were correlated primarily with the presence of plants, the water depth, and river kilometer, with sediment characteristics having relatively little influence (Fig. 2). The ordination separated the fauna roughly into four groups: (i) a small group of species (i.e., *Scolecolepides viridis, Monoculodes edwardsi, Chiridotea almyra, Chaoborus punctipennis, Littoridinops tenuipes, Rangia cuneata*) in the lower right of the ordination diagram, which were found chiefly near the downriver end of the study area, especially where salinity intrudes occasionally; (ii) a very large group of taxa (e.g., *Aulodrilus pigueti, Chironomus decorus* group species, *Phaenopsectra* sp., *Rheotanytarsus exiguus* group species, gastropods other than *Littoridinops tenuipes*) occupying most of the left half of the ordination

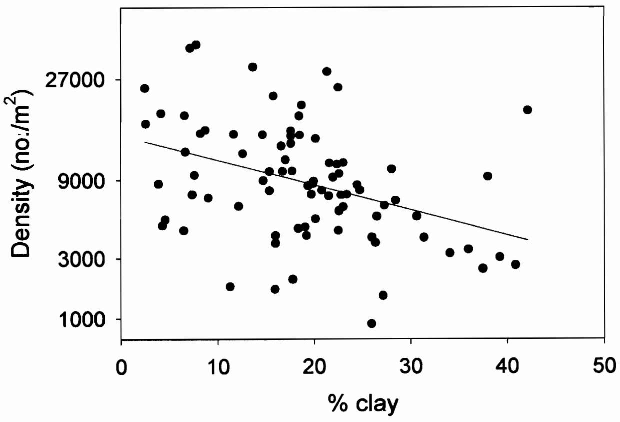

Fig. 3. Relationship between macrobenthic density and % clay in sediments of the Hudson River ($r^2 = 0.15$, $p < 0.01$). Y-axis is 4th-root scaled.

diagram, which were characteristically found upriver in shallow-water, vegetated habitats; (iii) three taxa (i. e., unionid mussels, *Manayunkia speciosa, Almyracuma proximoculi*) falling out along the positive Y-axis, which were found chiefly upriver but either indifferent to vegetation or found in unvegetated sites; and (iv) a large cluster of species (e. g., *Hydrolimax grisea, Limnodrilus hoffmeisteri, Gammarus fasciatus, Coelotanypus scapularis, Pisidium* sp.) that were widespread in the Hudson and indifferent to the main environmental variables, and which fall out near the origin in ordination space. Despite the clear separation of the fauna into these groups, only 19 % of the variance in community composition was explained by the first two CCA axes, so factors (e. g., predation, disturbance, sediment dynamics) other than the simple environmental variables we measured must have had a strong influence on the zoobenthos.

Average density of macroinvertebrates was about 10,000/m^2, but was highly variable from sample to sample. Some of this variation was related to sediment texture, with clayey sediments supporting low densities of macroinvertebrates (Fig. 3). Other measured environmental variables (i. e., loss on ignition, water depth, presence of rooted plants) were ineffective at predicting macrobenthic densities, although the presence of plants affected the response of macrobenthos to the zebra mussel invasion (see below).

Distribution of dominant species

The following section summarizes the distribution of the dominant benthic species in the Hudson River. We show the distribution of the species along the length of the river, from our data and the survey of Simpson et al. (1984, 1986). Correlations between major environmental features and the abundance of the species are presented, drawn largely from surveys done in 1990–92 before the zebra mussel invasion. Taxa for which no environmental correlations are presented were uncorrelated with all the environmental variables that we measured. Finally, we show the response of the species to the zebra mussel invasion. Responses to the zebra mussel invasion are discussed in a later section of the paper as well.

Turbellaria

Two species of flatworms were common in the Hudson: *Hydrolimax grisea* and *Dugesia tigrina.* Both species probably are predators or scavengers. In addition, we occasionally collected various microturbellarians, which presumably were numerous in the Hudson but too small to be collected regularly on a 0.5-mm mesh sieve. *H. grisea*, a little-known species of lowland rivers of the eastern United States (Smith & Menzie 1994), was common throughout the study area, in both shallow and deep water (Fig. 4). It was especially abundant on sediments dominated by fine sands. *D. tigrina* had a much more restricted distribution, and was found almost exclusively in shallow, vegetated areas. Flatworms had a complex response to the zebra mussel invasion (Fig. 5). Both species showed more negative responses in

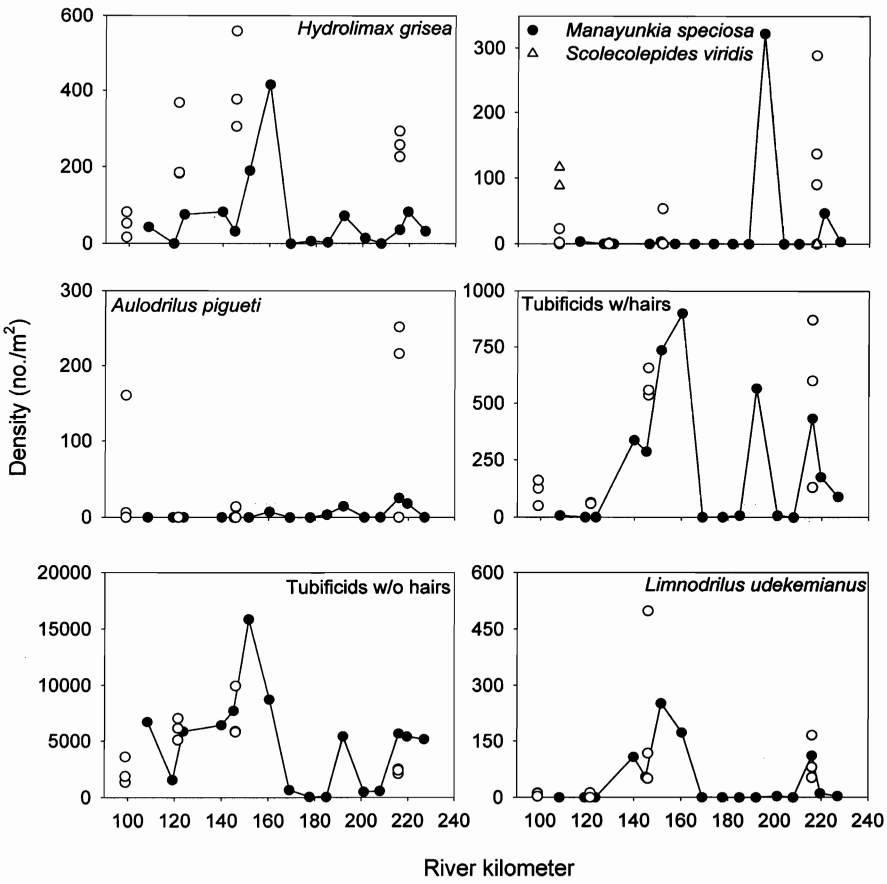

Fig. 4. Density of *Hydrolimax grisea* (Turbellaria), *Manayunkia speciosa* and *Scolecolepides viridis* (Polychaeta), and several oligochaetes along the freshwater tidal Hudson River. Black dots show data from the navigation channel in 1983 (Simpson et al. 1986), white dots show annual means for four cross-channel transects in 1990–92. For *H. grisea*, data from 1983 are for all flatworms, most of which presumably were *H. grisea*. Note the differences in scale among the Y-axes.

deep water than in shallow water; in addition, the mean density of *H. grisea* declined while that of *D. tigrina* increased. Thus, the overall effect of the invasion was to favor flatworm populations living in plant beds over those living on unvegetated sediments in deep water.

Nematoda

Most nematodes are far too small to be retained on a 0.5-mm mesh sieve (e.g., Hummon 1981). Nevertheless, large nematodes showed up regularly in our samples.

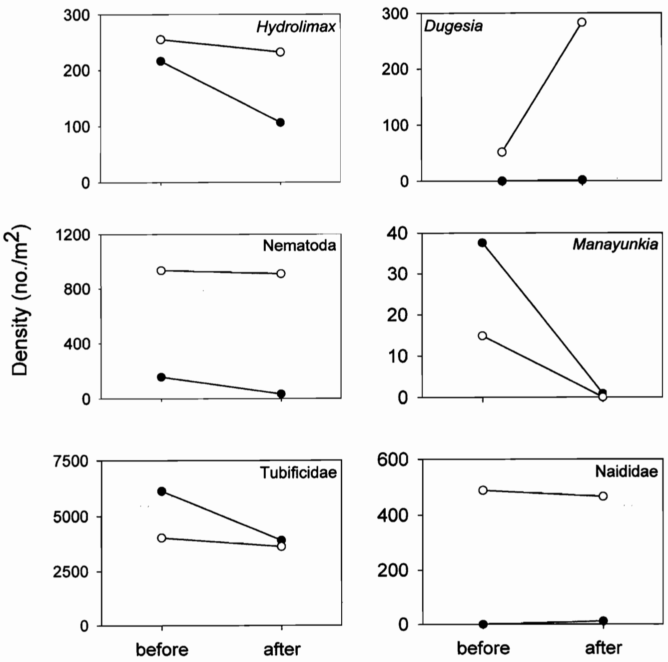

Fig. 5. Mean densities of flatworms (*Hydrolimax grisea* and *Dugesia tigrina*), nematodes, and tubificid and naidid oligochaetes at deepwater (black circles) and shallow-water (white circles) stations before and after the zebra mussel invasion in the Hudson River. The p-values for temporal change and the interaction between habitat and zebra mussel invasion are as follows: *Hydrolimax* (0.09, 0.13), *D. tigrina* (0.09, 0.09), Nematoda (> 0.2, 0.03), *Manayunkia* (> 0.2, > 0.2), Tubificidae (> 0.2, 0.10), Naididae (> 0.2, > 0.2). Note the differences in scale among the Y-axes.

We slide-mounted and identified nematodes only in 1991. We found (in order of decreasing abundance) *Dorylaimus* cf. *stagnalis,* Mermithidae, *Idiodorylaimus novazealandiae, Tobrilus* cf. *aberrans, Laimydorus* cf. *pseudostagnalis*, and *Hofmaenneria* sp. *D. stagnalis* was by far the most abundant of these large nematodes (Appendix 1). The mermithids are parasites of aquatic insects, and the dorylaimoids bear spears, and presumably feed on macrophytes, algae, or small animals. Nematodes were much more abundant in macrophyte beds than in deep water (Fig. 5), and tended to prefer silty sediments. Nematode densities in deepwater sediments declined by 78% following the zebra mussel invasion, while those in shallow-water, vegetated sites were essentially unchanged (Fig. 5).

Annelida

The Annelida of the freshwater tidal Hudson River included polychaetes, oligochaetes, and leeches. Several species of leeches were found in low numbers on soft

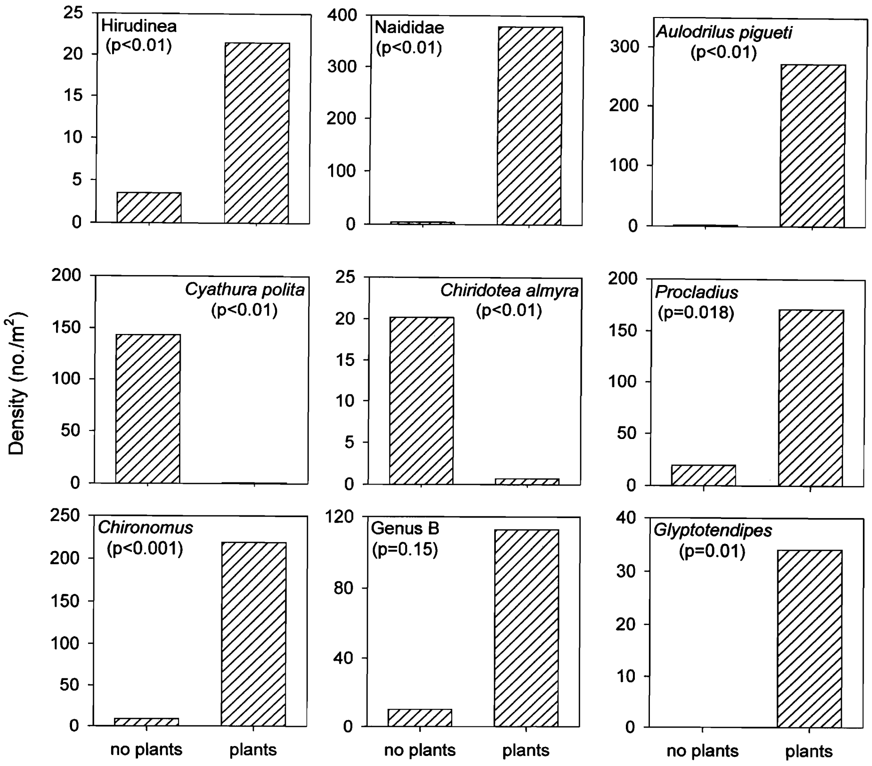

Fig. 6. Densities of selected taxa of zoobenthos in unvegetated (n = 24) and vegetated (n = 4) sites in the freshwater tidal Hudson in 1990–92. Note the differences in scale among the Y-axes.

sediments (Appendix 1) and rocky shores (Strayer & Smith 2000). They were more abundant among vegetation than in unvegetated sediments (Fig. 6).

Two species of polychaetes occurred in the study area. *Manayunkia speciosa* was abundant in the upper estuary and scattered elsewhere (Fig. 4). Its abundance was uncorrelated with the environmental variables that we measured. The biology of *M. speciosa* is poorly known, but it may suspension-feed on phytoplankton (Manoleli 1975; Davies 1991). *Scolecolepides viridis*, the other polychaete we found, is a brackish-water species that was abundant at Newburgh in some years (Fig. 4). It was abundant further downriver in the Hudson (Ristich et al. 1977; Weinstein 1977) and presumably ranges up into the lower parts of the freshwater estuary in dry years.

Oligochaetes were the most abundant macroinvertebrates in the freshwater tidal Hudson. Although the coarse mesh (0.5 mm) that we used probably underestimated the importance of the smaller naidids, the fauna appeared to consist primarily of tubificids, especially *Limnodrilus hoffmeisteri* (Appendix 1). Several of the species

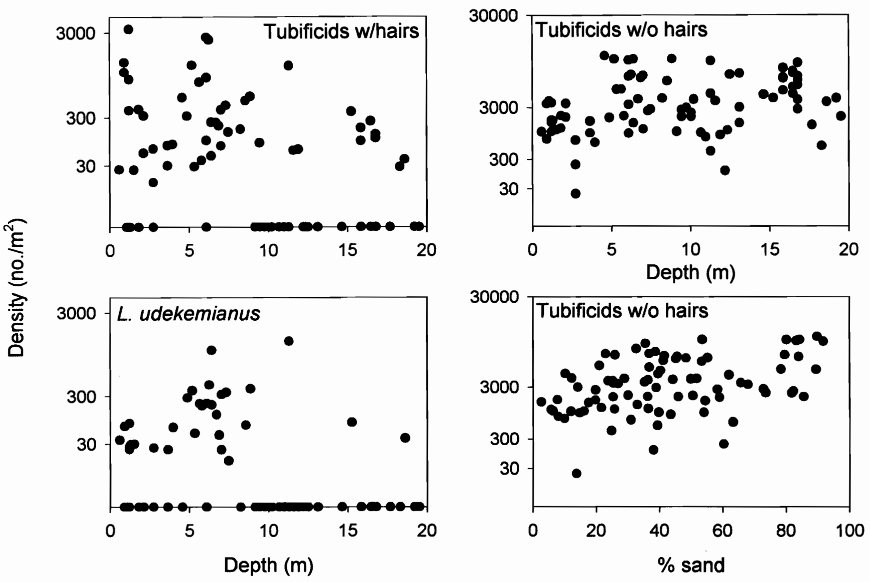

Fig. 7. Densities of selected oligochaetes as a function of environmental variables. Statistics are as follows: tubificids with hairs ($r^2 = 0.18$, $p < 0.01$), *Limnodrilus udekemianus* ($r^2 = 0.13$, $p < 0.01$), tubificids without hairs (depth: $r^2 = 0.16$, $p < 0.01$; % sand: $r^2 = 0.09$, $p < 0.01$). Note the differences in scale among the Y-axes.

of tubificids are unidentifiable as immatures, and were so combined for analysis into two broad categories: those with hair setae (i. e., *Ilyodrilus templetoni, Potamothrix vejdovskyi*, and *Tubifex tubifex*) and those without hair setae (i. e., *Isochaetides freyi, Limnodrilus hoffmeisteri*, and *Potamothrix moldaviensis*). Further, it appears that some of these species may have been dealt with inconsistently in the two major studies of the macrobenthos of the freshwater Hudson. Thus, among species with hair setae, Simpson et al. (1984, 1986) reported *Ilyodrilus templetoni*, while we found *Potamothrix vejdovskyi* and *Tubifex tubifex.* Amon species without hair setae, Simpson et al. (1984, 1986) reported *Isochaetides freyi*, while we found *Potamothrix moldaviensis.* Presumably, the species did not actually shift between the two studies, but rather were identified differently by the different groups of investigators. These apparent identification problems are another reason for combining the tubificid species into broad categories for analysis.

