IPRenewal NPEmails

From: Gray, Dara F [DGray@entergy.com]
Sent: Wednesday, July 06, 2011 5:36 PM
To: Julie.Crocker@Noaa.Gov; Stuyvenberg, Andrew; Imboden, Andy; Turk, Sherwin
Cc: Dacimo, Fred R.; Sutton, Kathryn M.; ezoli@goodwinprocter.com; Dowell, Kelli; Mark Mattson; Caputo, Charles; Curry, John J
Subject: RE: Benthic Invertebrate Studies
Attachments: Strayer- Hudson River Benthic inverts 2006.pdf

Julie and Drew
Attached is a recent (2006) report on the subject, as you requested When reviewing this, it probably would be helpful to note that Indian Point is located at kilometer 69.
Also, I hope to have the final thermal information to you tomorrow afternoon.
Again, please remember that we are more than happy to assist you in your evaluation and also please let me know if you have any questions.
Thanks

From: Gray, Dara F
Sent: Tuesday, July 05, 2011 6:19 PM
To: 'Julie.Crocker@Noaa.Gov'; 'Stuyvenberg, Andrew'; Imboden, Andy; Turk, Sherwin
Cc: Dacimo, Fred R.; 'Sutton, Kathryn M.'; 'ezoli@goodwinprocter.com'; Dowell, Kelli; Mark Mattson; Caputo, Charles; Curry, John J
Subject: FW: Zebra Mussel Reports for 2003-2010

Hi Julie and Drew,
Here are the monitoring reports from our "zebra mussel monitoring program" as promised. If you would like a copy of the SOP, please let me know. We hope to have the remainder of the thermal information to you tomorrow. (although it will likely be piece-meal given our email restrictions). Please let me know if you have any questions.
Thanks

From: Mark Mattson [mailto:mmattson@normandeau.com]
Sent: Tuesday, June 28, 2011 7:17 PM
To: Gray, Dara F
Cc: Zoli, Elise N
Subject: Zebra Mussel Reports for 2003-2010

PRIVILEGED & CONFIDENTIAL,
ATTORNEY-CLIENT COMMUNICATION,
ATTORNEY WORK PRODUCT,
PREPARED IN CONNECTION WITH/ANTICIPATION OF LITIGATION

Dara – attached are the eight most recent annual zebra mussel monitoring reports for IPEC (2003 through 2010). Each annual report presents the cumulative summary of monthly monitoring at the IPEC unit 3 intake and the bio boxes in plant at Unit 2 and Unit 3 of the total biomass of the entire biofouling community (wet weight), and number of each type of mussel species found on the settling plates during each incubation period. Let me know if you also think we should include the project SOP, and I'll have that made into a PDF and send it along. Take care. Mark

><((((:> ><((((:> ><((((:> ><((((:>
Mark T. Mattson, Ph.D., Vice President
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The Hudson River Estuary

Edited by

Jeffrey S. Levinton

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City University of New York

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Color plates precede Chapter 1.

19 The Benthic Animal Communities of the Tidal-Freshwater Hudson River Estuary

David L. Strayer

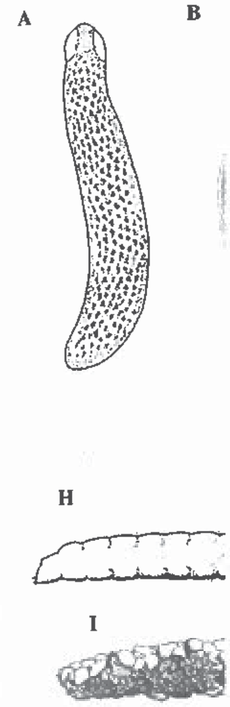
ABSTRACT Benthic animals (those that live in or on sediments or vegetation) are of key importance in the Hudson River ecosystem. They are the major source of food to the Hudson's fish and regulate the abundance and composition of phytoplankton in the river. Benthic animals probably are important in mixing sediments, an activity that may affect the movement and ultimate fate of toxins in the river, although this process is not well studied in the Hudson. The benthic animal community of the Hudson is diverse, containing several hundred species of worms, mollusks, crustaceans, insects, and other invertebrates. These animals represent a wide array of life histories, feeding types, distributions, and adaptations. Community structure and population density vary greatly from place to place in the Hudson, and are determined chiefly by salinity, the presence of rooted plants, and the nature of the sediment (hard vs. soft). Nevertheless, a great deal of site-to-site variation in benthic community structure in the Hudson and other large rivers is unexplained. Human activities (especially water pollution and alteration of the channel for navigation) probably had large effects on the benthic communities of the Hudson, but these effects have not been well documented. The recent invasion of the Hudson by the zebra mussel (*Dreissena polymorpha*) profoundly changed the benthic communities of the river, altering their composition and function in the ecosystem.

Introduction

Benthic animals (collectively called the zoobenthos) are a diverse community of animals living in or on sediments, aquatic plants, or other solid surfaces under the waters. The zoobenthos of the Hudson is one of the most diverse communities in the river, containing several hundred species of varied habits. Benthic animals play key roles in the river's ecosystem. They are the predominant food for many of the river's fish, regulate populations of phytoplankton and zooplankton, and probably are important in determining the movement and fate of nutrients and toxins in the river. Despite this importance, much remains unknown about the Hudson's benthic animals and their roles in the river's ecosystem. My goal in this chapter is to describe the animals that make up the Hudson's zoobenthos, discuss how different habitats within the river support different kinds of benthic animals, review how benthic animal communities in the river have changed over time, especially in response to the zebra mussel invasion, and evaluate the importance of benthic animals in the Hudson's ecosystem.