Most oligochaete taxa were found throughout the freshwater tidal Hudson, with markedly lower densities in the sandy middle reaches (RKM 150–200) of the river (Fig. 4). Densities of most oligochaete taxa were correlated only weakly with measured environmental variables. Tubificids with hair setae (presumably chiefly *Potamothrix vejdovskyi* and *Tubifex tubifex*) and *Limnodrilus udekemianus* were more abundant in shallow water than in deep (although not showing a strong association with vegetation), while tubificids without hair setae (presumably chiefly

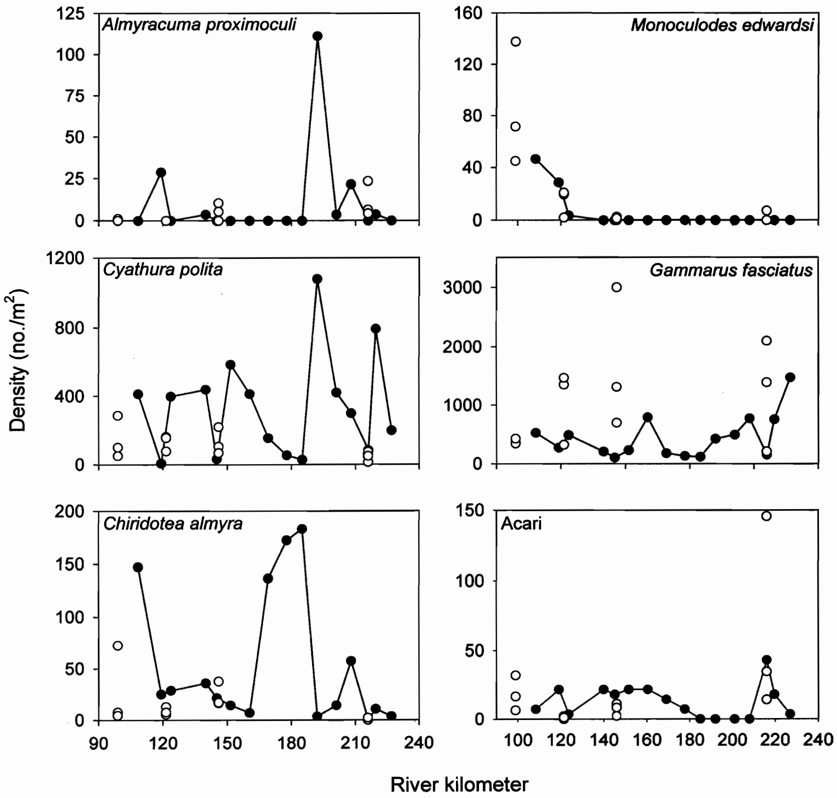

Fig. 8. Densities of macrobenthic crustaceans and mites along the freshwater tidal Hudson River. Black dots show data from the navigation channel in 1983 (SIMPSON et al. 1986), white dots show annual means for four cross-channel transects in 1990–92. Note differences in scale among the Y-axes.

Limnodrilus hoffmeisteri) showed an opposite pattern (Fig. 7). In addition, tubificids without hairs tended to be most abundant in sandy sediments (Fig. 7). Consistent with these results, FINDLAY et al. (1989) noted that *L. hoffmeisteri* seemed to be missing entirely from the muddy shallow-water sediments of Tivoli South Bay. In contrast to the weak patterns shown in Fig. 7, several species of oligochaetes were strongly associated with vegetated habitats. *Aulodrilus pigueti* and all of the naidids lived almost exclusively among macrophytes (Fig. 6), and *Aulodrilus limnobius*, although too scarce to show a strong pattern, seemed to follow the same pattern.

None of the annelids had a clear response to the zebra mussel invasion. Leeches were too sporadic to exhibit a statistically detectable response to zebra mussels. *Manayunkia speciosa* nearly disappeared from the Hudson after the zebra mussel invasion, but this change was not statistically significant (Fig. 5). Oligochaetes had a marginally significant divergence between shallow-water and deepwater sites in

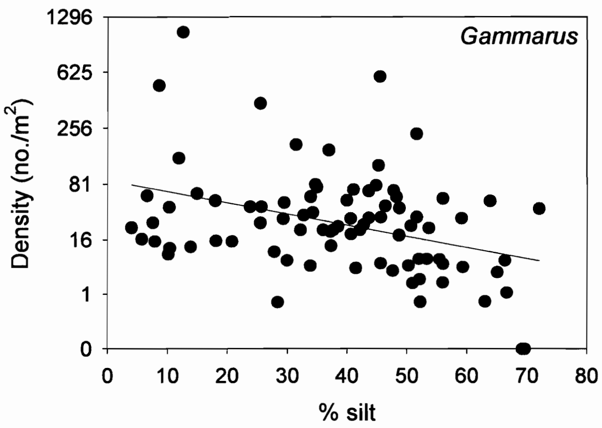

Fig. 9. Density of *Gammarus fasciatus* as a function of silt content of the sediment ($r^2 = 0.14$, $p < 0.01$). The Y-axis is 4th-root scaled.

their response to the invasion (Fig. 5). There was no detectable difference between the responses of tubificids and naidids (Fig. 5).

Crustacea

Two important groups of crustaceans escaped our sampling methods: the numerous microcrustaceans (ostracods, cladocerans, and copepods – see Yozzo & Steineck 1994) and the large, mobile species such as the blue crab and grass shrimp. Only a few macrobenthic crustaceans were common in our samples.

Cumaceans usually are thought of as entirely marine or brackish-water animals, but *Almyracuma proximoculi* lived at low density throughout the freshwater estuary (Fig. 8). It was perhaps most abundant in the upper estuary, and tended to be most abundant in sandy, shallow-water sediments low in organic matter. However, no measured environmental variable effectively predicted its density.

Two species of isopods were common in the freshwater tidal Hudson: *Cyathura polita* and *Chiridotea almyra.* Both are thought of as brackish-water forms, but as Simpson et al. (1985) pointed out, they were widespread in the freshwater Hudson (Fig. 8). Both species were far more abundant on unvegetated sediments than in the vegetated shallows (Fig. 6). In addition, we occasionally collected *Asellus* sp.

We collected three amphipod species in the study area. *Gammarus fasciatus* was one of the most abundant benthic animals in the freshwater tidal Hudson (Fig. 8), and was an important food for many species of fish in the estuary (Table 9). It was found across all habitats, but tended to be less abundant on very silty sediments (Fig. 9). *Monoculodes edwardsi* is a brackish-water to marine species (Bousfield 1973) that was common in the lower part of the study area (Fig. 8). It occasionally was found further upriver. *Corophium lacustre*, another widespread brackish-water

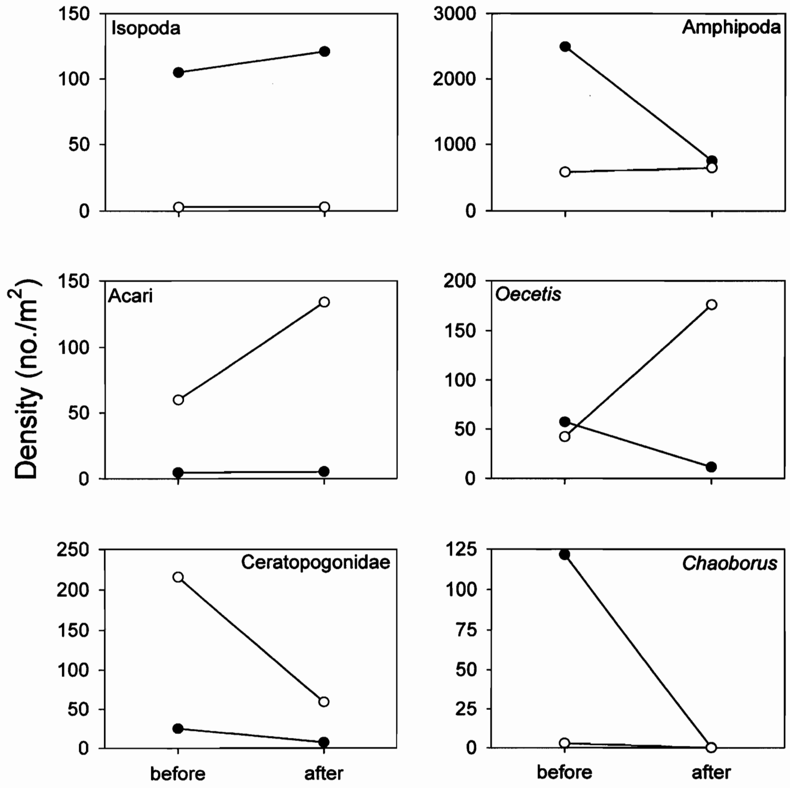

Fig. 10. Mean densities of macrobenthic crustaceans, mites, and non-chironomid insects at deepwater (black circles) and shallow-water (white circles) stations before and after the zebra mussel invasion in the Hudson River. The p-values for temporal change and the interaction between habitat and zebra mussel invasion are as follows: isopods (> 0.2, > 0.2), amphipods (> 0.2, 0.02), Acari (> 0.2, > 0.2), *Oecetis* (> 0.2, 0.03), Ceratopogonidae (0.10, > 0.2), *Chaoborus* (0.02, 0.03). Note the differences in scales among the Y-axes.

amphipod, appeared in small numbers at the lower end of the study area in the dry year of 1991.

Isopod densities and distribution were unaffected by the zebra mussel invasion (Fig. 10). In contrast, amphipod densities fell steeply in deepwater, unvegetated habitats while rising modestly in the vegetated shallows (Fig. 10).

Acari

Mites were found in small numbers along the length of the freshwater tidal Hudson (Fig. 8). They were associated with vegetation, where there was a large but statistically insignificant rise in density after the zebra mussel invasion (Fig. 10). We did not identify the mites that we collected, but earlier surveys (SIMPSON et al.

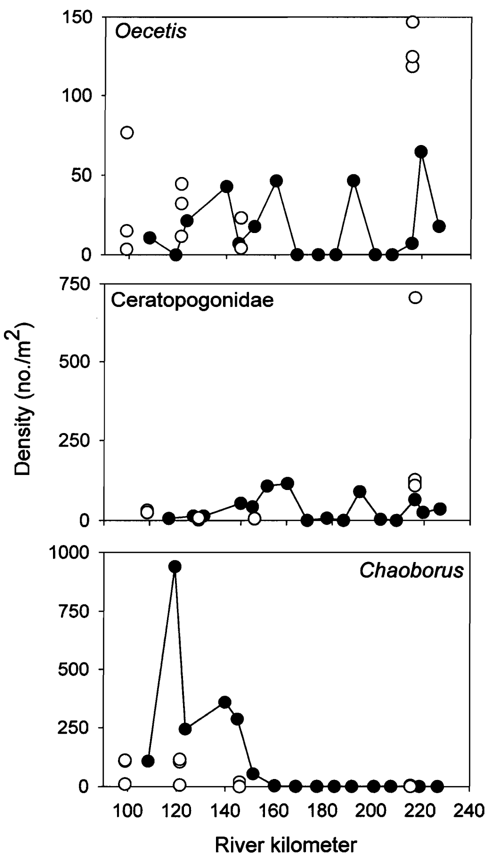

Fig. 11. Densities of benthic insects other than chironomids along the freshwater tidal Hudson River. Black dots show data from the navigation channel in 1983 (SIMPSON et al. 1986), white dots show annual means for four cross-channel transects in 1990–92. Note the differences in scales among the Y-axes.

1984, 1986; BODE et al. 1986) reported several common genera (Appendix 1). Presumably, other taxa are present as well.

Insecta

The insects were the most diverse group in the Hudson zoobenthos, with > 100 species recorded from the estuary (Table 3). Many of these species live along the edges of the estuary on rocky shorelines and among vegetation, with only dipterans and a single species of caddisfly being abundant in the main channel.

Oecetis inconspicua (Trichoptera: Leptoceridae) was the sole non-dipteran insect that was abundant in the freshwater tidal Hudson. It was widespread along the length of the freshwater estuary (Fig. 11), and had a striking response to the zebra mussel invasion (Fig. 10). Although it was not associated with vegetation prior to the invasion, densities of this animal rose steeply in vegetated habitats while simultaneously falling in unvegetated habitats, so densities are now strongly related to the presence of vegetation.

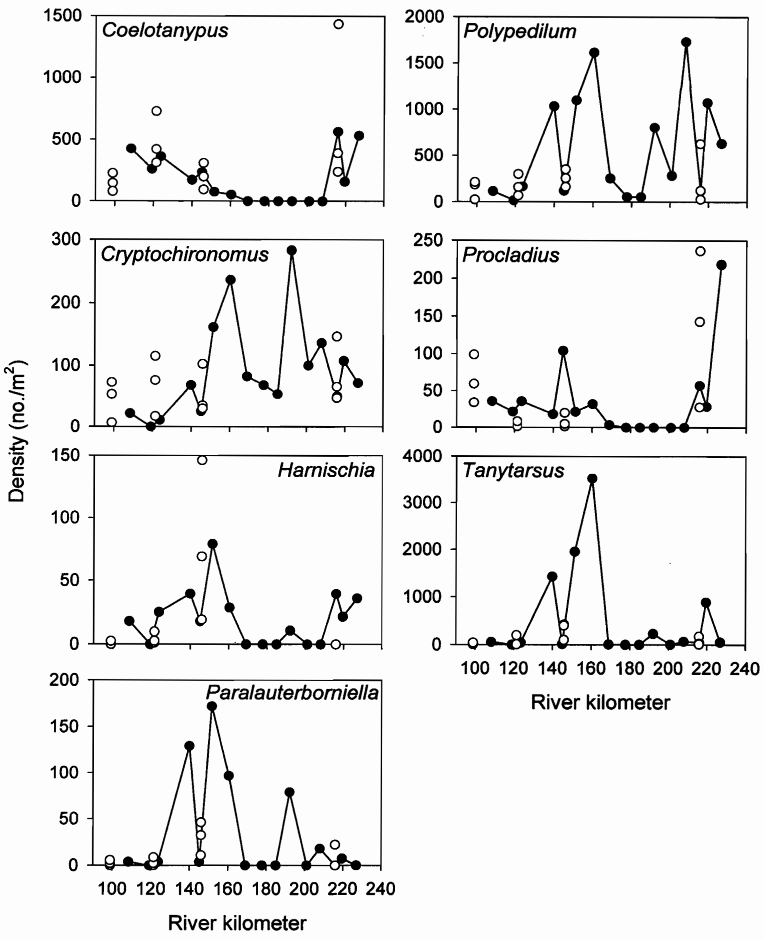

Fig. 12. Density of the chironomids *Coelotanypus scapularis, Cryptochironomus* spp., *Harnischia curtilamellata, Paralauterborniella nigrohalterale, Polypedilum* spp., *Procladius* spp., and *Tanytarsus guerlus* group spp. along the freshwater tidal Hudson River. Black dots show data from the navigation channel in 1983 (Simpson et al. 1986), white dots show annual means for four cross-channel transects in 1990–92. Note the differences in scales among the Y-axes.