Sources of Information

Studies of the Hudson's zoobenthos have been spotty, limiting our insight into this part of the ecosystem. The earliest naturalists collected specimens from the Hudson and made incidental observations on benthic animals (e.g., Say, 1821; Lea, 1829; Dekay, 1844; Gordon, 1986), but the first systematic survey of the Hudson's zoobenthos was done by Townes (1937), who made a few collections from the middle estuary as part of the Conservation Department's survey of New York's fisheries resources. In the 1970s, the Boyce Thompson Institute (Ristich, Crandall, and Fortier, 1977; Weinstein, 1977) surveyed the benthos of the lower estuary (Manhattan to Poughkeepsie), and in 1983–84 researchers from the New York State Department of Health (Simpson et al., 1984, 1985, 1986; Bode et al., 1986) made a detailed study of the zoobenthos of the main channel of the freshwater Hudson from Troy to New Hamburg. Two vegetated areas (Bowline Pond – Menzie, 1980, and Tivoli South Bay – Findlay, Schoeberl, and Wagner, 1989) were studied during the same time period. Finally, my colleagues and I have studied the zoobenthos of the freshwater tidal section of the river (Troy to Newburgh) since 1990, a period that included the zebra mussel invasion (Strayer et al., 1994, 1996, 1998; Strayer and Smith, 1996, 2000, 2001).



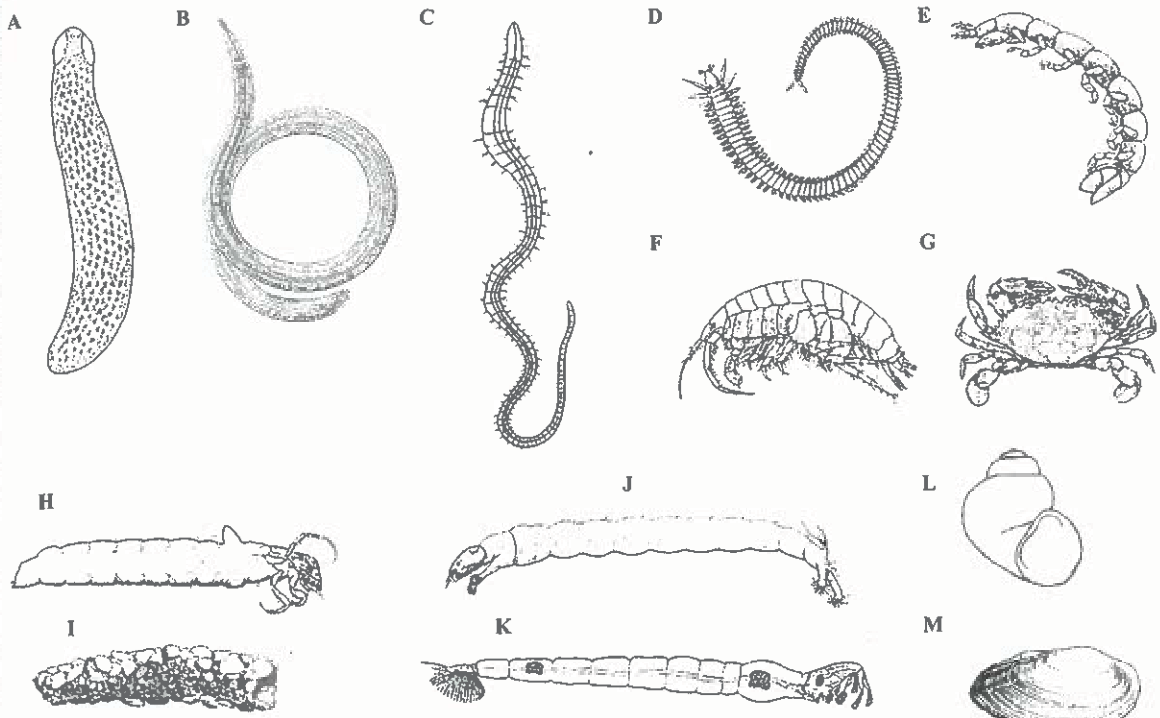


Figure 19.1. Some benthic animals that are common in the Hudson River. A. the flatworm *Hydrolimax grisea*, B. the nematode *Dorylaimus stagnalis*, C. a tubificid oligochaete, D. the polychaete *Eteone heteropoda*, E. the isopod *Cyathura polita*, F. the amphipod *Leptocheirus plumulosus*, G. the blue crab *Callinectes sapidus*, H. the caddisfly *Oecetis inconspicua*, and I. its case, J. the chironomid *Ablabesmyia*, K. the phantom midge *Chaoborus*, L. the snail *Amnicola limosa*, M. the mussel *Anodonta implicata*. From Thorne and Swanger (1936), Hyman and Jones (1959), Burch (1975), Weinstein (1977), Oliver and Roussel (1983), Fryer (1991), Jokinen (1992), and Wiggins (1996).

In addition to these large studies, a number of studies more limited in scope (e.g., Hirschfield, Rachlin, and Leff, 1966; Howells, Musnick, and Hirschfield, 1969; Williams, Hogan, and Zo, 1975; Crandall, 1977; Yozzo and Steineck, 1994) have contributed information on the Hudson's zoobenthos. Together, these studies offer a moderately clear picture of benthic animal communities of the freshwater tidal river in 1983–2000, a glimpse into communities of the lower river in the mid-1970s, and only hints of the benthic communities that lived anywhere in the river before 1970.

Further, most of the studies in the Hudson have been focused on the macrofauna (animals large enough to be caught on a 0.5–1 mm mesh screen), and have excluded the numerous smaller animals as well as larger mobile forms such as crabs and shrimp. Typically, these excluded forms constitute 5–75 percent of benthic biomass, production, and diversity (e.g., Strayer, 1985; Hakenkamp, Morin, and Strayer, 2002). Consequently, benthic animals in the Hudson are more numerous and more diverse than existing studies on the Hudson suggest.

Biology of the Zoobenthos

Approximately three hundred species of macrobenthic animals have been recorded from the Hudson River (Ristich et al., 1977; Simpson et al., 1986; Strayer and Smith, 2001). This fauna includes animals with a wide array of body sizes and shapes (Fig. 19.1), life histories, and ecological habits. In terms of numbers, biomass, and species richness, the most important groups in the Hudson's zoobenthos are annelids, mollusks, crustaceans, and insects.

Three major groups of annelids are common in the Hudson: leeches, oligochaetes, and polychaetes. Although leeches are well known (and reviled!) as bloodsuckers, only a few species of leeches are parasites of humans and other vertebrates. Most leech species are scavengers or predators of invertebrates. About ten species of leeches have been reported from the freshwater parts of the Hudson. Leech densities usually are low in the Hudson, but these animals may be locally important as predators in plant beds, where their densities are highest. Most oligochaetes and polychaetes burrow in soft sediments or crawl on vegetation or rocks and are deposit-feeders, feeding on sediment bacteria and organic matter. Many species are macroscopic, and reach lengths of 3–30 mm as adults. Polychaetes are predominately marine, and are dominant in the polyhaline and mesohaline parts of the Hudson (river kilometer (RKM) 0–75). Only one species (the microscopic *Manayunkia speciosa*) lives in the freshwater part of the estuary. Oligochaetes live throughout the river, but are especially common in the freshwater estuary (RKM 100–248), where they often constitute >75 percent of macrobenthic animals. Scientists have thus far found twenty to thirty species each of oligochaetes and polychaetes in the Hudson.

Mollusks (clams, mussels, and snails) are among the most familiar of the benthic animals in the Hudson. About fifty species have been reported from the river. Bivalve mollusks (clams and mussels) feed either on phytoplankton and other suspended material (suspension-feed) or on organic matter deposited on the sediments (deposit-feed). While some bivalves are among the largest invertebrates in the river, reaching >10 cm long, others never reach 5 mm long, even as adults. The life cycles of our bivalves are highly varied. Most of the brackish-water species have free-living larvae, but most freshwater species either have larvae that are parasitic on fish (pearly mussels) or no larvae at all (pea clams). The pearly mussels may live for decades. Some of the bivalves in the Hudson are edible (for example, oysters, mussels), and have been fished in prehistoric (e.g., Schaper, 1989) and recent times (because of widespread contamination, it is probably not a good idea to eat mollusks from the river today). Most of the Hudson's snails graze on attached algae or deposit feed on organic sediments; a few are able to suspension feed. Several alien mollusk species have been introduced to the Hudson (e.g., the zebra mussel *Dreissena polymorpha*, the dark false mussel *Mytilopsis leucophaeta*, the Atlantic rangia *Rangia cuneata*, the faucet snail, *Bithynia tentaculata*) and are now common in the river.

Although only about thirty species of benthic crustaceans (isopods, amphipods, barnacles, and decapods) have been reported from the Hudson, the crustaceans are among the most important benthic animals in the river. They often are abundant, and many are especially choice food for fish (Table 19.1). Isopods (relatives of the familiar terrestrial pill bug) are common on unvegetated sediments throughout the river. Amphipods (scuds, sideswimmers) are small shrimp-like crustaceans common throughout the river that are one of the most important fish foods in the river (Table 19.1). Barnacles live on rocky shorelines as far north as Beacon (RKM 99). The decapods (crabs, crayfish, and shrimp) are another important fish food, but have received little study in the Hudson. Crayfish live in freshwater habitats, grass shrimp (*Paleomonetes*) live in brackish habitats, and blue crabs (*Callinectes sapidus*) migrate from the lower estuary as far north as Troy in some summers. Blue crabs (color plate 7) are widely fished for food in the Hudson and elsewhere; in recent years, the commercial catch in the river was ~40,000 kg/yr (NYSDEC, 1993). Many marine crustaceans have free-swimming larvae, and larval crabs and barnacles are common in the plankton on the lower Hudson. In contrast, most freshwater crustaceans have no larval stage, and develop directly from egg to juvenile to adult.

Benthic insects are common in the Hudson, especially in freshwater habitats. The chironomid midges (larvae of non-biting flies) are by far the most abundant and species-rich of the insects (color plate 8). Chironomid densities in the freshwater Hudson typically are ~1,000/m^2. More than 70 species of chironomids have been identified from the Hudson, and true diversity probably exceeds 100 species. The chironomids are a diverse group that includes predators, suspension-feeders, and grazers. Other insects that may be locally abundant in the freshwater Hudson include Ephemeroptera (mayflies), Odonata (damselflies),

Table 19.1. Importance of benthic invertebrates in the diets of some Hudson River fishes.