Chironomids were moderately abundant (1000/m^2) and very diverse (at least 71 species) in the Hudson (Table 3). As is usually the case in large, warmwater rivers (Lindegaard 1995; Pinder 1995), the fauna was dominated by Chironominae and Tanypodinae. Before the zebra mussel invasion, the most abundant genera were *Coelotanypus, Polypedilum, Tanytarsus, Phaenopsectra* (s. l., including *Tribelos*), *Cryptochironomus*, and *Procladius* (Appendix 1), all common genera of warmwater rivers and lakes. If our study had included samples from winter and early spring, we probably would have found many additional species of orthoclads, which can

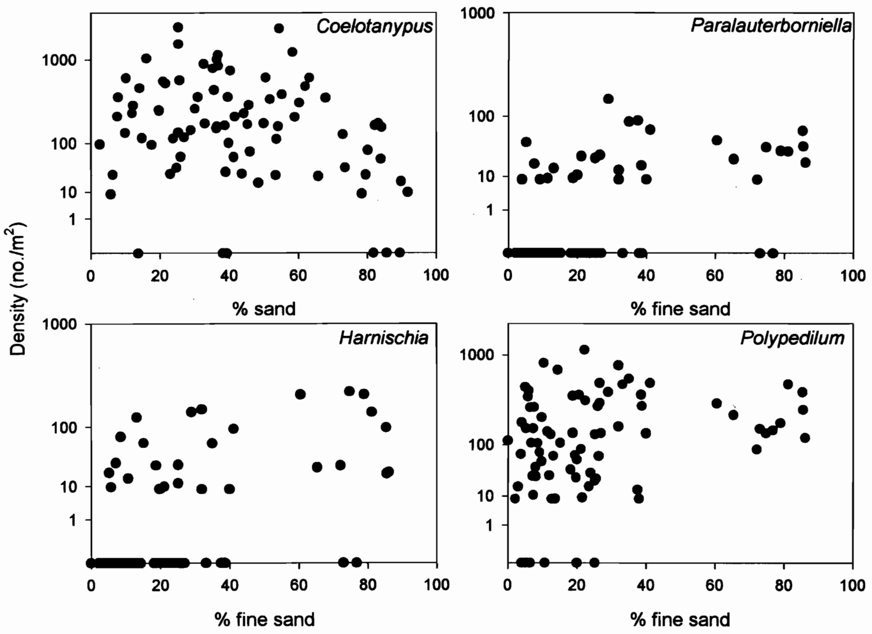

Fig. 13. Densities of selected chironomids as a function of sediment granulometry. Statistics as follows: *Coelotanypus scapularis* ($r^2 = 0.08$, $p < 0.01$); *Harnischia curtilamellata* ($r^2 = 0.26$, $p < 0.01$); *Paralauterborniella nigrohalterale* ($r^2 = 0.28$, $p < 0.01$); *Polypedilum* spp. ($r^2 = 0.11$, $p < 0.01$). Note the differences in scales among the Y-axes.

seasonally dominate the chironomid communities of even warmwater rivers (e.g., Beckett 1992). The Hudson's fauna was dominated by predatory species, which constituted almost half of chironomid numbers. The remainder of the fauna consisted of collector-gatherers that probably feed on detritus, algae, and microbes (Berg 1995; Merritt & Cummins 1996). Two of the genera probably are suspension-feeders. *Rheotanytarsus* feeds on small particles trapped on the silk net that it builds on the end of its larval retreat (Walshe 1951; Schröder 1988). Some members of the large genus *Tanytarsus* likewise feed on suspended particles (Benke et al. 1984; Merritt & Cummins 1996). In the Hudson, both *Rheotanytarsus* and *Tanytarsus* had gut contents of small, uniform organic particles rather than the heterogeneous mix characteristic of other non-predatory chironomids, and we suspect that both fed on suspended food.

Several chironomid genera showed distinct patterns in density along the length of the river (Fig. 12), typically having reduced densities in the sandy middle part (RKM 150–200) of the estuary. The predatory *Cryptochironomus* was a striking exception to this pattern, with highest densities in this sandy midreach of the river. Several genera had weak but statistically significant relationships between population

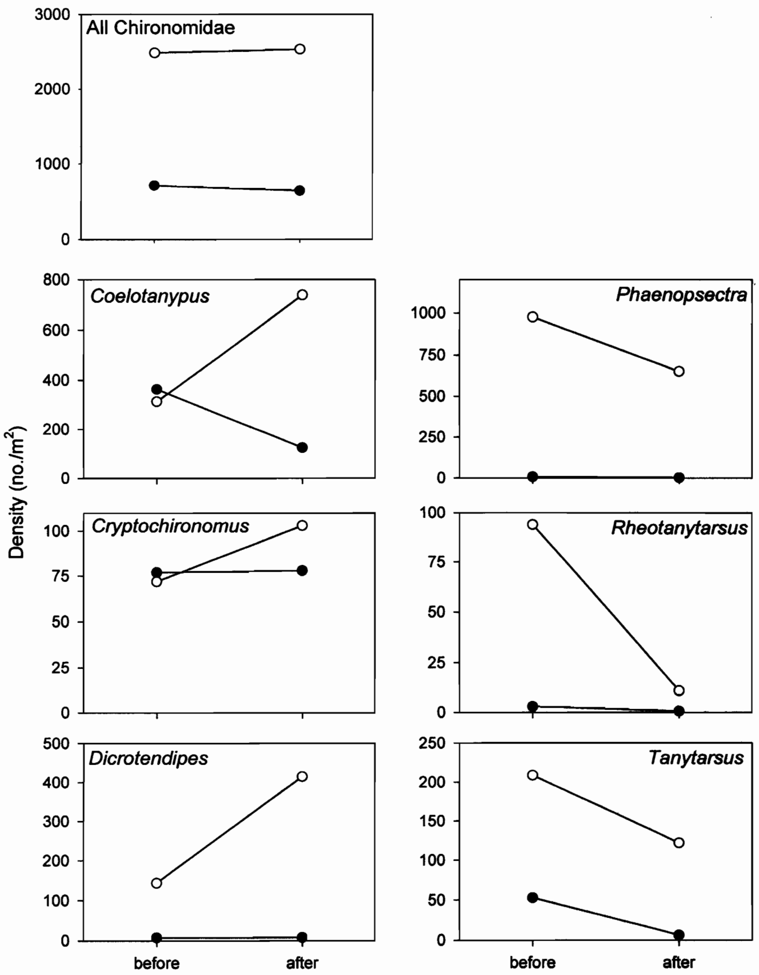

Fig. 14. Mean densities of all Chironomidae and selected chironomid genera at deepwater (black circles) and shallow-water (white circles) stations before and after the zebra mussel invasion in the Hudson River. The p-values for temporal change and the interaction between habitat and zebra mussel invasion are as follows: Chironomidae (> 0.2, > 0.2), *Coelotanypus* (> 0.2, 0.009), *Cryptochironomus* (> 0.2, 0.20), *Dicrotendipes* (> 0.2, 0.12), *Phaenopsectra* (> 0.2, 0.04), *Rheotanytarsus* (0.09, > 0.2), *Tanytarsus* (0.09, > 0.2). Neither the effect of the zebra mussel invasion nor the interaction between habitat and the zebra mussel invasion was significant (p = 0.2) for *Procladius* spp., *Chironomus decorus* group species, *Polypedilum* spp., or Chironomini Genus B. Note the difference in scales among the Y-axes.

density and sediment grain size (Fig. 13), none strong enough to suggest that grain size per se was an important limiting factor in the Hudson. *Procladius, Chironomus, Dicrotendipes,* Chironomini Genus B (as defined by PINDER & REISS 1983), *Glyptotendipes, Phaenopsectra, Rheotanytarsus*, and *Tanytarsus* all were strongly associated with shallow-water, vegetated habitats (Figs. 6, 14).

Chironomids had a complicated response to the zebra mussel invasion. As a whole, chironomids had no response to the invasion (Fig. 14). However, the dominant genera showed three kinds of responses. The two presumed suspension-feeders, *Tanytarsus guerlus* group species and *Rheotanytarsus exiguus* group species, declined steeply (69 % and 87 %, respectively) across all habitats after the invasion (Fig. 14). Four genera (*Coelotanypus, Cryptochironomus, Dicrotendipes*, and *Phaenopsectra*) had divergent responses in deepwater and shallow-water sites to the invasion, with more negative changes in the deepwater sites (Fig. 14). Finally, four genera (*Procladius, Chironomus*, Chironomini Genus B, and *Polypedilum*) had no detectable response to the invasion. Other genera were too rare to be analysed.

Two other groups of dipterans were also common in the river. Ceratopogonids, represented by several species (Appendix 1), were common throughout the length of the study area (Fig. 11). These predatory dipterans were more abundant in the vegetated shallows than in deep water, and may have declined generally across all habitats after the zebra mussel arrived (Fig. 10). *Chaoborus punctipennis*, formerly abundant in deepwater sediments in RKM 100–150 (Figs. 10, 11), appears to have disappeared from the river as a result of the zebra mussel invasion (Fig. 10). In fact, since 1992, we have collected only a single individual (in 1993) of this once-common species.

Gastropoda

Three more or less distinct gastropod communities occurred in different habitats in the Hudson. The soft, unvegetated sediments of the main channel generally contained few gastropods (Table 4). The exception to this pattern was the tiny hydrobiid *Littoridinops tenuipes*, which was abundant in the deepwater stations in Newburgh and, in the very dry summer of 1991, at Poughkeepsie. Macrophyte beds

Table 4. Mean densities (no./m^2) of gastropods at shallow- and deep-water stations, 1990–96.

Species	Shallow	Deep
Ferrissia spp.	160	15
Amnicola limosa	157	1
Littoridinops tenuipes	39	92
Valvata tricarinata	17	0
Gyraulus parvus	11	2
Probythinella lacustris	7	1
Micromenetus dilatatus	3	0
Physella sp.	0.4	0

throughout the freshwater estuary supported dense gastropod populations, especially of *Ferrissia fragilis* and *Amnicola limosa* (Table 4). Finally, rocky shorelines supported dense and diverse gastropod communities (Appendix 1; STRAYER & SMITH 2000). In addition to the species we found in 1990–97, several species reported from the Hudson in the late 19th century (*Lioplax subcarinata, Gillia altilis, Birgella subglobosa, Cincinnatia integra*) apparently have disappeared from the Hudson (STRAYER 1987). These are all prosobranchs that probably were sensitive to pollution and habitat destruction, and may have been especially common in the complex of shallow-water habitats upriver that were destroyed by navigational improvements. We could discern no indirect effect of the zebra mussel invasion on gastropods in the Hudson, although zebra mussels have had strong direct impacts of gastropod communities that live in zebra mussel beds in other ecosystems (e. g., STEWART & HAYNES 1994; HOWELL et al. 1996; RICCIARDI et al. 1997; STEWART et al. 1998a).

Bivalvia

Four families of bivalves lived in the freshwater tidal Hudson: pearly mussels (Unionidae), fingernail clams (Sphaeriidae), zebra mussels (Dreissenidae), and surf clams (Mactridae). The latter two families are not native to the Hudson.

Unionid mussels, formerly a dominant part of the Hudson's zoobenthos, have declined as a result of human activities. In the 1890s, eight species were known from the river (records of *Pyganodon cataracta* are not supported by museum specimens and probably are based on misidentifications of *Anodonta implicata*) (STRAYER 1987). Between the 1890s and the 1990s, two of these species disappeared (*Lasmigona subviridis* and *Strophitus undulatus*) and three other species that apparently were abundant became scarce (*Lampsilis radiata, L. cariosa*, and *Ligumia nasuta*). We can only guess at the reasons for these declines, but likely candidates include gross organic pollution in the upper estuary (BOYLE 1979) and widespread habitat modification. In particular, many shallow side channels and marshes were filled, dredged, or cut off from the main channel to aid navigation. These shallow-water habitats may have been especially important for the five affected species, which often are found in small streams or lake shallows (e. g., STRAYER & JIRKA 1997). By 1991–92, only three species of unionids (*Elliptio complanata, Anodonta implicata*, and *Leptodea ochracea*) were still common in the Hudson estuary (Figs. 15, 16). Nevertheless, these three species were abundant, especially in RKM 213–248, and so constituted most of zoobenthic biomass and were the dominant suspension-feeders in the estuary, with filtration rates locally exceeding 2 $m^3 m^{-2} d^{-1}$ (STRAYER et al. 1994). Beginning late in 1992, zebra mussels reduced phytoplankton biomass by about 80 % (CARACO et al. 1997), and unionid populations declined sharply (Fig. 16, STRAYER & SMITH 1996). As of 1998, only one unionid species (*Elliptio complanata*) maintained a large (but diminished) population in the Hudson estuary (Fig. 15).

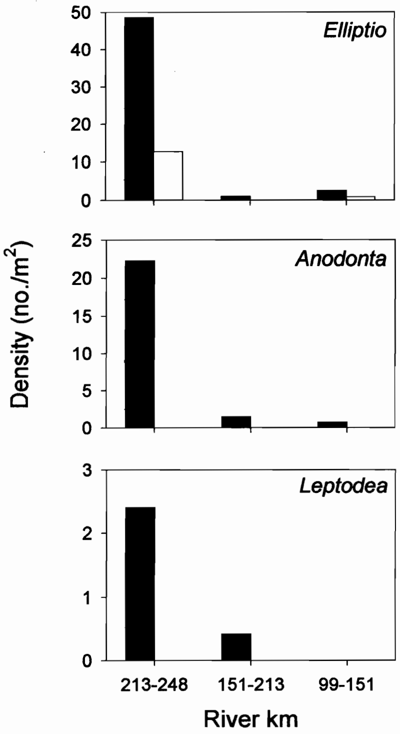

Fig. 15. Density of unionid mussels in three sections of the freshwater tidal Hudson River before (black bars = 1991–92) and after (white bars = 1998) the zebra mussel invasion. Note the difference in scales among the Y-axes.

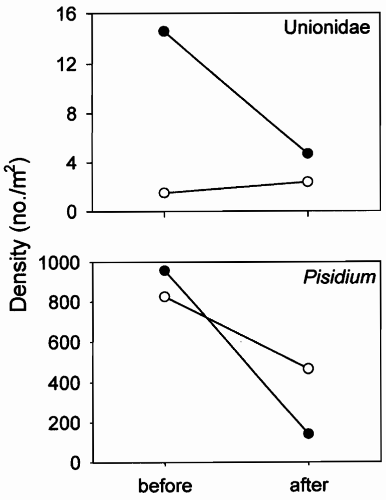

Fig. 16. Mean densities of Unionidae and *Pisidium* sp. at deepwater (black circles) and shallow-water (white circles) stations before and after the zebra mussel invasion in the Hudson River. The p-values for temporal change and the interaction between habitat and zebra mussel invasion are as follows: Unionidae (0.001, > 0.2), *Pisidium* (0.03, 0.14). Note the difference in scales between the Y-axes.

A small *Pisidium* sp. (possibly including more than one species) was abundant throughout much of the freshwater tidal Hudson River. It tended to be less abundant in clay-rich, highly organic sediments. Simpson et al. (1984, 1986) found *Pisidium* to be scarce or absent above RKM 170, but we found dense populations at Castleton (RKM 216) in 1990–96 (Fig. 17). *Pisidium* populations dropped sharply following the zebra mussel invasion (Fig. 16), presumably reflecting a loss of their phytoplankton food. In addition to this *Pisidium* sp., sparse populations ($< 30/\text{m}^2$) of *Sphaerium striatinum* and *Pisidium amnicum* were collected from the upper part of the estuary (RKM 213–248) in 1991–92.