Fish species	% of diet	Dominant items in diet	Source
Shortnose sturgeon (YOY)	100 (V)	Chironomids	Carlson and Simpson, 1987
Shortnose sturgeon	100 (V)	Chironomids, mollusks, oligochaetes	Curran and Ries, 1937
Atlantic sturgeon	100 (V)	Chironomids, oligochaetes	Curran and 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 and Schmidt, 1988
Tomcod	99 (N)	Amphipods	McLaren et al., 1988
Banded killifish	>50 (N)	Microcrustaceans, chironomids	Richard and Schmidt, 1986
White perch	91–99 (N)	Amphipods	Curran and Ries, 1937; Bath and O'Connor, 1985
Striped bass (YOY)	85 (N)	Amphipods	Townes, 1937; Gardinier and Hoff, 1983
Striped bass (yearlings)	76 (N)	Amphipods	Gardinier and Hoff, 1983
Striped bass (2-yr old)	14 (N)	Fish	Gardinier and Hoff, 1983
Tessellated darter	>50 (N)	Chironomids, microcrustaceans	Duryea and Schmidt, 1986

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
Modified from Strayer and Smith (2001).

Trichoptera (caddisflies), Coleoptera (beetles), Ceratopogonidae (no-see-ums), and Chaoboridae (phantom midges).

While annelids, mollusks, crustaceans, and insects dominate the Hudson's zoobenthos, many other animals are present. Porifera (sponges), Cnidaria (hydras, jellyfish), Turbellaria (flatworms), Nematoda (roundworms), and Acari (mites) may be locally abundant in the Hudson and add to its biological richness.

The Hudson's fauna resembles that of other tidal rivers in northeastern North America, from the James to the St. Lawrence. The macrozoobenthos of the freshwater parts of these rivers is usually strongly dominated by *Limnodrilus hoffmeisteri* and other tubificid oligochaetes, and often contains dense populations of predatory chironomids (for example, *Coelotanypus scapularis, Procladius* spp., *Cryptochironomus* spp.) and sphaeriid clams (Massengill, 1976; Crumb, 1977; Vincent, 1979; Ettinger, 1982; Diaz, 1989). Most of the freshwater species in these tidal rivers also occur widely in lakes and warm water rivers, but the fauna is distinctive in two ways. Several species common in the Hudson and other northeastern estuaries (for example, the cumacean crustacean *Almyracuma proximoculi*, the amphipod *Monoculodes edwardsi*, the isopods *Chiridotea almyra* and *Cyathura polita*, and the snail *Littoridinops tenuipes*) usually live in oligohaline estuaries and coastal waters, and introduce a distinctively estuarine element to the "freshwater" fauna. Also, net-spinning caddisflies and burrowing mayflies, two groups of suspension-feeding insects that are important in many large rivers worldwide, are 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.

Spatial Variation in the Hudson Zoobenthos

Benthic communities vary enormously from place to place along the Hudson, in terms of both the number and kinds of animals that are present. Four factors are correlated with this variation: position along the course of the river, salinity, the presence or absence of rooted plants, and the nature of the bottom (hard vs. soft).

It appears that the density of benthic macroinvertebrates in the Hudson follows a W-shaped pattern, with peaks near Manhattan, Kingston, and Albany, and deep, broad troughs between these peaks (Fig. 19.2). This pattern is very strong, with densities in the peaks about 100-fold higher than

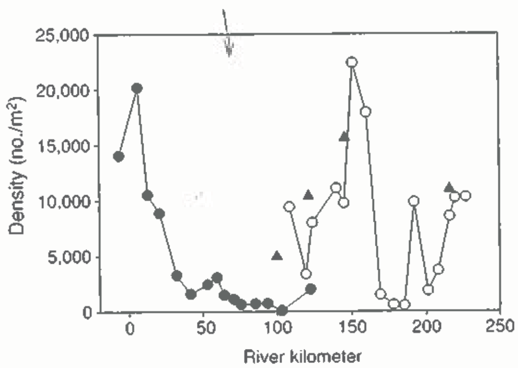


Figure 19.2. Long-river variation in density of benthic macroinvertebrates in the Hudson River. Data from mid-channel samples from Ristich et al. (1977) (black circles) and Simpson et al. (1984) (white circles), and from cross-channel transects in 1990–92 by Strayer et al. (unpublished). Because the three studies were done at different times and used different methods, the data are not exactly comparable across studies.

in the troughs. The W-shaped pattern may arise through a combination of stress and food subsidies. Unstable salinities in RKM 20–100 and unstable, sandy sediments in RKM 170–210 may suppress benthic communities (cf. Simpson et al., 1986). Inputs of sewage from New York City, and of phytoplankton from the Bight and near RKM 150 (Cole, Caraco, and Peierls, 1992) may further contribute to the development of the peaks.

The composition of benthic communities in the Hudson is a strong function of salinity (Fig. 19.3). Near Manhattan, the fauna is dominated by characteristically marine animals (polychaetes, bivalves such as *Mya* and *Macoma*), while above Newburgh, the benthos is dominated by freshwater species of oligochaetes, insects, and bivalves. In the intermediate zone of moderate and fluctuating salinity, the fauna contains a few species (for example, the polychaete *Marenzelleria viridis*, the amphipod *Leptocheirus plumulosus*) that thrive in brackish water. Nevertheless, there is a good deal of blurring of the fauna along the salinity gradient, and it is common to find supposedly marine or brackish-water animals (e.g., the crab *Callinectes sapidus*, the cumacean *Almyracuma proximoculi*) well into the freshwater Hudson (Simpson et al., 1985).

The nature of the substratum also has a strong influence on the character of the zoobenthos (Table 19.2). Compared to nearby unvegetated habitats, beds of rooted vegetation support diverse communities that are rich in insects and snails. Dozens of species of benthic animals in the Hudson are essentially confined to plant beds (Strayer and Smith, 2001). Likewise, rocky bottoms support more diverse communities than unvegetated soft sediments, including animals like mayflies and beetles that are rare elsewhere in the river. In contrast, the communities of various kinds of soft sediments (that is, sand vs. mud) differ little from one another, at least in the freshwater part of the Hudson (Strayer and Smith, 2001).

Nevertheless, most of the site-to-site variation in benthic communities in the Hudson and other large rivers is unexplained by factors like salinity, rooted plants, the grain size and organic content of the sediments. For example, the amphipod

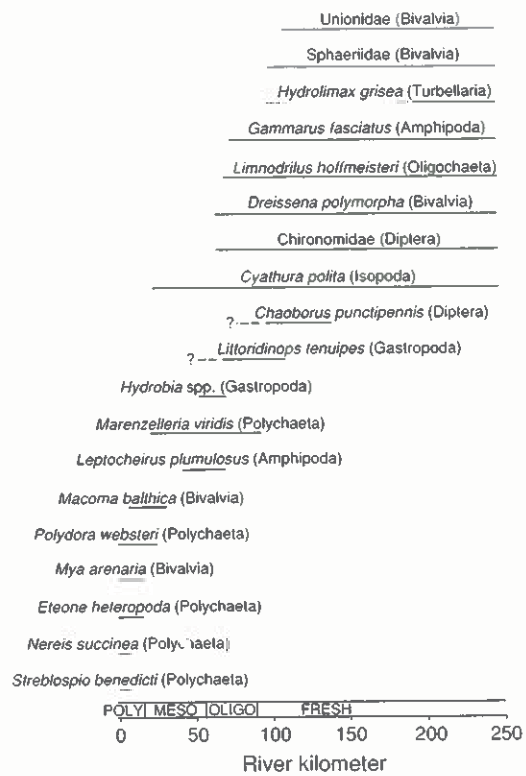


Figure 19.3. Approximate longitudinal distribution of dominant benthic animals in the Hudson River estuary, showing succession along the salinity gradient. The typical late-summer salinity zonation is shown just above the X-axis. FRESH = freshwater (< 0.5 ppt), MESO = mesohaline (5–18 ppt), OLIGO = oligohaline (0.5–5 ppt), POLY = polyhaline (18–30 ppt). Based on Ristich et al. (1977), Weinstein (1977), Simpson et al. (1986), and Strayer and Smith (2001). Uncertainties indicated by dashes and question marks.

Table 19.2. Composition of macrobenthic communities in three habitats of the freshwater tidal Hudson near Kingston, based on % numerical abundance

Taxon	Soft bottom	Beds of submersed vegetation	Rocky shoreline
Oligochaeta	70%	41%	9.2%
Amphipoda	13%	0.4%	3.7%
Bivalvia	6.8%	16%	0.5%
Diptera	5.6%	21%	45%
Turbellaria	2.9%	1.7%	5.5%
Others	1.3%	0.4%	3.1%
Nematoda	0.6%	18%	20%
Non-dipteran insects	0.1%	0.3%	6.3%
Gastropoda	0.02%	2.3%	7.1%

From Strayer and Smith (2000, 2001).

Gammarus tigrinus is common throughout the freshwater tidal Hudson River. Like other benthic animals, its local density varies from place to place by more than 1,000-fold. Of this variation, 11 percent can be attributed to sampling error, 14 percent can be explained by environmental variables like bottom type, and 75 percent remains unexplained (Strayer and Smith, 2001). This unexplained variation could be due to biological factors (e.g., sediment bacteria, amphipod behavior, fish predation), disturbance history, unmeasured characteristics of the environment (e.g., local current regime, sediment stability), and so on. Understanding the causes and consequences of spatial variation in large-river benthic communities represents a major research challenge.

Temporal Variation in the Hudson Zoobenthos

Benthic communities vary over time in response to season, disturbances, species invasions, human alteration of riverine habitats, long-term climate change, and so on. Unfortunately, very little is known about how the Hudson's benthos varies over time. Based on work done in other rivers and estuaries, we can assume that there are significant seasonal changes in the community (for example, Wolff, 1983; Beckett, 1992). The Hudson's zoobenthos must have changed greatly over the past one hundred to two hundred years in response to pollution and habitat alteration by humans. Further, it seems likely that there has been natural long-term variation in the benthic community. However, we know almost nothing about the nature of these changes. The only temporal change in the zoobenthos that has been well studied in the Hudson is its response to the zebra mussel invasion.

Zebra mussels first appeared in the river in May 1991 and by the end of 1992 constituted over half of heterotrophic biomass in the freshwater tidal Hudson (Strayer, Chapter 21, this volume). They reduced the biomass of phytoplankton and small zooplankton by 80–90 percent (Caraco et al., 1997; Pace, Findlay, and Fischer, 1998; Chapter 9, this volume; Chapter 16, this volume), changed the species composition of the remaining phytoplankton (Smith et al., 1998), increased water clarity by 45 percent (Caraco et al., 1997), changed concentrations of dissolved oxygen and plant nutrients (Caraco et al., 2000), and increased numbers of bacterioplankton (Findlay, Pace, and Fischer, 1998).

The zoobenthos showed three kinds of response to the zebra mussel invasion. First, there was an overall depletion of the zoobenthos other than zebra mussels (Fig. 19.4, upper). Riverwide, we estimated a loss of about 4,000 animals/m^2 (Strayer and Smith, 2001), or roughly three benthic animals lost for every zebra mussel that appeared. Taken together with losses in the zooplankton (Pace et al., 1998), we estimated that about half of the biomass of invertebrates useful for fish forage was lost from the Hudson with the zebra mussel invasion (Strayer and Smith, 2001).