The Dreissenidae included two introduced species in the freshwater Hudson estuary. *Mytilopsis leucophaeta*, a species from the American Southeast, appeared in the Hudson in the 1930s (Rehder 1937; Jacobson 1953; Mills et al. 1997), and

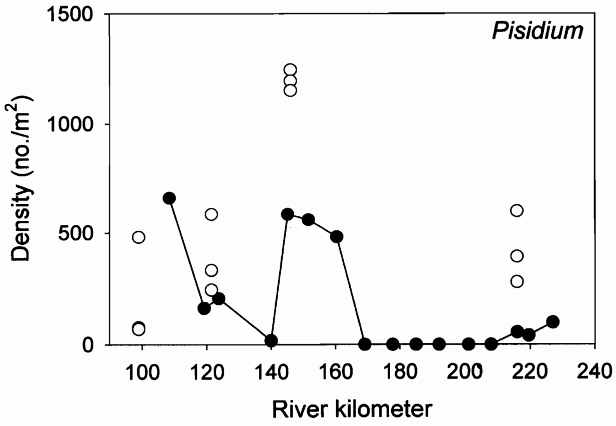

Fig. 17. Density of *Pisidium* sp. along the freshwater tidal Hudson River. Black dots show data from the navigation channel in 1983 (Simpson et al. 1986), white dots show annual means for four cross-channel transects in 1990–92.

was widespread and common on rocky shores in the oligohaline part of the estuary, extending upriver to RKM 100–110 (Walton 1996). We routinely saw it on rocky shores at Beacon (RKM 99), and occasionally in our surveys of the soft-bottom fauna at Newburgh. The chronology and effects of the zebra mussel (*Dreissena polymorpha*) invasion of the Hudson were described in detail by Strayer et al. (1996, 1998, 1999), Strayer & Smith (1996), Caraco et al. (1997, 2000), Pace et al. (1998), and Findlay et al. (1998). Briefly, zebra mussels were first seen in the Hudson in May 1991, near Catskill (RKM 178), and spread rapidly throughout the entire freshwater and oligohaline estuary by the end of 1992. Since September 1992, zebra mussels have constituted over half of heterotrophic biomass and $>95\%$ of suspension-feeding activity in the freshwater Hudson, causing wide-reaching changes in the ecosystem. Zebra mussels were found in low densities (usually $< 100/m^2$) on soft sediments in the Hudson, but were abundant on rocky sediments in deep water (usually $> 10{,}000/m^2$) and along shorelines ($100–1000/m^2$) (Strayer & Smith 2000). They also colonized unionid mussels and rooted plants such as *Vallisneria americana.*

Finally, another introduced bivalve, *Rangia cuneata*, sometimes occurred in the lower parts of the freshwater tidal Hudson. This is another southeastern species that appeared in the Hudson in the 1980s (Mills et al. 1997). It was very common in the oligohaline and mesohaline parts of the Hudson (Thomas Lake, pers. comm.), and just reached the "freshwater" estuary in dry years. At the end of the very dry summer of 1991, we collected an average of $42/m^2$ at Newburgh. These animals all were young-of-year and did not appear in samples taken in subsequent years.

Environmental correlates of zoobenthic distribution in the Hudson River

A central goal of our research was to describe how environmental variables affect the distribution and abundance of benthic animals in the Hudson. Broadly speaking, the composition of the zoobenthos in the Hudson was related chiefly to the salinity of the water and whether the site was vegetated or not. Nonetheless, a great deal of variation in the structure of the zoobenthos was unexplained by these or other measured environmental variables.

As is the case in many estuaries (e.g., Nekrasova 1972; Wolff 1973, 1983; Diaz 1989), salinity has been recognized as a major factor structuring the zoobenthos of the Hudson (e.g., Townes 1937; Ristich et al. 1977; Weinstein 1977). Although our study was nearly restricted to the freshwater part of the river, we saw evidence of the importance of salinity in the appearance of brackish-water species such as *Scolecolepides viridis* (Polychaeta), *Monoculodes edwardsi* (Amphipoda), *Littoridinops tenuipes* (Gastropoda), and *Rangia cuneata* (Bivalvia) near the lower part of the freshwater estuary, especially during dry summers (Figs. 2, 4, 8). The strong relationship between the zoobenthos and the salinity regime suggests that the geographic ranges of zoobenthic species in the Hudson should respond sensitively to projected changes in salinity resulting from changes in freshwater flow or sea level from human-induced climate change.

Within the freshwater estuary, we found large differences in the zoobenthos between vegetated, shallow-water sites and unvegetated, deepwater sites (Fig. 2). Many taxa (e.g., *Dugesia tigrina,* Nematoda, Naididae, Hirudinea, Acari, *Chironomus decorus* group species, *Glyptotendipes lobiferus, Rheotanytarsus exiguus* group species, most gastropods) had their chief habitat in the vegetated shallows (e.g., Figs. 5, 6, 10, 14, Table 4). Conversely, a few taxa (e.g., Isopoda, *Chaoborus*

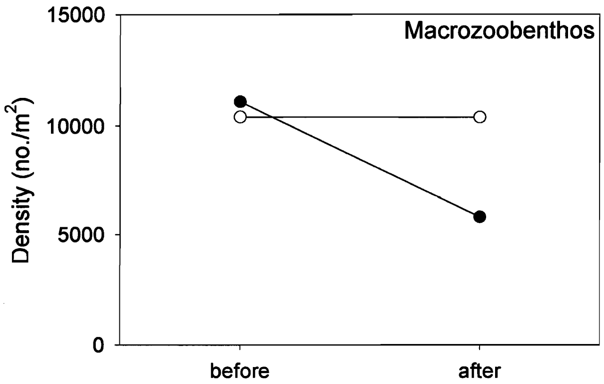

Fig. 18. Mean densities of all macrozoobenthos at deepwater (black circles) and shallow-water (white circles) stations before and after the zebra mussel invasion in the Hudson River. The interaction between habitat and the zebra mussel invasion is significant ($p < 0.02$), but there is no difference in densities between pre- and post-invasion years ($p > 0.2$).

punctipennis, Unionidae) lived primarily in unvegetated, deepwater sites (e. g., Figs. 6, 10, 16). The relationship between vegetation and fauna was strongly asymmetric, with many more species favoring the vegetated shallows than the unvegetated deepwater sites. Perhaps more profoundly, zoobenthic communities in these two kinds of habitats responded differently to the zebra mussel invasion, with shallow-water populations typically increasing while deepwater populations fell (i. e., Figs. 5, 10, 14, 16, 18). Thus, not only did shallow-water and deepwater communities differ in structure, but they also differed markedly in their reaction to a perturbation.

Surprisingly, sediment grain size and organic content were relatively ineffective at predicting the distribution and abundance of benthic animals in the Hudson. Overall community composition was related only weakly to sediment variables (Fig. 2), and although densities of many species were correlated with grain size or organic content of the sediment (e. g., Figs. 7, 9, 13), such correlations invariably were weak. In contrast, SIMPSON et al. (1986) concluded that the composition and abundance of the Hudson's zoobenthos was determined chiefly by sediment grain size. They showed that main-channel sites between RKM 169 and 208 were dominated by well-sorted fine sands and supported macroinvertebrate communities of low density and richness. We were unable to detect any strong correlations between sediment grain size and the zoobenthos at our sampling sites in the Hudson. Specifically, we did not find that sediments with a high content of fine sand had low density or richness. Thus, we conclude that the sandy middle reaches of the Hudson support an impoverished zoobenthos, but that this impoverishment is probably not a result of the sediment grain size per se, but rather to some other unfavorable feature (e. g., bed mobility) of this region. Despite the apparent lack of influence of grain size on zoobenthos in fine-grained sediments, there was a strong difference between zoobenthic communities of fine-grained sediments and nearby rocky sediments (STRAYER & SMITH 2000, and unpublished). Rocky sediments often supported dense populations of Ephemeroptera, Trichoptera, Gastropoda, and *Dreissena polymorpha* that typically were scarce on fine-grained sediments in the Hudson.

Thus, we can recognize three major controls on the composition of the zoobenthos of the Hudson: salinity, presence of plants, and grain size (i. e., rocky vs. fine-grained). If we combine information on the response of the Hudson zoobenthos to these three environmental variables, we can recognize a series of idealized communities in the different habitats of the river (Table 5).

Nevertheless, a great deal of variation in zoobenthic community composition remains unexplained by these three variables (and all other measured variables). This unexplained variation could have several causes. First, our estimates of animal densities at a sampling site had large errors. Replicate samples taken from an anchored boat at one site often differed from one another by a factor of 10 or more. We do not believe that this small-scale variance, although large and interesting in its own right, was primarily responsible for the weak relationships between the zoobenthos and environmental variables. For instance, in the case of the amphipod *Gammarus fasciatus*, within-site sampling error accounted for only 11 % of the

Table 5. Dominant macrobenthic animals living in the major habitats of the Hudson River estuary in 1970–2000, idealized from this study, Williams et al. (1975), Crandall (1977), Ristich et al. (1977), Weinstein (1977), Menzie (1980), Findlay et al. (1989), and Strayer & Smith (2000).

Salinity zone	Fine-grained sediments in deep water	Vegetated shallows	Rocky sediments
Freshwater (< 0.5 psu or ppt)	*Hydrolimax grisea* (Turbellaria) *Limnodrilus hoffmeisteri* (Oligochaeta) *Potamothrix vejdovskyi* (Oligochaeta) *Cyathura polita* (Isopoda) *Gammarus fasciatus* (Amphipoda) *Chaoborus punctipennis*^{a} (Diptera) *Coelotanypus scapularis* (Diptera) *Polypedilum* spp. (Diptera) *Elliptio complanata*^{a} (Bivalvia) *Anodonta implicata*^{a} (Bivalvia) *Pisidium* sp.^{a} (Bivalvia)	*Hydrolimax grisea* (Turbellaria) *Dugesia tigrina* (Turbellaria) *Dorylaimus* cf. *stagnalis* (Nematoda) *Limnodrilus hoffmeisteri* (Oligochaeta) Naididae (Oligochaeta) *Gammarus fasciatus* (Amphipoda) Acari *Oecetis inconspicua* (Trichoptera) Ceratopogonidae^{a} (Diptera) *Ablabesmyia* sp. (Diptera) *Chironomus decorus* (Diptera) *Coelotanypus scapularis* (Diptera) *Cricotopus* sp. (Diptera) *Dicrotendipes* spp. (Diptera) *Harnischia* sp. (Diptera) *Phaenopsectra* sp. (Diptera) *Polypedilum* spp. (Diptera) *Procladius* sp. (Diptera) *Rheotanytarsus exiguus* gr.^{a} (Diptera) *Tanytarsus guerlus* gr.^{a} (Diptera) *Amnicola limosa* (Gastropoda) *Ferrissia* spp. (Gastropoda) *Pisidium* sp.^{a} (Bivalvia)	Naididae (Oligochaeta) *Gammarus fasciatus* (Amphipoda) *Stenacron* sp. (Ephemeroptera) *Hydroptila* sp. (Trichoptera) *Orthotrichia* sp. (Trichoptera) *Dicrotendipes* sp. (Diptera) *Glyptotendipes* sp. (Diptera) *Orthocladius* sp. (Diptera) *Polypedilum* spp. (Diptera) Ceratopogonidae^{a} (Diptera) *Bithynia tentaculata* (Gastropoda) *Amnicola limosa* (Gastropoda) *Gyraulus parvus* (Gastropoda) *Ferrissia* spp. (Gastropoda) *Dreissena polymorpha* (Bivalvia)
Oligohaline (0.5–5 psu or ppt)	Nematoda *Hypaniola grayi* (Polychaeta) *Scolecolepides viridis* (Polychaeta) Oligochaeta *Cyathura polita* (Isopoda) *Gammarus* spp. (Amphipoda)	Nematoda Oligochaeta Acari *Corophium lacustre* (Amphipoda) *Gammarus daiberi* (Amphipoda) *Leptocheirus plumulosus* (Amphipoda)	*Hypaniola grayi* (Polychaeta) Oligochaeta *Cyathura polita* (Isopoda) *Corophium lacustre* (Amphipoda) *Gammarus* spp. (Amphipoda) *Melita nitida* (Amphipoda)

Table 5, continued.

Salinity zone	Fine-grained sediments in deep water	Vegetated shallows	Rocky sediments
Oligohaline (0.5–5 psu or ppt)	*Leptocheirus plumulosus* (Amphipoda) *Monoculodes edwardsi* (Amphipoda) *Balanus improvisus* (Cirripedia) Chironomidae (Diptera) *Littoridinops tenuipes* (Gastropoda) *Mytilopsis leucophaeta* (Bivalvia)	*Monoculodes edwardsi* (Amphipoda) *Chironomus decorus* (Diptera) *Cricotopus sylvestris* (Diptera) *Dicrotendipes modestus* (Diptera) *Polypedilum halterale* (Diptera) *Polypedilum illinoense* (Diptera) *Procladius sublettei* (Diptera) *Rheotanytarsus* sp. (Diptera) *Tanytarsus* sp. (Diptera) Gastropoda *Mytilopsis leucophaeta* (Bivalvia)	*Rhithropanopeus harrissi* (Decapoda) *Balanus improvisus* (Cirripedia) Chironomidae (Diptera) *Hydrobia* spp. (Gastropoda) *Mytilopsis leucophaeta* (Bivalvia)
Mesohaline (5–18 psu or ppt)	*Scolecolepides viridis* (Polychaeta) *Streblospio benedicti* (Polychaeta) Oligochaeta *Cyathura polita* (Isopoda) *Edotea triloba* (Isopoda) *Leptocheirus plumulosus* (Amphipoda) Cumacea *Balanus improvisus* (Cirripedia) *Hydrobia* spp. (Gastropoda) *Macoma balthica* (Bivalvia) *Mya arenaria* (Bivalvia)	not studied	not studied
Polyhaline (18–30 psu or ppt)	*Eteone heteropoda* (Polychaeta) *Nereis succinea* (Polychaeta) *Polydora websteri* (Polychaeta) *Streblospio benedicti* (Polychaeta) Oligochaeta *Etodea triloba* (Isopoda) *Balanus balanoides* (Cirripedia) *Balanus subalbidus* (Cirripedia) *Mya arenaria* (Bivalvia) *Macoma balthica* (Bivalvia)	not studied	not studied

[a] abundance greatly reduced after the zebra mussel invasion

variance in 4th-root transformed densities among sites (cf. Fig. 9). Thus, most of the variance in animal densities (perhaps 75–90 % for most species in the Hudson) was accounted for neither by measured environmental variables (which typically explained 5–20 % of variance) nor by sampling error. Similarly large and unexplained local variation in zoobenthic communities has been reported from other rivers (e. g., HAAG & THORP 1991; SCHÖNBAUER 1998; SEYS et al. 1999). Additional causes for variation in benthic populations include unmeasured environmental variables, history, and biological interactions. Although we measured many variables conventionally thought to influence benthic animals, there are of course many additional variables that could affect the zoobenthos. For instance, functional properties of the sediment (e. g., coherence, penetrability) or local hydraulic variables could control benthic communities. Historical factors, especially disturbance history, can have a strong influence on benthic communities that is not revealed by one-time measurements of environmental variables. In the Hudson, scour or fill from tidal currents, floods, or dredging could affect the zoobenthos. Finally, the biological community in which the zoobenthos is embedded is itself highly patchy. Microbial resources, feeding by mobile predators, and interactions within the zoobenthos are capable of generating strong spatial structure in benthic populations. The relative importance of these various factors (other than sampling error) has not been assessed, but is an important challenge for understanding the large-river zoobenthos.

Effects of the zebra mussel invasion on the Hudson River zoobenthos

The zebra mussel invasion caused deep and widespread changes in the zoobenthos of the Hudson. Zoobenthic species showed two kinds of responses. First, a few species declined across all sites in the river. Almost all of the species that showed such widespread declines are planktivores (*Rheotanytarsus exiguus* group species, Fig. 14; *Tanytarsus guerlus* group species, Fig. 14; *Chaoborus punctipennis*, Fig. 10; Unionidae, Fig. 16; Sphaeriidae, Fig. 16; and perhaps *Manayunkia speciosa*, Fig. 5), and presumably were affected by the 70–90 % losses of phytoplankton and zooplankton that followed the zebra mussel invasion of the Hudson (CARACO et al. 1997; PACE et al. 1998). The single exception to this pattern was the Ceratopogonidae, which showed a marginally significant decline across all habitats (Fig. 10), but are not thought to be planktivorous.

A much more common pattern of response to the zebra mussel invasion was a graded response according to habitat, with much more negative changes in abundance in deepwater habitats than in vegetated shallow-water habitats. This pattern was shown by many benthic taxa, including flatworms (Fig. 5), nematodes (Fig. 5), *Gammarus fasciatus* (Fig. 10), *Oecetis inconspicua* (Fig. 10), several chironomids (Fig. 14), and the zoobenthos as a whole (Fig. 18). As we suggested elsewhere (STRAYER et al. 1998, 1999), this divergence between deepwater and shallow-water sites may have arisen because the increase in primary production by macrophytes and attached algae in the river shallows offset the loss in edible particles sedimenting through the water column. Thus, deepwater sites may have suffered a loss in sedimenting food, leading to a decline in zoobenthos. This decline would be consistent with studies done on other ecosystems demonstrating the importance of freshly settling phytoplankton to benthic animals (e.g., Jonasson 1972; Kajak 1988; Johnson et al. 1989; Johnson & Wiederholm 1992; Goedkoop & Johnson 1996). In the shallows, sedimenting particles would likewise decline, but could be supplemented by local increases in production by macrophytes and attached algae as a result of the increase in water clarity caused by the zebra mussel invasion (Caraco et al. 1997). Based on P-I curves for macrophytes in the Hudson (Harley & Findlay 1994), Caraco et al. (2000) estimated that net primary production in macrophyte beds may have doubled after the zebra mussel invasion.