Second, the response of benthic species to the zebra mussel invasion depended on their trophic group. Species that feed on plankton (that is, suspension-feeders plus the phantom midge *Chaoborus punctipennis*, which eats small zooplankton) declined much more severely than species that feed on benthic food (that is, predators and deposit-feeders) (Fig. 19.4, middle). Since the zebra mussel invasion, benthic planktivores have declined by 46–100 percent, and several formerly common species appear to be on the verge of disappearing from the Hudson. Because these benthic planktivores constituted more than half of heterotrophic biomass in the freshwater tidal Hudson River before the zebra mussel invasion, these large losses may have important ecological ramifications.

Third, the habitat occupied by benthic animals determined their response to the zebra mussel invasion. The zoobenthos of deep-water (>3 m deep), unvegetated, soft-bottom habitats declined sharply, while the zoobenthos of shallow-water, vegetated, soft-bottom habitats did not change (Fig. 19.4, bottom). Together, trophic group and habitat accounted for 51 percent of the variation in the response of benthic species to the zebra mussel invasion (Strayer and Smith, 2001).

It appears that loss of planktonic food, especially phytoplankton, was responsible for the large effects of the zebra mussel invasion on the Hudson's zoobenthos. Several pieces of evidence point to this conclusion: (a) benthic animals that feed on plankton declined, while those that feed on benthos did not (Fig. 19.4); (b) the body condition (body mass for a given body length) of unionid mussels declined, suggesting that they were receiving insufficient food (Strayer and Smith, 1996); and (c) population declines and body conditions of unionid mussels (which eat plankton) were uncorrelated with fouling rates by zebra mussels, suggesting that exploitative competition (rather than interference competition) was involved (Strayer and Smith, 1996). Thus, even though phytoplankton production forms only a small part of organic matter inputs to the Hudson, it appears to be of key importance in supporting higher trophic levels.

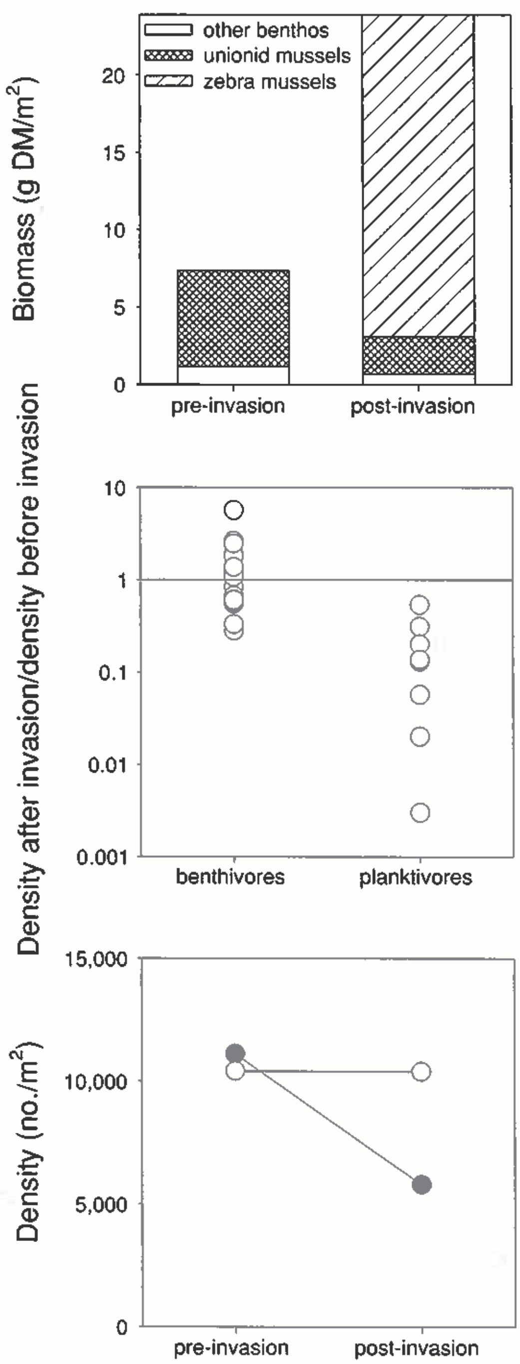


Figure 19.4 Effects of the zebra mussel invasion on the macrobenthos of the freshwater tidal Hudson River. Upper. Biomass of various parts of the community before and after the invasion. Middle. Effect of the zebra mussel invasion on populations of benthic animals in the freshwater tidal Hudson River according to trophic group. Each point represents the change in density of a taxon (usually a species) between 1990–92 and 1993–97 (animals other than unionids) or 1993–99 (unionids). The mean change for planktivores was significantly different than that for benthivores (t-test, $p < 0.0001$). Lower. Mean densities of all macrobenthos at deep water (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 ($p < 0.02$). Based on Strayer and Smith (2001).

Table 19.3. Outputs of organic carbon from the freshwater tidal Hudson River. Because the different terms in the budget were estimated at different times and using different methods and assumptions, the overall budget is very approximate.

	Output (g C/m²-yr)
Phytoplanktonic respiration	230
Submerged macrophyte respiration	10
Bacterial respiration	220
Zooplanktonic respiration	10
Macrozoobenthic respiration (before zebra mussel)	**8**
Macrozoobenthic respiration (after zebra mussel)	**110**
Export to downriver at RKM 100	360
Burial in sediments	40

Modified from Howarth, Schneider, and Swaney (1996), Caraco et al. (2000), and Strayer and Smith (2001).

Importance of Benthic Animals in the Hudson River Ecosystem

We know enough to assess the roles of benthic animals in the Hudson ecosystem only for the freshwater parts of the estuary, although there is no reason to doubt that they are important further downriver. Furthermore, because we have essentially no information about the meiofauna and mobile epifauna in the river, all of our assessments underestimate the importance of benthic animals in the Hudson.

Most often, when ecologists speak of the "importance" of a group of organisms, they are referring vaguely to their abundance, biomass, or contribution to metabolic processes in the ecosystem. There are approximately 10,000 benthic animals/m² of river bottom, and these animals constitute more than half of heterotrophic biomass in the ecosystem (e.g., Strayer et al., 1996). With the arrival of the zebra mussel, zoobenthic respiration changed from a minor term to a major term in the organic carbon budget of the Hudson (Table 19.3), which was large enough to significantly reduce dissolved oxygen concentrations in the freshwater tidal Hudson (Caraco et al., 2000). However, these conventional assessments give limited insight into the roles that benthic animals play in the Hudson River ecosystem. It may be more useful to consider three specific roles that benthic animals play in the Hudson ecosystem: as suspension feeders, as forage for fish, and as sediment mixers.

Suspension-feeders feed on particles that are suspended in the water column, and thus have the potential to affect the number and kind of phytoplankton and other suspended particles. Prior to the arrival of the zebra mussel, benthic animals (chiefly unionid mussels) were responsible for a little more than half of suspension-feeding activity in the freshwater tidal Hudson (Fig. 19.5), and may have exercised modest control over plankton in the upper river (RKM 213–248) (Caraco et al., 1997, Strayer et al., 1994). After the zebra mussel invasion, the activity of benthic suspension-feeders became enormous, and was a primary control on the amount and kind of phytoplankton in the freshwater estuary (Caraco et al., 1997; Cole and Caraco, Chapter 9, this volume), with effects that ramified into many other parts of the ecosystem (Findlay et al., 1998; Pace et al., 1998; Strayer et al., 1999; 2001; Caraco et al., 2000).

Benthic animals also serve as an important source of food to higher trophic levels, particularly fish. Except for very early life stages, every fish that has been the subject of a detailed dietary study in the Hudson has been found to feed

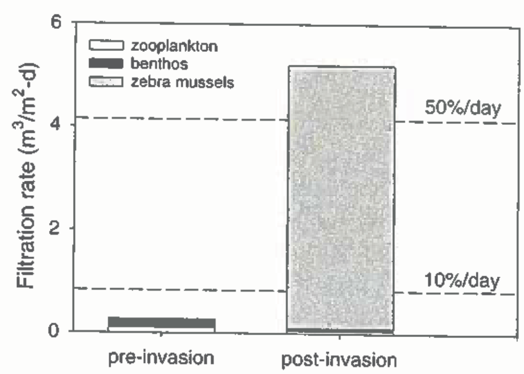


Figure 19.5. Estimated filtration rates of all suspension-feeders, averaged over the entire freshwater tidal Hudson River, before and after the zebra mussel invasion. The dashed lines show the percentage of the water in the freshwater tidal estuary that would theoretically be cleared of particles by suspension-feeders feeding at such rates, if particle retention were perfectly efficient. Based on Strayer and Smith (2001).

primarily on benthic animals, or on benthivorous fish (Table 19.1). Thus, benthic animals form the main link between phytoplankton, macrophytes, and allochthonous inputs at the base of the Hudson's food chain, and fish at its top. Because the zebra mussel invasion radically reduced the biomass of invertebrates that serve as fish food in the Hudson (Pace et al., 1998; Strayer and Smith, 2001), we might expect to see consequent changes in the Hudson's fish communities.

Finally, the feeding, burrowing, and movement of benthic animals mix sediments. Such mixing activities may alter exchanges of materials between sediment and overlying water (e.g., McCall and Tevesz, 1982; Robbins, 1982; Van de Bund et al., 1994). Although sediment mixing by benthic animals has not been investigated in the Hudson, its benthos is dominated by animals that are known to be effective sediment mixers (i.e., tubificid oligochaetes, chironomids, amphipods, and unionid mussels – Robbins, 1982; Van de Bund, Goedkoop, and Johnson, 1994; McCall et al., 1995), and many important substances in the river (notably PCBs) are associated with the sediments. Thus, it seems likely that benthic animals play important roles as sediment mixers in the Hudson.

The role of benthic animals in the Hudson ecosystem is thus larger and more complex than would be suggested from a conventional assessment of biomass or metabolism. The overall importance of the zoobenthos in the ecosystem differs across specific roles, as does the importance of different members of the zoobenthos. Thus, bivalves are important suspension-feeders, amphipods are especially important as fish food, and oligochaetes probably are important in mixing sediments. Even this brief consideration of a few specific roles of benthic animals shows that they form a vital part of the Hudson River ecosystem.