As a result of these two kinds of responses, the overall riverwide response of a benthic species would be expected to depend on two variables: whether it was planktivorous and whether it lived chiefly in deep water or shallow water. Because of their direct connection to the plankton, planktivorous species would be expected to decline more steeply than other species. Species that lived chiefly in deep water would be expected to decline more severely than species that lived in shallow water; in fact, the latter species might increase as a result of the zebra mussel invasion. An ANCOVA showed that these variables were highly effective predictors of zoobenthic response to the zebra mussel invasion ($r^2 = 0.51$, $p = 0.00003$). Planktivorous

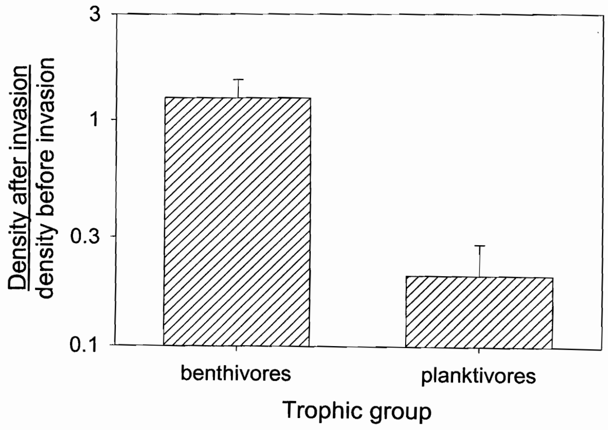

Fig. 19. Response of zoobenthic taxa to the zebra mussel invasion in the Hudson River, as a function of trophic group. Planktivores include *Manayunkia speciosa, Chaoborus punctipennis, Rheotanytarsus exiguus* group species, *Tanytarsus guerlus* group species, Unionidae, and Sphaeriidae; benthivores are all other taxa. Trophic group is a significant determinant ($p = 0.0004$) of response in an ANCOVA with group and habitat use (cf. Fig. 20) as independent variables ($r^2 = 0.51$; $p = 0.00003$).

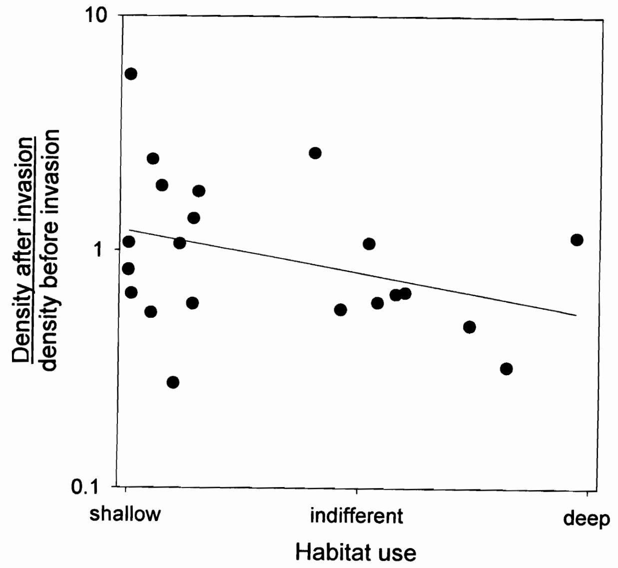

Fig. 20. Effect of the zebra mussel invasion on riverwide mean densities of major taxa of benthivorous macroinvertebrates in the freshwater tidal Hudson River, as a function of habitat use. Habitat use is a simple weighted average of densities in shallow- and deepwater sediments before the zebra mussel invasion, scaled from 0 (species that lived entirely in shallow-water sites) to 1 (species that lived entirely in deepwater sites). Habitat use is a significant determinant (p = 0.043) of response in an ANCOVA with trophic group (cf. Fig. 19) and habitat use as independent variables ($r^2 = 0.51$; p = 0.00003).

taxa declined more steeply than non-planktivorous taxa (Fig. 19), and taxa that lived chiefly in deep water declined more severely than those that lived in shallow water (Fig. 20). Populations of many species living in shallow water did in fact increase after the zebra mussel invasion (Fig. 20).

A few of the most sensitive taxa appear to have disappeared altogether from the freshwater tidal Hudson. While it is difficult to demonstrate that these species have been entirely extirpated from the Hudson, they are at least so rare now that they are ecologically negligible. Two species of unionids, *Anodonta implicata* and *Leptodea ochracea*, which formerly constituted a large fraction of zoobenthic biomass in the Hudson (STRAYER et al. 1994) have not been collected since 1997. Three rarer unionids that used to live in the Hudson (i. e., *Ligumia nasuta, Lampsilis cariosa*, and *Lampsilis radiata*) have not been seen since the zebra mussel invasion either, and probably have vanished from the river. Perhaps the most striking loss was that of *Chaoborus punctipennis*, a formerly abundant species that we have not collected from the Hudson since 1993. What is unusual about the case of *Chaoborus* is that this species and the zebra mussel scarcely overlapped spatially in the Hudson. *Chaoborus* lived on soft sediments in RKM 100–150 (Fig. 11), while zebra mussels lived chiefly on hard sediments in RKM 175–210 (STRAYER et al. 1996; CARACO et al. 1997). Nevertheless, the effects of zebra mussels extended for tens of kilometers downriver of their population center. The reach of the Hudson downriver of the zebra mussel population is too deep and turbid to allow phytoplankton to grow (Cole et al. 1992; Caraco et al. 1997). Before the zebra mussel arrived, RKM 100–150 contained phytoplankton and zooplankton that was produced upriver and exported downriver into the reach. Zebra mussel grazing removed phytoplankton from RKM 175–210, so plankton could be neither produced nor imported into RKM 100–150. Thus, both phytoplankton and zooplankton (especially microzooplankton) remained depressed for many kilometers downriver of the main zebra mussel population (Caraco et al. 1997; Pace et al. 1998). *Chaoborus* feeds on zooplankton and large, motile phytoplankton (e. g., Moore 1988; Moore et al. 1994), and the survival of early instars may be very sensitive to the abundance of small zooplankton (Neill 1988). The severe (~ 90%; Pace et al. 1998) loss of microzooplankton seems the likeliest mechanism by which the zebra mussel invasion caused the extirpation of *Chaoborus* in the Hudson. Thus, the effects of a midriver zebra mussel population were propagated downriver by the hydrologic and morphological characteristics of the Hudson to eliminate a *Chaoborus* population tens of kilometers downriver.

Several studies (e. g., Stewart & Haynes 1994; Ricciardi et al. 1997; Stewart et al. 1998a, b; Horvath et al. 1999; Kuhns & Berg 1999) have shown that zebra mussels cause large, local increases in macroinvertebrate densities in zebra mussel beds. This increase is due to both the shelter and the food provided by zebra mussels. Such studies may lead to the simplistic idea that zebra mussels (or other benthic suspension-feeders) divert resources from the plankton to the benthos. Studies done at small scales within zebra mussel beds neglect events that occur beyond the boundaries of these beds. In most lakes and rivers, zebra mussel beds constitute a small part of the benthic habitat. As the widespread decline in benthic populations in deepwater habitats in the Hudson showed, zebra mussels may divert resources from the benthos as well as the plankton. The overall effect of zebra mussels on the benthos will depend on the relative sizes of zebra mussel beds (where zoobenthos increases), deepwater areas outside of zebra mussel beds (where zoobenthos decreases), and shallow-water vegetated areas outside of zebra mussel beds (where zoobenthos may either increase or decrease). Thus, from the perspective of the whole ecosystem, zebra mussels may divert resources either towards or away from the benthos. A full accounting of the effects of the zebra mussel on the zoobenthos requires knowledge of changes in all three of these habitats, not just in the zebra mussel beds themselves. In the Hudson, we have measurements of the effects of the zebra mussel invasion on deepwater and shallow-water benthos, but not in the zebra mussel beds themselves, because no data exist on the zoobenthos of rocky bottoms prior to the zebra mussel invasion. Nonetheless, it is possible to use data from other ecosystems (Stewart & Haynes 1994; Ricciardi et al. 1997) to estimate the changes that might have occurred on rocky bottoms in the Hudson. Because rocky bottoms constitute only 7% of the area of the freshwater tidal

Table 6. Mean riverwide changes in macrobenthic densities in the Hudson River associated with the zebra mussel invasion. Figures are based on observed trends in vegetated and unvegetated habitats in the Hudson, and the mean of changes observed in zebra mussel beds in Lake Ontario (Stewart & Haynes 1994) and the St. Lawrence River (Ricciardi et al. 1997).

Taxon Habitat	Observed change (no./m^2) due to zebra mussel invasion			
	Unvegetated sites	Vegetated sites	Zebra mussel beds	Areally weighted riverwide mean
Area (%)	78	15	7	100
Turbellaria	−77	+207	+125	−27
Nematoda	−124	−28	+4	−101
Annelida	−2225	−418	+414	−1769
Isopoda	+16	0	+12	+13
Amphipoda	−1743	+66	+756	−1297
Acari	+1	+74	0	+12
Trichoptera	−46	+134	+16	−15
Chironomidae	−96	+211	+334	−20
Ceratopogonidae	−18	−275	0	−55
Chaoborus	−119	0	0	−92
Gastropoda	+94	+94	+588	+129
Sphaeriidae	−817	−360	+7	−691
Unionidae	−10	+1	0	−8
Total macrozoobenthos	−5164	−294	+2256	−3921

Hudson, this overall assessment of zebra mussel effects is not highly sensitive to the estimates of change in these rocky bottoms. When such a comprehensive accounting is made in the Hudson, we find that the zebra mussel invasion led to large declines in zoobenthos at the whole-ecosystem level (Table 6). The overall effect of zebra mussels on the rest of the zoobenthos has thus been strongly negative when viewed from the perspective of the entire Hudson ecosystem, in contrast to the conclusion that might be reached from narrower studies that focus only on events within the zebra mussel beds.

In terms of biomass, deepwater sites in the Hudson lost about half of their zoobenthos other than zebra mussels, while shallow water sites gained about 10 %, resulting in a riverwide loss of about 40 % of benthic biomass. Coupled with a loss of about 70 % of zooplankton biomass (Pace et al. 1998), we estimate that about half of the invertebrate biomass available for fish forage disappeared from the Hudson as a result of the zebra mussel invasion (Fig. 21).

Comprehensive assessment of the effects of the *Dreissena* invasion on the zoobenthos have been made at only a few sites (Howell et al. 1996; Dermott & Kerec 1997; Nalepa et al. 1998). All of these sites were on soft substrata in the Great Lakes, most were in water > 10 m deep, and most supported dense populations of zebra mussels. Thus, these sites differed from the Hudson in many ways. Nevertheless, these studies found many of the same changes in the zoobenthos that we found in the Hudson. Typically, animals that feed on suspended or freshly

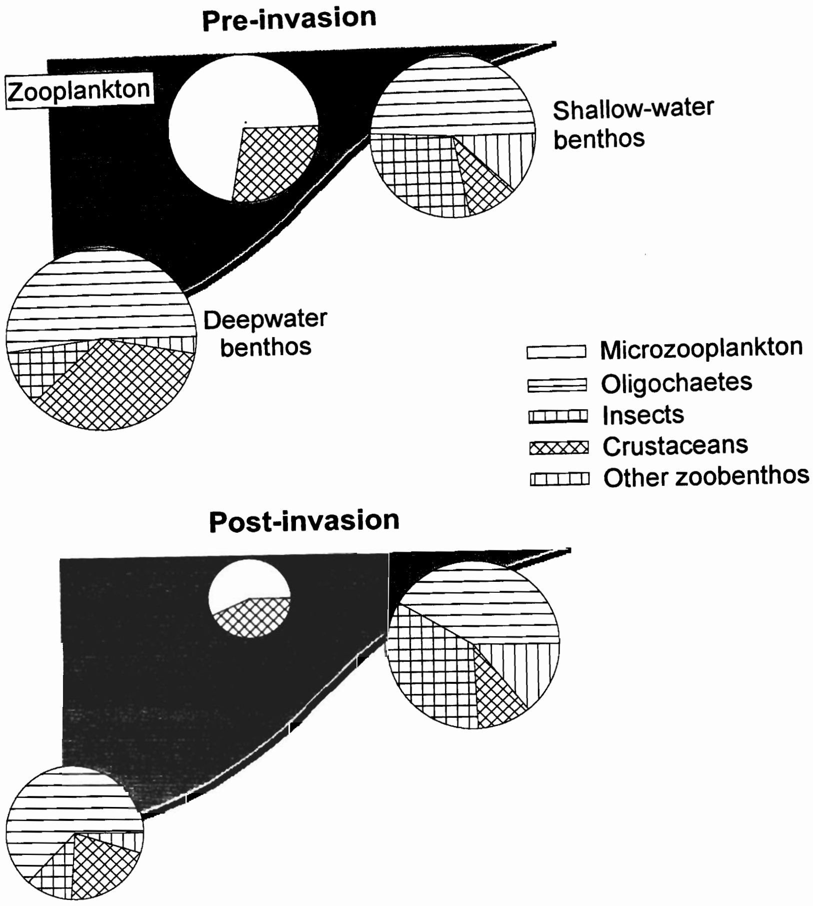

Fig. 21. Changes in the invertebrate forage base in three habitats in the Hudson River in response to the zebra mussel invasion. The biomass of invertebrates in each habitat (in g DM/m^2) is proportional to the area of the circle. Favored forage items (crustaceans and insects; cf. Table 9) are shown in cross-hatching. Data exclude unionids and zebra mussels, which are eaten by few fish species. Zooplankton data from PACE et al. (1998).

settled plankton (i.e., the amphipod *Diporeia*, sphaeriids, suspension-feeding chironomids, the polychaete *Manayunkia*) declined sharply. Some deposit-feeding animals (i.e., tubificid oligochaetes) declined, but these declines were modest, and often not statistically significant. Animals that used *Dreissena* beds for food or shelter (i.e., gammarid amphipods, meiofauna) increased. Overall, the *Dreissena* invasion caused biomass of macrozoobenthic animals other than *Dreissena* to fall. Thus, many of the changes we observed in the Hudson may occur generally in fresh waters.

Roles of the zoobenthos in the Hudson River ecosystem

Conventional assessments of the ecological roles of the biota focus on biomass, production, and respiration. Of these variables, only biomass has been measured for the Hudson River zoobenthos, but production and respiration can be roughly estimated from biomass data and approximate turnover ratios (Table 7). Compared to zoobenthic data from other lakes and rivers (Rasmussen & Kalff 1987; Plante & Downing 1989; Benke 1993), zoobenthic biomass, respiration, and production in the Hudson were moderately low. Production and respiration of the zoobenthos were roughly equal to those of the zooplankton before the zebra mussel invasion (Lints et al. 1992). In the context of the whole ecosystem, both zoobenthic and zooplanktonic production and respiration were dwarfed by those of the microbes (Lints et al. 1992). After the zebra mussel invasion, increases in metabolic activity by zebra mussels overwhelmed the decreases in the metabolic activity of the rest of the zoobenthos (Table 7), so that zoobenthic respiration became an important part of the whole-ecosystem oxygen budget (Caraco et al. 2000). Nevertheless, these metabolic variables are inadequate to express fully the role of the zoobenthos (or any other part of the biota) in an ecosystem. In particular, it often is possible to assess more specific roles that the zoobenthos plays in the ecosystem. Here, we briefly discuss three such roles: suspension-feeding activity, food for fish, and sediment mixing.

Suspension-feeding links the zoobenthos to the overlying water column. Only two major groups of benthic animals in the Hudson were suspension feeders: bivalves and tanytarsine midges (the polychaete *Manayunkia speciosa* probably suspension-feeds as well, but was quantitatively unimportant in the Hudson). Other typically abundant freshwater suspension-feeders (e.g., net-spinning Trichoptera, Simuliidae, burrowing mayflies) were strikingly absent from the Hudson estuary. Before the zebra mussel invasion, riverwide clearance rates of benthic suspension-feeders were modest (Table 8) and about equal to downstream flushing. Zooplankton grazing rates were likewise small ($\sim$ 0.1 $m^3/m^2/d$) on a riverwide basis (Caraco et al. 1997). Despite these modest clearance rates, suspension-feeders probably were

Table 7. Estimated biomass, production, and respiration of the macrozoobenthos in the freshwater tidal Hudson River. Biomass based on individual dry masses measured by Simpson et al. (1984, 1986) and this study, and converted to carbon by multiplying by 0.5. Production estimated from biomass by assuming annual P/B of 0.2 for the Unionidae (Strayer et al. 1994), 1 for *Dreissena* (Stanczykowska 1976; Waters 1977; Cleven & Frenzel 1993), and 5 for the remainder of the macrozoobenthos (Waters 1977). Respiration estimated by assuming a net growth efficiency of 30% (cf. Schroeder 1981). Figures are areally weighted means for the freshwater tidal Hudson.

	Pre-invasion	Post-invasion	
		excluding *Dreissena*	including *Dreissena*
Biomass (g C/m^2)	3.7	1.6	12
Production (g $C/m^2/yr$)	3.8	2.3	32
Respiration (g $C/m^2/yr$)	8.9	5.4	111

Table 8. Estimated clearance rates (areally weighted means, $m^3/m^2/d$, summer growing season) for benthic suspension-feeders in the freshwater tidal Hudson River, before and after the zebra mussel invasion. Rate for *Dreissena* and unionids estimated by applying laboratory clearance rates (Kryger & Riisgard 1988; Roditi et al. 1996) to densities and sizes of animals observed in the Hudson (Strayer et al. 1994, 1996). Actual clearance rates for sphaeriids and tanytarsines are poorly known, but were roughly estimated as follows. Clearance rates for *Pisidium* were assumed to be 1 ml/individual/hr (Hinz & Schiel 1972; Lopez & Holopainen 1987). For tanytarsines, we assumed a mean area of the catch net of 1.4×10^{-5} m^2 (cf. Walshe 1951), a flow velocity of 1 cm/s, and an ingestion efficiency of 1% (comparable to the low rates reported for passive suspension-feeding insects by Schröder 1988).

Taxon	Pre-invasion	Post-invasion
Dreissena	0	5.1
Unionidae	0.14	0.05
Sphaeriidae	0.02	0.005
Tanytarsini	0.01	0.004
Total zoobenthos	0.17	5.2

abundant enough to affect phytoplankton and other suspended particles at particular time and places. For example, the planktonic cladoceran *Bosmina freyi* developed dense populations in the freshwater estuary in June (Pace et al. 1992), and unionid bivalves were abundant ($75/m^2$) in RKM 213–248 (Strayer et al. 1994). With the arrival of zebra mussels, clearance rates by benthic suspension-feeders rose by 10–100 fold (Table 8), changing the Hudson from an ecosystem where benthic suspension-feeding was of modest, local importance to a system where benthic suspension-feeding was a dominant process. In shallow, well mixed aquatic ecosystems, changes in benthic suspension-feeders can strongly affect the amount and composition of suspended particles (and vice versa) (e.g., Cohen et al. 1984; Alpine & Cloern 1992; Ulanowicz & Tuttle 1992; Dame 1996). In the Hudson, the zebra mussel invasion caused large changes in populations of planktonic bacteria, algae, and animals (Caraco et al. 1997; Findlay et al. 1998; Pace et al. 1998; Smith et al. 1998).

Most species of fish in the Hudson that are not piscivorous fed heavily on benthic animals (Table 9). Amphipods, chironomids, and microcrustaceans were especially important in fish diets, perhaps because they were abundant and often active at and above the sediment surface, where they are easily captured by fish. In contrast, the abundant oligochaetes and mollusks in the Hudson appeared to be less important in fish diets, perhaps because they burrow or are protected by thick shells, although the absence of indigestible hard structures in oligochaetes may make them hard to detect in routine gut analyses. Presumably, many benthic animals are captured as they drift or emerge through the water column, when they are especially vulnerable to fish predation (Townes 1937). It is not possible to estimate exactly what fraction of fish production was supported by benthic invertebrates, but based on Table 9, it is reasonable to guess that well over half of fish production in the freshwater tidal Hudson was supported by benthic invertebrates. The zebra mussel invasion caused

Table 9. Importance of benthic invertebrates in the diets of some Hudson River fishes. Importance is expressed as % of number (N) or volume (V) of items in the gut contents that were benthic invertebrates. YOY = young-of-year fish.

Fish species	% of diet	Dominant items in diet	Source
shortnose sturgeon (YOY)	100 (V)	chironomids	Carlson & Simpson 1986
shortnose sturgeon	100 (V)	chironomids, mollusks, oligochaetes	Curran & Ries 1937
Atlantic sturgeon	100 (V)	chironomids, oligochaetes	Curran & Ries 1937
Blueback herring (YOY)	49 (V)	copepods	Limburg 1988
American shad (YOY)	~ 65 (N, V)	chironomids, *Chaoborus*	Townes 1937; Limburg 1988
spottail shiner	>50 (N)	microcrustaceans, chironomids	Smith & Schmidt 1988
tomcod	99 (N)	amphipods	McLaren et al. 1988
banded killifish	>50 (N)	microcrustaceans, chironomids	Richard & Schmidt 1986
white perch	91–99 (N)	amphipods	Curran & Ries 1937; Bath & O'Connor 1985
striped bass (YOY)	85 (N)	amphipods	Townes 1937; Gardinier & Hoff 1983
striped bass (1–2 yr)	76 (N)	amphipods	Gardinier & Hoff 1983
tesselated darter	>50 (N)	chironomids, microcrustaceans	Duryea & Schmidt 1986

large changes in the amount and kind of forage invertebrates available to fish in the Hudson (Fig. 21).

Benthic animals also play an important role in mixing sediments and altering exchanges of materials between sediment and overlying water (e.g., McCall & Tevesz 1982; Robbins 1982; van de Bund et al. 1994). Burrowing animals and deposit-feeders such as tubificid oligochaetes, chironomids, amphipods, and unionid mussels have been especially implicated in sediment mixing (Robbins 1982; van de Bund et al. 1994; McCall et al. 1995). Although biological sediment mixing has not been estimated in the freshwater Hudson estuary, the abundance of tubificids, amphipods, and unionids suggests that such mixing may have been substantial. The declines in populations of these animals (Figs. 5, 10, 16) after the zebra mussel invasion may have substantially reduced such biological sediment mixing in the Hudson, and well as altering its spatial distribution.

Further, sediment-water exchanges may be affected by bivalves and their spent shells, either because the bivalves alter sediment roughness and thereby near-bottom turbulence or because the bivalves and their shells protect fine sediments from erosion. The large, dense unionid beds formerly present in the upper river are disappearing (Fig. 15), and the large accumulations of empty unionid shells in this reach subsequently are declining (STRAYER et al. unpublished). At the same time, although most zebra mussels in the Hudson were attached to rocks (STRAYER et al. 1996), many empty shells and small colonies of zebra mussels have appeared on soft sediments. The net effects of the changes in bivalve populations on sediment dynamics have not been measured, but could be large and spatially variable in the Hudson. Thus, the zebra mussel invasion changed populations of sediment mixers and bivalves in the Hudson, which probably caused large changes in sediment-water exchanges in the Hudson. Unfortunately, these changes have not been measured, nor can even the direction of change easily be estimated.

Thus, the role of benthic animals in the Hudson ecosystem was larger and more complex than would be suggested from a simple assessment of metabolic parameters. The overall importance of the zoobenthos in the ecosystem differed across roles, and the importance of different members of the zoobenthos differed across roles. Thus, amphipods were especially important as fish food, while unionids were important suspension-feeders, although neither had very large production or respiration. Assessment of specific roles is more likely to give a satisfactory assessment of the roles of benthic animals than is a simple inspection of metabolic parameters.

Finally, regardless of what measure is used to assess ecological role, the zebra mussel invasion changed the importance of the zoobenthos in the Hudson ecosystem. Overall biomass, production, respiration, and clearance rates rose substantially, while availability of fish forage fell by about half. Sediment mixing probably changed as well, although this role has not been assessed in the Hudson, so even the direction of the change is not known. Thus, the zebra mussel invasion had profound effects on the functions as well as the composition of the zoobenthos.

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Literature cited

ABOOD, K. A., APICELLA, G. A. & WELLS, A. W. (1992): General evaluation of Hudson River freshwater flow trends. – In: SMITH, C. L. (ed.): Estuarine research in the 1980s: 3–28. State University of New York Press.

ALPINE, A. E. & CLOERN, J. E. (1992): Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. – Limnol. Oceanogr. **37**: 946–955.

ANDRASSY, I. (1981): Revision of the order Monhysterida (Nematoda) inhabiting soil and inland waters. – Opusc. Zool. **17/18**: 13–47.

– (1988): The superfamily Dorylaimoidea (Nematoda) – a review. Family Dorylaimidae. – Opusc. Zool. **23**: 3–63.

ASHIZAWA, D. & COLE, J. J. (1994): Long-term temperature trends of the Hudson River: a study of the historical data. – Estuaries **17**: 166–171.

BATH, D. W. & O'CONNOR, J. M. (1985): Food preferences of white perch in the Hudson River estuary. – N.Y. Fish Game J. **32**: 63–70.

BECKETT, D. C. (1992): Phenology of the larval Chironomidae of a large temperate Nearctic river. – J. Freshwat. Ecol. **7**: 303–316.

BECKETT, D. C., BINGHAM, C. R. & SANDERS, L. G. (1983): Benthic macroinvertebrates of selected habitats of the lower Mississippi River. – J. Freshwat. Ecol. **2**: 247–261.

BENKE, A. C. (1993): Concepts and patterns of invertebrate production in running waters. – Verh. Int. Verein. Limnol. **25**: 15–38.

BENKE, A. C., VAN ARSDELL, T. C. & GILLESPIE, D. M. (1984): Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. – Ecol. Monogr. **54**: 25–63.

BERG, M. B. (1995): Larval food and feeding behavior. – In: ARMITAGE, P. D., CRANSTON, P. S. & PINDER, P. C. V. (eds.): The Chironomidae: biology and ecology of non-biting midges: 136–168. Chapman & Hall.

BODE, R. W., NOVAK, M. A., FAGNANI, J. P. & DENICOLA, D. M. (1986): The benthic macroinvertebrates of the Hudson River from Troy to Albany, New York. – Final Report to the Hudson River Foundation, New York, 145 pp.

BOTTS, P. S. PATTERSON, B. A. & SCHLOESSER, D. W. (1996): Zebra mussel effects on benthic invertebrates: physical or biotic? – J. N. Amer. Benthol. Soc. **15**: 179–184.

BOUSFIELD, E. L. (1973): Shallow-water gammaridean Amphipoda of New England. – Cornell University Press, 312 pp.

BOYLE, R. H. (1979): The Hudson River: a natural and unnatural history. Expanded edition. – W. W. Norton, New York.

BRINKHURST, R. O. (1986): Guide to the freshwater aquatic microdrile oligochaetes of North America. – Can. Spec. Publ. Fish. Aquat. Sci. **84**: 1–259.

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.

CARLSON, D. M. & SIMPSON, K. W. (1987): Gut contents of juvenile shortnose sturgeon in the Upper Hudson River estuary. – Copeia **1987**: 196–202.

CASPERS, N. (1991): The actual biocoenotic zonation of the River Rhine exemplified by the chironomid midges (Insecta, Diptera). – Verh. Int. Verein. Limnol. **24**: 1829–1834.

CLEVEN, E. J. & FRENZEL, P. (1993): Population dynamics and production of *Dreissena polymorpha* (PALLAS) in River Seerhein, the outlet of Lake Constance (Obersee). – Arch. Hydrobiol. **127**: 395–407.

COHEN, R. R. H., DRESLER, P. V., PHILLIPS, E. J. P. & CORY, R. L. (1984): The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. – Limnol. Oceanogr. **29**: 170–180.

COLE, J. J., CARACO, N. F. & PEIERLS, B. (1992): Can phytoplankton maintain a positive carbon balance in a turbid, freshwater, tidal estuary? – Limnol. Oceanogr. **37**: 1608–1617.

COOPER, J. C., CANTELMO, F. R. & NEWTON, C. E. (1988): Overview of the Hudson River estuary. – Amer. Fish. Soc. Monogr. **4**: 11–24.

CRANDALL, M. E. (1977): Epibenthic invertebrates of Croton Bay in the Hudson River. – N.Y. Fish Game J. **24**: 178–186.

CRUMB, S. E. (1977): Macrobenthos of the tidal Delaware River between Trenton and Burlington. – Chesapeake Sci. **18**: 253–265.

Curran, H. W. & Ries, D. T. (1937): Fisheries investigations in the lower Hudson River. – In: Moore, E. (ed.): A biological survey of the lower Hudson watershed. Suppl. 26th Ann. Rep. St. N.Y. Conserv. Dept.: 124–145.

Dame, R. F. (1996): Ecology of marine bivalves: an ecosystem approach. – CRC Press, 254 pp.

Davies, R. W. (1991): Annelida: leeches, polychaetes, and acanthobdellids. – In: Thorp, J. H. & Covich, A. P. (eds.): Ecology and classification of North American freshwater invertebrates: 437–479. Academic Press.

Dermott, R. & Kerec, D. (1997): Changes in the deepwater benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979–1993. – Can. J. Fish. Aquat. Sci. **54**: 922–930.

Diaz, R. J. (1989): Pollution and tidal benthic communities of the James River estuary, Virginia. – Hydrobiologia **180**: 195–211.

Downing, J. A. (1979): Aggregation, transformation, and the design of benthos sampling programs. – J. Fish. Res. Bd. Canada **36**: 1454–1463.

Dudgeon, D. (2000): Going with the flow: large-scale hydrological changes and prospects for riverine biodiversity in tropical Asia. – BioScience **50**: 793–806.

Duryea, M. & Schmidt, R. E. (1986): Feeding biology of tesselated darter (*Etheostoma olmstedi atromaculatus*) at Tivoli North Bay, Hudson River, New York. – In: Blair, E. A. & Cooper, J. C. (eds.): Polgar Fellowship reports of the Hudson River National Estuarine Research Reserve Program, 1986. Hudson River Foundation, New York: pp. III-1 to III-19.

Ebsary, B. A. (1982): Canadian species of *Tobrilus* (Nematoda: Tobrilidae) with description of three new species. – Can. J. Zool. **60**: 3048–3062.

Effler, S. W., Boone, S. R., Siegfried, C. A., Walrath, L. & Ashby, S. L. (1997): Mobilization of ammonia and phosphorus by zebra mussels (*Dreissena polymorpha*) in the Seneca River, New York. – In: D'Itri, F. M. (ed.): Zebra mussels and aquatic nuisance species: 187–207. Ann Arbor Press.

Ettinger, W. S. (1982): Macrobenthos of the freshwater tidal Schuylkill River at Philadelphia, Pennsylvania. – J. Freshwat. Ecol. **1**: 599–606.

Findlay, S., Pace, M. L. & Fischer, D. T. (1998): Response of heterotrophic planktonic bacteria to the zebra mussel invasion of the tidal freshwater Hudson River. – Microb. Ecol. **36**: 131–140.

Findlay, S., Pace, M. & Lints, D. (1991): Variability and transport of suspended sediment, particulate and dissolved organic carbon in the tidal freshwater Hudson River. – Biogeochemistry **12**: 149–169.

Findlay, S., Schoeberl, K. & Wagner, B. (1989): Abundance, composition, and dynamics of the invertebrate fauna of a tidal freshwater wetland. – J. N. Amer. Benthol. Soc. **8**: 140–148.

Fruget, J. F. (1992): Ecology of the lower Rhône after 200 years of human influence: a review. – Regul. Rivers Res. Mgmt. **7**: 233–246.

Gardinier, M. N. & Hoff, T. B. (1983): Diet of striped bass in the Hudson River estuary. – N.Y. Fish Game J. **29**: 152–165.

Gee, G. W. & Bauder, J. W. (1986): Particle size analysis. – In: Klute, A. (ed.): Methods of soil analysis. Part 1. Physical and mineralogical methods: 383–411. American Society of Agronomy.

Gladden, J. B., Cantelmo, F. R., Croom, J. M. & Shapot, R. (1988): Evaluation of the Hudson River ecosystem in relation to the dynamics of fish populations. – Amer. Fish. Soc. Monogr. **4**: 37–52.