The relative importance of the two major groups of invertebrates – zooplankton and zoobenthos – differs across types of aquatic ecosystems. Pace et al. (1992) pointed out that zooplankton densities are lower in advective habitats such as estuaries and rivers than in still-water habitats such as lakes. In contrast, because benthic animals are not carried en masse downriver by water flow, we would expect that benthic animal densities could be just as high in rivers and estuaries as in lakes. Available data support this idea, and further show

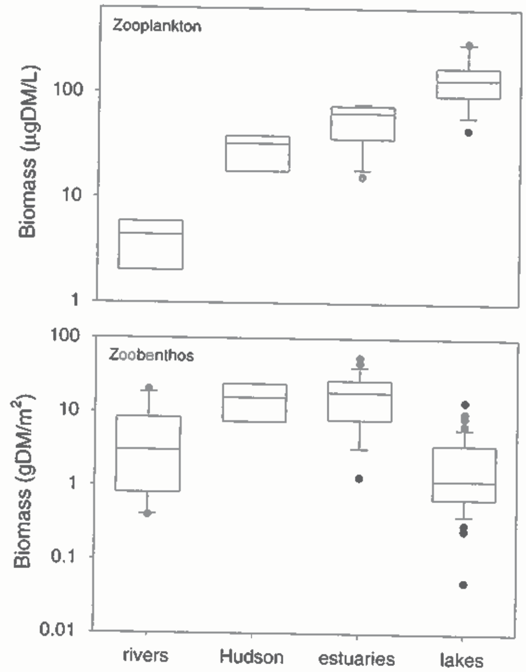


Figure 19.6. Biomass of zooplankton and zoobenthos in large rivers, the freshwater tidal Hudson River, estuaries, and lakes. Boxes show 25th and 75th percentiles (horizontal line is the median), whiskers show 5th and 95th percentiles, and dots show outliers. For zoobenthos, sample sizes are as follows: large rivers (10), Hudson River (2; i.e., pre- and post zebra mussel invasion), estuaries (23), and lakes (41). Zooplankton data from Pace, Findlay, and Lints (1992); zoobenthos data compiled from various sources.

that benthic biomass is especially high in estuaries (Fig. 19.6). Perhaps estuaries support higher benthic biomass than lakes because estuaries have greater inputs of physical energy (especially tidal currents), which leads to better vertical mixing and higher rates of food supply to the sediments (Nixon, 1988). The beneficial effects of physical energy may be reduced in rivers because of high temporal variance in energy supply rates, leading to scour, fill, and disturbance of the benthos. Further, food quality may be lower in rivers than in estuaries because of greater relative inputs of detrital allochthonous material of low nutritional quality. Thus, although site-to-site variation will be high, zoobenthos/zooplankton ratios might be highest in rivers, intermediate in estuaries, and lowest in lakes.

Traditionally, the ecological communities of the sediments and open water are considered separately, probably because the different habitats

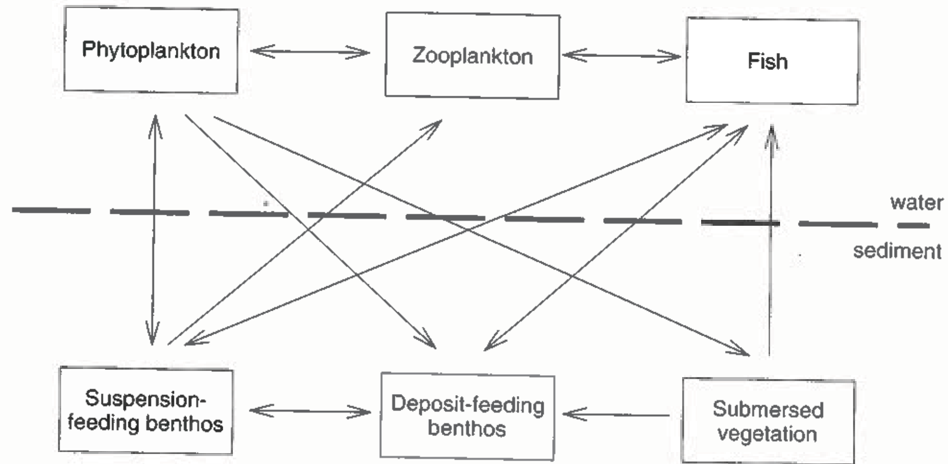


Figure 19.7. Diagram of the major community interactions in aquatic ecosystems such as the Hudson River. Arrows show the hypothesized direction of control. Note that many interaction arrows cross the sediment-water interface.

are studied by different groups of scientists using different methods. Nevertheless, connections between the benthos and the overlying water of the Hudson are numerous and strong (Fig. 19.7). Benthic suspension-feeders, especially bivalves, can regulate the amount and kind of plankton (Dame, 1996; Strayer et al., 1999), as was shown most clearly by the zebra mussel invasion of the Hudson (Cole and Caraco, Chapter 9, this volume; Pace and Lonsdale, Chapter 16, this volume). The benthic animal community in turn depends on the amount and kind of plankton as a key food source. Seasonal, interannual (Johnson, Bostrom, and van de Bund, 1989), or long-term changes in the plankton can cause large changes in the zoobenthos. In the Hudson, the removal of edible suspended particles by zebra mussels led to large changes in the zoobenthos (Fig. 19.4). Benthic plant communities likewise depend on the amount of suspended particles, which regulate the amount of light that penetrates to the sediments. A concrete example of this link was the possible increase in rooted plants (Caraco et al., 2000; Findlay et al., Chapter 17, this volume) and associated animals (Fig. 19.4) after zebra mussels reduced plankton biomass in the Hudson. Further, rooted plants may negatively influence phytoplankton, through a complex series of interactions (Scheffer, 1998). Finally, as shown in Table 19.1, benthic prey dominates fish diets in the Hudson, so that there may be strong reciprocal links between fish and zoobenthos in aquatic ecosystems (e.g., Strayer, 1991). Thus, many aquatic ecosystems, especially shallow, well mixed habitats like the Hudson, function more as unified systems than as the isolated boxes suggested by compartmentalized research studies and textbook diagrams.

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