Goedkoop, W. & Johnson, R. K. (1996): Pelagic-benthic coupling: profundal benthic community response to spring diatom deposition in mesotrophic Lake Erken. – Limnol. Oceanogr. **41**: 636–647.

Gosner, K. L. (1971): Guide to identification of marine and estuarine invertebrates, Cape Hatteras to Bay of Fundy. – Wiley-Interscience, 693 pp.

Haag, K. H. & Thorp, J. H. (1991): Cross-channel distribution patterns of zoobenthos in a regulated reach of the Tennessee River. – Regul. Rivers Res. Mgmt. **6**: 225–233.

Harley, M. T. & Findlay, S. (1994): Photosynthesis-irradiance relationships for three species of submersed macrophytes in the tidal freshwater Hudson River. – Estuaries **17**: 200–205.

Hart, C. W. & Fuller, S. L. H. (eds.) (1974): Pollution ecology of freshwater invertebrates. – Academic Press, 389 pp.

Hinz, W. & Schiel, H.-G. (1972): Zur Filtrationsleistung von *Dreissena, Sphaerium* und *Pisidium* (Eulamellibranchiata). – Oecologia **11**: 45–54.

Hirschfield, H. I., Rachlin, J. W. & Leff, E. (1966): A survey of the invertebrates from selected sites of the lower Hudson River. – In: Eisenbud, M. & Stevens, D. B. (eds.): Hudson River ecology: 220–257. Hudson River Valley Commission.

Horvath, T. G., Martin, K. M. & Lamberti, G. A. (1999): Effect of zebra mussels, *Dreissena polymorpha*, on macroinvertebrates in a lake-outlet stream. – Am. Midl. Nat. **142**: 340–347.

Howell, E. T., Marvin, C. H., Bilyea, R. W., Kauss, P. B. & Somers, K. (1996): Changes in environmental conditions during *Dreissena* colonization of a monitoring station in eastern Lake Erie. – J. Great Lakes Res. **22**: 744–756.

Howells, G. P., Musnick, E. & Hirschfield, H. I. (1969): Invertebrates of the Hudson River. – In: Howells, G. P. & Lauer, G. J. (eds): Hudson River ecology: proceedings of a symposium: 262–280. New York State Department of Environmental Conservation.

Hummon, W. D. (1981): Extraction by sieving: a biased procedure in studies of stream meiobenthos. – Trans. Am. Microsc. Soc. **100**: 278–284.

Humpesch, U. H. (1996): Case study – the River Danube in Austria. – Arch. Hydrobiol. Suppl. **113**: 239–266.

Hyman, L. H. (1959): Order Tricladida. – In: Edmondson, W. T. (ed.): Fresh-water biology, 2nd ed.: 326–334. John Wiley.

Jacobson, M. K. (1953): *Congeria leucophaeta* (Conrad) in the Hudson River. – Nautilus **66**: 125–128.

Johnson, R. K., Bostrom, B. & van de Bund, W. (1989): Interactions between *Chironomus plumosus* and the microbial community in surficial sediments of a shallow, eutrophic lake. – Limnol. Oceanogr. **34**: 992–1003.

Johnson, R. W. & Wiederholm, T. (1992): Pelagic-benthic coupling: the importance of diatom interannual variability for population oscillations of *Monoporeia affinis*. – Limnol. Oceanogr. **37**: 1596–1607.

Jonasson, P. M. (1972): Ecology and production of the profundal zoobenthos in relation to phytoplankton in Lake Esrom. – Oikos Suppl. **14**: 1–148.

Kajak, Z. (1988): Consideration on benthos abundance in freshwater, its factors and mechanisms. – Int. Rev. ges. Hydrobiol. **73**: 5–19.

Karatayev, A. Y., Burlakova, L. E. & Padilla, D. K. (1997): The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities in eastern Europe. – J. Shellfish Res. **16**: 187–203.

Kryger, J. & Riisgard, H. U. (1988): Filtration rate capacities in 6 species of European freshwater bivalves. – Oecologia **77**: 34–38.

Kuhns, L. A. & Berg, M. B. (1999): Benthic invertebrate community responses to round goby (*Neogobius melanostomus*) and zebra mussel (*Dreissena polymorpha*) invasion in southern Lake Michigan. – J. Great Lakes Res. **25**: 910–917.

Leuven, R. S. E. W., Brock, T. C. M. & van Druten, H. A. M. (1985): Effects of preservation on dry- and ash-free dry weight biomass of some common aquatic macroinvertebrates. – Hydrobiologia **127**: 151–159.

Limburg, K. E. (1988): Studies of young-of-the-year river herring and American shad in the Tivoli Bays, Hudson River, New York. – In: Waldman, J. R. & Blair, E. A. (eds.): Polgar Fellowship reports of the Hudson River Research Reserve Program, 1987: pp. VII-1 to VII-62.

Limburg, K. E., Moran, M. A. & McDowell, W. H. (1986): The Hudson River ecosystem. – Springer-Verlag, 331 pp.

Lindegaard, C. (1995): Classification of water-bodies and pollution. – In: Armitage, P. D., Cranston, P. S. & Pinder, P. C. V. (eds.): The Chironomidae: biology and ecology of non-biting midges: 385–404. Chapman & Hall.

Lints, D., Findlay, S. E. G. & Pace, M. L. (1992): Biomass and energetics of consumers in the lower food web of the Hudson River. – In: Smith, C. L. (ed.): Estuarine research in the 1980s: 446–457. State University of New York Press.

Lopez, G. R. & Holopainen, I. J. (1987): Interstitial suspension-feeding by *Pisidium* spp. (Pisidiidae: Bivalvia): a new guild in the lentic benthos? – Am. Malacol. Bull. **5**: 21–29.

MacIsaac, H. J. (1996): Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. – Amer. Zool. **36**: 287–299.

Malmqvist, B., Wotton, R. S. & Zhang, Y. (2001): Suspension feeders transform massive amounts of seston in large northern rivers. – Oikos **92**: 35–43.

Mancroni, W. J., Daley, M. W. & Dey, W. (1992): Recent trends and patterns in selected water quality parameters in the mid-Hudson River estuary. – In: Smith, C. L. (ed.): Estuarine research in the 1980s: 59–81. State University of New York Press.

Manoleli, D. (1975): On the distribution, biology, and origin of Polychaeta from the Danube and Danube delta, Romania. – Trav. Mus. Hist. Nat. Grigore Antipa **16**: 25–34 (only abstract seen).

Massengill, R. R. (1976): Benthic fauna: 1965–1967 versus 1968–1972. – In: Merriam, D. & Thorpe, L. M. (eds.): The Connecticut River ecological study: the impact of a nuclear power plant. – Amer. Fish. Soc. Monogr. **1**: 39–59.

McCall, P. L. & Tevesz, M. J. S. (1982): The effects of benthos on physical properties of freshwater sediments. – In: McCall, P. L. & Tevesz, M. J. S. (eds.): Animal-sediment relations: the biogenic alteration of sediments: 105–176. Plenum Press.

McCall, P. L., Tevesz, M. J. S., Wang, X. & Jackson, J. R. (1995): Particle mixing rates of freshwater bivalves: *Anodonta grandis* (Unionidae) and *Sphaerium striatinum* (Pisidiidae). – J. Great Lakes Res. **21**: 333–339.

McLaren, J. B., Peck, T. H., Dey, W. P. & Gardinier, M. (1988): Biology of Atlantic tomcod in the Hudson River estuary. – Am. Fish. Soc. Monogr. **4**: 102–112.

Menzie, C. A. (1980): The chironomid (Insecta: Diptera) and other fauna of a *Myriophyllum spicatum* L. plant bed in the lower Hudson River. – Estuaries **3**: 38–54.

Merritt, R. W. & Cummins, K. W. (eds.) (1996): An introduction to the aquatic insects of North America, 3rd ed. – Kendall/Hunt, 862 pp.

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. – 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.

Moog, O., Humpesch, U. H. & Konar, M. (1995): The distribution of benthic invertebrates along the Austrian stretch of the River Danube and its relevance as an indicator of zoogeographical and water quality patterns – part 1. – Arch. Hydrobiol. Suppl. **101**: 121–213.

Moore, M. (1988): Differential use of food resources by the instars of *Chaoborus punctipennis*. – Freshwat. Biol. **19**: 249–268.

Moore, M., Yan, N. D. & Pawson, T. (1994): Omnivory of the phantom midge (*Chaoborus* spp.) and its potential significance for freshwater planktonic food webs. – Can. J. Zool. **72**: 2055–2065.

Nalepa, T. F., Hartson, D. J., Fanslow, D. L., Lang, G. A. & Lozano, S. J. (1998): Declines in benthic macroinvertebrate populations in southern Lake Michigan, 1980–1993. – Can. J. Fish. Aquat. Sci. **55**: 2402–2413.

Neill, W. E. (1988): Community responses to experimental nutrient perturbations in oligotrophic lakes: the importance of bottlenecks in size-structured populations. – In: Ebenman, B. & Persson, L. (eds.): Size-structured populations: ecology and evolution: 236–255. Springer-Verlag.

Nekrasova, M. Y. (1972): Zoobenthos stock and production in Gulf of Taganrog. – Hydrobiol. J. **8**: 30–36.

Neves, R. J., Bogan, A. E., Williams, J. D., Ahlstedt, S. A. & Hartfield, P. W. (1997): Status of aquatic mollusks in the southeastern United States: a downward spiral of diversity. – In: Benz, G. W. & Collins, D. E. (eds): Aquatic fauna in peril: the southeastern perspective: 43–86. Lenz Design & Communications.

Oliver, D. R., Dillon, M. E. & Cranston, P. S. (1990): A catalog of Nearctic Chironomidae. – Research Branch, Agriculture Canada, Ottawa.

Oliver, D. R. & Roussel, M. E. (1983): The insects and arachnids of Canada, part 11: the genera of larval midges of Canada (Diptera: Chironomidae). – Biosystematics Research Unit, Agriculture Canada, 263 pp.

Pace, M. L., Findlay, S. E. G. & Fischer, D. T. (1998): Effects of an invasive bivalve on the zooplankton community of the Hudson River. – Freshwat. Biol. **39**: 103–116.

Pace, M. L., Findlay, S. E. G. & Lints, D. (1992): Zooplankton in advective environments: the Hudson River community and a comparative analysis. – Can. J. Fish. Aquat. Sci. **49**: 1060–1069.

Peckarsky, B. L., Fraissinet, P. R., Penton, M. A. & Conklin, D. J. (1990): Freshwater macroinvertebrates of northeastern North America. – Cornell University Press, 442 pp.

Pennak, R. W. (1989): Fresh-water invertebrates of the United States, third edition. – Wiley-Interscience, 628 pp.

Pinder, L. C. V. (1995): The habitats of chironomid larvae. – In: Armitage, P. D., Cranston, P. S. & Pinder, P. C. V. (eds.): The Chironomidae: biology and ecology of non-biting midges: 107–135. Chapman & Hall.

Pinder, L. C. V. & Reiss, F. (1983): The larvae of Chironominae (Diptera: Chironomidae) of the Holarctic region – keys and diagnoses. – Entomol. Scand. Suppl. **19**: 293–435.

Plante, C. & Downing, J. A. (1989): Production of freshwater invertebrate populations in lakes. – Can. J. Fish. Aquat. Sci. **46**: 1489–1498.

Rasmussen, J. B. & Kalff, J. (1987): Empirical models for zoobenthic biomass in lakes. – Can. J. Fish. Aquat. Sci. **44**: 990–1001.

Rehder, H. A. (1937): *Congeria leucophaeta* (Con.) in the Hudson River. – Nautilus **50**: 143.

Ricciardi, A., Whoriskey, F. G. & Rasmussen, J. B. (1997): The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. – Can. J. Fish. Aquat. Sci. **54**: 2596–2608.

Richard, E. & Schmidt, R. E. (1986): Feeding biology of the banded killifish (*Fundulus diaphanus*) at Tivoli North Bay, Hudson River, New York. – In: Blair, E. A. & Cooper, J. C. (eds.): Polgar Fellowship reports of the Hudson River National Estuarine Research Reserve Program, 1986: pp. II-1 to II-20. Hudson River Foundation, New York.

Ristich, S. S., Crandall, M. E. & Fortier, J. (197): Benthic and epibenthic macroinvertebrates of the Hudson River. I. Distribution, natural history and community structure. – Est. Coast. Mar. Sci. **5**: 255–266.

Robbins, J. A. (1982): Stratigraphic and dynamic effects of sediment reworking by Great Lakes zoobenthos. – Hydrobiologia **92**: 611–622.

Roditi, H. A., Caraco, N. F., Cole, J. J. & Strayer, D. L. (1996): Filtration of Hudson River water by the zebra mussel (*Dreissena polymorpha*). – Estuaries **19**: 824–832.

Rohmann, S. O. (1985): Tracing a river's toxic pollution: a case study of the Hudson River. – INFORM, 154 pp.

Rohmann, S. O. & Lilienthal, N. (1987): Tracing a river's toxic pollution: a case study of the Hudson River. Phase II. – INFORM, 209 pp.

Rosenberg, D. M. & Resh, V. H. (eds.) (1993): Freshwater biomonitoring and benthic macroinvertebrates. – Chapman & Hall, 488 pp.

Schönbauer, B. (1998): The Austrian Danube, a deep, fast flowing river: A) zoobenthos of the main channel. – Verh. Int. Verein. Limnol. **26**: 1129–1135.

Schroeder, L. A. (1981): Consumer growth efficiencies: their limits and relationships to ecological energetics. – J. Theor. Biol. **93**: 805–828.

Schröder, P. (1988): Quantitative Aspekte zur Ernährungsbiologie passiver Filterer (Larven der Simuliidae, Chironomiden und netzbauenden Trichopteren). – Arch. Hydrobiol. Suppl. **77**: 183–270.

Seys, J., Vincx, M. & Meire, P. (1999): Spatial distribution of oligochaetes (Clitellata) in the tidal freshwater and brackish parts of the Schelde estuary (Belgium). – Hydrobiologia **406**: 119–132.

Simpson, K. W., Bode, R. W., Fagnani, J. P. & Denicola, D. M. (1984): The freshwater macrobenthos of the main channel, Hudson River, part B: biology, taxonomy and distribution of resident macrobenthic species. – Final report to the Hudson River Foundation, New York, 203 pp.

Simpson, K. W., Fagnani, J. P., Bode, R. W., Denicola, D. M. & Abele, L. E. (1986): Organism-substrate relationships in the main channel of the lower Hudson River. – J. N. Amer. Benthol. Soc. **5**: 41–57.

Simpson, K. W., Fagnani, J. P., Denicola, D. M. & Bode, R. W. (1985): Widespread distribution of some estuarine crustaceans (*Cyathura polita, Chiridotea almyra, Almyracuma proximoculi*) in the limnetic zone of the lower Hudson River, New York. – Estuaries **8**: 373–380.

Smith, D. G. (1995): Keys to the freshwater macroinvertebrates of Massachusetts, 2nd ed. – Privately published, 243 pp.

Smith, D. G. & Menzie, C. C. (1994): *Hydrolimax grisea* (Platyhelminthes: Plagiostomidae) in southern New England, with notes on the anatomy of its pharynx. – Trans. Am. Microsc. Soc. **113**: 258–262.

Smith, S. & Schmidt, R. E. (1988): Trophic status of the spottail shiner (*Notropis hudsonius*) in Tivoli North Bay, a Hudson River freshwater tidal marsh. – In: Waldman, J. R. & Blair, E. A. (eds.): Polgar Fellowship reports of the Hudson River Research Reserve Program, 1987: pp. VI-1 to VI-25.

Smith, T. E., Stevenson, R. J., Caraco, N. F. & Cole, J. J. (1998): Changes in phytoplankton community structure during the zebra mussel (*Dreissena polymorpha*) invasion of the Hudson River (New York). – J. Plankt. Res. **20**: 1567–1579.

Stanczykowska, A. (1976): Biomass and production of *Dreissena polymorpha* (Pall.) in some Masurian lakes. – Ekol. Pol. **24**: 103–112.

Stewart, T. W. & Haynes, J. M. (1994): Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena*. – J. Great Lakes Res. **20**: 479–493.

Stewart, T. W., Miner, J. G. & Lowe, R. L. (1998a): Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic matter production and shell-generated habitat. – J. N. Amer. Benthol. Soc. **17**: 81–94.

– (1998b): Macroinvertebrate communities on hard substrates in western Lake Erie: structuring effects of *Dreissena*. – J. Great Lakes Res. **24**: 868–879.

Strayer, D. (1987): Ecology and zoogeography of the freshwater mollusks of the Hudson River basin. – Malacol. Rev. **20**: 1–68.

– (2001): Endangered freshwater invertebrates. – In: Levin, S. A. (ed.): Encyclopedia of biodiversity **2**: 425–439. Academic Press.

Strayer, D. L., Caraco, N. F., Cole, J. J., Findlay, S. & Pace, M. L. (1999): Transformation of freshwater ecosystems by bivalves: a case study of zebra mussels in the Hudson River. – BioScience **49**: 19–27.

Strayer, D. L., Hunter, D. C., Smith, L. C. & Borg, C. K. (1994): Distribution, abundance, and roles of freshwater clams (Bivalvia, Unionidae) in the freshwater tidal Hudson River. – Freshwat. Biol. **31**: 239–248.

Strayer, D. L. & Jirka, K. J. (1997): The pearly mussels of New York state. – Mem. N.Y. St. Mus. **26**: 1–114 + pls. 1–27.

Strayer, D. L., Powell, J., Ambrose, P., Smith, L. C., Pace, M. L. & Fischer, D. T. (1996): Arrival, spread, and early dynamics of a zebra mussel (*Dreissena polymorpha*) population in the Hudson River estuary. – Can. J. Fish. Aquat. Sci. **53**: 1143–1149.

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.

– (2000): Macroinvertebrates of a rocky shore in the freshwater tidal Hudson River. – Estuaries **23**: 359–366.

Strayer, D. L., Smith, L. C. & Hunter, D. C. (1998): Effects of the zebra mussel (*Dreissena polymorpha*) invasion on the macrobenthos of the freshwater tidal Hudson River. – Can. J. Zool. **76**: 419–425.

Thorne, G. & Swanger, H. H. (1936): A monograph of the nematode genera *Dorylaimus* Dujardin, *Aporcelaimus* n. g., *Dorylaimoides* n. g. and *Pungentus* n. g. – Capita Zool. **6** (4): 9–223.

Thorp, J. H. & Covich, A. P. (eds.) (1991): Ecology and classification of North American freshwater invertebrates. – Academic Press, 911 pp.

TOWNES, H. K. (1937): Studies on the food organisms of fish. – In: MOORE, E. (ed.): A biological survey of the lower Hudson watershed. Suppl. 26th Ann. Rep. St. N.Y. Conserv. Dept.: 217–230.

ULANOWICZ, R.E. & TUTTLE, J.H. (1992): The trophic consequences of oyster stock rehabilitation in Chesapeake Bay. – Estuaries **15**: 298–306.

VAN DE BUND, W., GOEDKOOP, W. & JOHNSON, R. K. (1994): Effects of deposit-feeder activity on bacterial production and abundance in profundal lake sediment. – J.N. Amer. Benthol. Soc. **13**: 532–539.

VINCENT, B. (1979): Étude du benthos d'eau douce dans le haut-estuaire du Saint-Laurent (Québec). – Can. J. Zool. **57**: 2171–2182.

WALSHE, B.M. (1951): The feeding habits of certain chironomid larvae (subfamily Tendipedinae). – Proc. Zool. Soc. London **121**: 63–79.

WALTON, W. C. (1996): Occurrence of zebra mussel (*Dreissena polymorpha*) in the oligohaline Hudson River, New York. – Estuaries **19**: 612–618.

WATERS, T. F. (1977): Secondary production in inland waters. – Adv. Ecol. Res. **10**: 91–164.

WEINSTEIN, L. H. (ed.) (1977): An atlas of the biologic resources of the Hudson estuary. – Boyce Thompson Institute for Plant Research, 104 pp.

WELKER, M. & WALZ, N. (1998): Can mussels control the plankton in rivers? – A planktological approach applying a Lagrangian sampling strategy. – Limnol. Oceanogr. **43**: 753–762.

WIEDERHOLM, T. (ed.) (1983): Chironomidae of the Holarctic region: keys and diagnoses. Part 1. Larvae. – Ent. Scand. Suppl. **19**: 1–457.

WIGGINS, G. B. (1996): Larvae of the North American caddisfly genera (Trichoptera), second edition. – University of Toronto Press, 457 pp.

WILLIAMS, B. S., HOGAN, T. & ZO, Z. (1975): The benthic environment of the Hudson River in the vicinity of Ossining, New York, during 1972 and 1973. – N.Y. Fish Game J. **22**: 25–31.

WOLFF, W.J. (1973): The estuary as a habitat: an analysis of data on the soft-bottom macrofauna of the estuarine areas of the rivers Rhine, Meuse, and Scheldt. – Zool. Verh. **126**: 1–242.

– (1983): Estuarine benthos. – In: KETCHUM, B.H. (ed.): Estuaries and enclosed seas: 151–182. Elsevier.

YOZZO, D. & STEINECK, P. L. (1994): Ostracoda from tidal freshwater wetlands at Stockport, Hudson River estuary: abundance, distribution, and composition. – Estuaries **17**: 680–684.

ZIPPIN, C. (1958): The removal method of population estimation. – J. Wildl. Mgmt. **22**: 82–90.

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Appendix 1

Macrozoobenthos of the freshwater tidal Hudson River. The species list is compiled from several studies. Mean densities are given from Simpson et al.'s (1984, 1986) survey of 16 sites along the navigation channel (0.59-mm mesh) and our survey of four cross-channel transects (28 sites total; 0.5-mm mesh) in 1990–92. See methods for details. A "+" in the density column indicates that the taxon was taken in these two programs but not enumerated. Taxa not collected in these main-channel surveys but collected in Bode et al.'s (1986) survey of the upper estuary (Troy to Albany) or Strayer & Smith's (2000, and unpublished) study of the macrofauna of a rocky shoreline are listed in the table and indicated by a "u" or "r" superscript after the species name, respectively.

Taxon	Density (no./m^2)	
	Simpson et al.	This study
Cnidaria		
Cordylophora lacustris	0	+
Hydra sp.	0	+
Turbellaria	68	
Dugesia tigrina		7
Hydrolimax grisea		233
Nemertea	0.2	0
Nematoda	0	230[a]
Dorylaimus cf. *stagnalis*		114[a]
Hofmaenneria sp.		0.8[a]
Idiodorylaimus novazealandiae		20[a]
Laimydorus cf. *pseudostagnalis*		3[a]
Mermithidae		17[a]
Tobrilus cf. *aberrans*		4[a]
Polychaeta		
Scolecolepides viridis	0	20
Manayunkia speciosa	24	32
Oligochaeta		
Arcteonais lomondi	19	5
Aulodrilus americanus	6	4
Aulodrilus limnobius	2	2
Aulodrilus pigueti	4	41
Aulodrilus pluriseta	0.2	0
Branchiura sowerbyi	0.9	0
Enchytraeidae		+
Ilyodrilus templetoni	222	0
Isochaetides freyi	418	0
Limnodrilus cervix	2	0
Limnodrilus hoffmeisteri	4357	4789[b]
Limnodrilus udekemianus	45	82
Nais behningi	0.4	0
Nais communis/variabilis	2	14
Potamothrix moldaviensis	0	4789[b]
Potamothrix vejdovskyi	0	293[h]
Pristinella sp.	0	0.9
Quistidrilus multisetosus	45	5
Ripistes parasita	0.9	0
Specaria josinae	0	3
Slavina appendiculata	3	1
Spirosperma ferox	0.4	0
Stylaria lacustris	0.2	34

Taxon	Density (no./m^2)	
	Simpson et al.	This study
Tubifex tubifex	0	293[h]
Vejdovskyella comata[u]		
Vejdovskyella intermedia	3	0
Lumbriculidae	28	0
Hirudinea	8	3
Alboglossiphonia heteroclita[u]		
Batracobdella phalera	+	
Glossiphonia complanata[u]		
Helobdella elongata	+	
Helobdella stagnalis	+	
Helobdella triserialis	+	
Marvinmeyeria lucida[u]		
Mooreobdella microstoma[u]		
Placobdella montifera	+	
Piscicolidae	+	
Entoprocta		
Urnatella gracilis	0	+
Ectoprocta[r]		
Mysidacea		
Neomysis americana	0	0.1
Cumacea		
Almyracuma proximoculi	11	3
Isopoda		
Asellus sp.	0.9	0.1
Chiridotea almyra	54	17
Cyathura polita	337	123
Amphipoda		
Gammarus fasciatus	445	1059
Monoculodes edwardsi	5	29
Corophium lacustre	0	1
Cirripedia		
Balanus improvisus	0	+
Decapoda		
Callinectes sapidus		+
Rhithopanopeus harrissi		0.4
Orconectes limosus		0.1
Acari	13	17
Hygrobates sp.[u]		
Lebertia sp.[u]		
Limnesia sp.	+	
?*Limnochares* sp.	+	
Unionicola sp.	+	
Collembola		
Isotomurus palustris	0.4	0
Odonata	0.4	4
Ischnura sp.	+	
Stylurus sp.	+	
Ephemeroptera	2	0.5
Caenis sp.	+	
Ephemerella serratoides[u]		
Hexagenia cf. *rigida*[u]		

Taxon	Density (no./m^2)	
	SIMPSON et al.	This study
Stenacron sp.[r]		
Stenonema sp.	+	
Tricorythodes sp.[u]		
Plecoptera		
Shipsa rotunda[r]		
Hemiptera	0.2	0.1
Trichoptera		
Ceraclea sp.	0.7	0
Cernotina sp.[r]		
Cheumatopsyche sp.	0.2	0
Cyrnellus fraternus[r]		
Hydropsyche scalaris[u]		
Hydroptila sp.[r]		
Nectopsyche sp.	0.4	0
Oecetis inconspicua	18	41
Orthotrichia sp.[r]		
Oxyethira sp.[r]		
Phylocentropus sp.[u]		
Neuroptera		
Sisyra sp.	0	0.1
Lepidoptera	0.2	0
Coleoptera	1	3
Anchytarsus sp.[r]		
Berosus sp.[r, u]		
Dubiraphia vittata	+	
Ectopria leechi[r]		
Macronychus cf. *glabratus*[u]		
Ochthebius sp.[r]		
Optioservus sp.	+	
Stenelmis sp.[r, u]		
Chironomidae[c]		
Ablabesmyia monilis	0.2	0
Ablabesmyia mallochi	0.2	0
Ablabesmyia simpsoni	9	0
Axarus festivus gr. sp.	0.9	0
Chaetocladius piger gr. sp.[u]		
Chironomus decorus gr. sp.	2	39
Cladopelma sp.[u]		
Cladotanytarsus sp.	0.4	0
Clinotanypus sp.	0	1
Coelotanypus scapularis	177	337
Corynoneura taris[u]		
Cricotopus bicinctus	0.9	0
Cricotopus sylvestris[u]		
Cricotopus trifascia[u]		
Cryptochironomus digitatus[u]		
Cryptochironomus fulvus gr. spp.	6	61
Cryptochironomus ponderosus	86	[c]
Cryptochironomus scimitaris gr. sp.[u]		
Cryptotendipes cf. *casuarius*[u]		
Cryptotendipes emorsus	0.4	0
Cryptotendipes pseudotener[u]		

Taxon	Density (no./m^2)	
	Simpson et al.	This study
Dicrotendipes modestus	0.7	17
Dicrotendipes neomodestus	3	[c]
Dicrotendipes sp. 3[u]		
Djalmabatista sp.		+
Einfeldia sp.		+
Endochironomus nigricans	0.2	0
Eukiefferiella claripennis gr. sp.[u]		
Eukiefferiella coerulescens gr. sp.	0.2	0
Genus B (Chironomini)	0	25
Glyptotendipes dreisbachi[u]		
Glyptotendipes lobiferus	0.2	5
Harnischia curtilamellata	20	24
Hayesomyia senata	9	+
Helopelopia cornuticaudata	0.2	0
Hydrobaenus cf. *pilipes*	0.2	0
Labrundinia sp.[r]		
Larsia canadensis	0.2	0
Microchironomus sp.	0.2	0
Microtendipes cf. *pedellus*[u]		
Nanocladius crassicornus	0.2	0
Nanocladius rectinervis	1	0
Nilothauma babiyi	0.2	+
Orthocladius carlatus[u]		
Parachironomus cf. *carinatus*[u]		
Parakiefferiella sp.	0.9	0
Paralauterborniella nigrohalterale	32	11
Paratanytarsus sp.[u]		
Paratendipes albimanus	0.2	0
Phaenopsectra obediens		106
Polypedilum convictum	0.7	201
Polypedilum halterale	398	[c]
Polypedilum halterale gr. sp.	80	[c]
Polypedilum illinoense	1	[c]
Polypedilum scalaenum	96	[c]
Polypedilum (Tripodura) sp.[u]		
Procladius bellus	13	41
Procladius sublettei	23	[c]
Psectrocladius sp.		+
Rheotanytarsus exiguus gr. sp.	0.7	11
Stempellinella sp.[u]		
Stenochironomus sp.		+
Stictochironomus sp.	0.4	0
Tanytarsus glabrescens gr. sp.[u]		
Tanytarsus guerlus gr. sp. 1	0.7	124
Tanytarsus guerlus gr. sp. 2	518	[c]
Tanytarsus sp. 3[u]		
Tanytarsus sp. 4[u]		
Thienemanniella cf. *fusca*[u]		
Tribelos jucundum	0.9	[d]
Xenochironomus xenolabis[u]		

Taxon	Density (no./m^2)	
	SIMPSON et al.	This study
Other Diptera		
Ceratopogonidae	36	56
Bezzia sp. 1	+	
Bezzia sp. 2	+	
Ceratopogon sp.[u]		
Probezzia sp. 1	+	
Probezzia sp. 2	+	
Sphaeromais longipennis	+	
Chaoborus punctipennis	125	47
Empididae[r]		
Ephydridae		
Hydrellia sp.[u]		
Psychodidae		
Psychoda sp.[u]		
Simuliidae		
Simulium vittatum[u]		
Tipulidae[r]		
Gastropoda[e]	7	
Amnicola limosa		8
Bithynia tentaculata[r]		
Elimia virginica		0.2
Ferrissia fragilis		17
Ferrissia rivularis		0.6
Fossaria sp.[r]		
Gyraulus deflectus[r]		
Gyraulus parvus		1
Helisoma anceps[r]		
Laevapex fuscus[r]		
Littoridinops tenuipes		79
Lyogyrus granum[r]		
Lyogyrus pupoidea[r]		
Micromenetus dilatatus		0.1
Physella ancillaria[r]		
Physella gyrina[r]		
Pomatiopsis lapidaria[r]		
Probythinella lacustris		3
Promenetus exacuous[r]		
Pyrgulopsis lustrica[r]		
Pseudosuccinea columella[r]		
Stagnicola catascopium[r]		
Valvata sincera		0.5
Valvata tricarinata		4
Bivalvia		
Unionidae[e]	64	[e]
Sphaeriidae[e]	225	[e]
Anodonta implicata		3[f]
Dreissena polymorpha		1747[g]
Elliptio complanata		5[f]
Lampsilis radiata		0.006[f]
Leptodea ochracea		0.4[f]
Ligumia nasuta		0.08[f]
Mytilopsis leucophaeta		0.3

Taxon	Density (no./m^2)	
	SIMPSON et al.	This study
Pisidium amnicum		0.2
Pisidium sp.		577
Rangia cuneata		4
Sphaerium striatinum		2
Total macrozoobenthos	8025	10409

[a] nematode totals are from 1990–92, while densities of individual species are for 1991, the only year in which nematodes were identified

[b] densities are for otherwise unidentifiable tubificid species without hair setae (chiefly *Limnodrilus hoffmeisteri*, but also *Potamothrix moldaviensis*)

[c] in 1990–92, chironomids were identified only to genus

[d] included under *Phaenopsectra* (OLIVER & ROUSSEL 1983)

[e] it appears that some of the molluscan identifications given by SIMPSON et al. (1984, 1986) and BODE et al. (1986) are unreliable, so we simply report their densities of all gastropods, unionids, and sphaeriids

[f] from 1991–92 (STRAYER et al. 1994)

[g] from 1993–96 (STRAYER et al. 1996 and unpublished)

[h] densities are for otherwise unidentifiable tubificid species with hair setae (*Tubifex tubifex* and *Potamothrix vejdovskyi*)