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Distribution, abundance, and roles of freshwater clams (Bivalvia, Unionidae) in the freshwater tidal Hudson River

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SUMMARY

1. An extensive series of PONAR grabs was used to determine the distribution and abundance of unionid clams in the freshwater tidal Hudson River.
2. The five species of unionids collected were distributed very unevenly within the river. Mean river-wide density and biomass of unionids were $8.0\,m^{-2}$ and $6.2\,g\,DM\,m^{-2}$ (shell-free), respectively.
3. The environmental variables that we measured (water depth, distance from shore, sediment granulometry and organic content, presence or absence of macrophytes, and the chlorophyll *a* and particulate organic matter content of the water) explained little of the variation in abundance of unionids.
4. The distributions of the various species of clams did not differ significantly with respect to the environmental variables measured.
5. We estimate that unionids filter a significant amount of water ($0.14\,m^3\,m^{-2}\,day^{-1}$, on average) in the Hudson River estuary, roughly equivalent in magnitude to downstream flushing.
6. We project that unionids will serve as a major substratum for the settlement of the zebra mussel (*Dreissena polymorpha*), which is now invading the estuary. We emphasize that unionids may play important non-trophic roles in large river ecosystems.

Introduction

Freshwater clams (Unionacea) are among the most characteristic and widespread of the riverine biota. Rivers have been a major site of evolution and diversification of these animals, and river systems world-wide support hundreds of species of these conspicuous animals. For a long time, it has been thought that unionaceans form a large part of the zoobenthos of large rivers (e.g. Hynes, 1970; Vannote *et al.*, 1980), and that their filtering activities might affect the functioning of river ecosystems. It is therefore ironic that almost all studies on the distribution and roles of freshwater clams have been done in lakes (e.g. James, 1985; Hanson, Mackay & Prepas, 1988; Nalepa & Gauvin, 1988) or small streams (e.g. Salmon & Green, 1983; Strayer & Ralley, 1993). Studies on large rivers have been confined to numerous non-quantitative surveys of distribution, zoogeography, and pollution ecology (e.g. Ortmann, 1925; van der Schalie & van der Schalie, 1950; Starrett, 1971; Taylor, 1989; Hornbach, Miller & Payne, 1992) and a few recent, detailed and quantitative studies on community composition, demography, and distribution of unionids within more or less well-defined clam beds (e.g. Miller & Payne, 1988, 1993; Way, Miller & Payne, 1989). Studies by Negus (1966) and Holland-Bartels (1990) are among the very few quantitative studies on unionaceans over large areas in rivers. Consequently, we know little about patterns of distribution and abundance of unionaceans in large rivers, about what factors regulate these patterns, and about the importance of these characteristically riverine animals in the functioning of river ecosystems.

Prior studies on the macrobenthos of the freshwater tidal Hudson River (Simpson *et al.*, 1984, 1986; Bode *et al.*, 1986) focused on insects, oligochaetes and crustaceans, but indicated that the river might con-

tain large populations of unionid clams. As part of a study of the macrobenthos of the Hudson River prior to the invasion of the zebra mussel, *Dreissena polymorpha*, we conducted a detailed study of unionids. Our interest in unionids arose for several reasons. The data collected by Simpson's group suggested that unionids might be abundant enough in the river to affect the functioning of the ecosystem. In addition, our preliminary calculations (Strayer & Smith, 1993) suggested that living unionids might serve as substrata for the settlement of large numbers of *Dreissena*. Finally, *Dreissena* can have a strong negative impact on unionids (Hebert *et al.*, 1991; Hunter & Bailey, 1992; Haag *et al.*, 1993). Specifically, our goals were: (i) to estimate the number and distribution of unionids in the freshwater tidal Hudson River; (ii) to correlate patterns of unionid abundance in the river with environmental variables; and (iii) to estimate the importance of unionids in the functioning of the Hudson River ecosystem.

In addition, we had originally planned to use the growth lines present in clam shells to conduct detailed studies of growth and age structure of the populations. Recently, it has been shown that such growth lines are not always annual, however (Downing, Shostell & Downing, 1992; Downing & Downing, 1993). In addition, the several dozen shell thin sections that we prepared following the method of Neves & Moyer (1988) had very poorly marked growth lines and are difficult to age in any case.

The Study Area

The study area was the entire freshwater part of the Hudson River estuary in eastern New York, from the head of tide at the Troy dam (RKM 248, i.e. 248 river kilometres above The Battery in New York City) to Newburgh (RKM 99). The freshwater tidal Hudson covers 140 km^2 and has a mean depth of 8.3 m (Gladden *et al.*, 1988). The estuary is well mixed vertically. Mean annual discharge is 384–533 $m^3 s^{-1}$, depending on position in the estuary (Abood, Apicella & Wells, 1992), but is dwarfed by twice-daily tidal flows (Limburg, Moran & McDowell, 1986). Tidal range varies from 0.8 to 1.6 m (Cooper, Cantelmo & Newton, 1988). The water in the Hudson is hard (pH 7.6, Ca^{2+} = 27 mg l^{-1}; Mancroni, Daley & Dey, 1992; D.L. Strayer, unpublished), rich in nutrients (NO_3-N = 0.7 mg l^{-1}, soluble reactive P = 3–30 μg l^{-1}; Findlay *et al.*, 1991a; Cole, Caraco & Peierls, 1992), and moderately turbid (suspended solids = 20 mg l^{-1}; Cole, Caraco & Peierls, 1991; Findlay, Pace & Lints, 1991b). Additional environmental attributes of our sampling sites are given in Table 1.

Materials and Methods

Our sampling was done in two stages. In July–August 1991, we established twelve transects approximately evenly spaced over the length of the study area (Fig. 1). In June–July 1992 we sampled nine additional transects located randomly in a region shown by our 1991 samples to have a high density of unionids, to increase the precision of our estimate of unionid numbers in the river. Although *Dreissena* appeared in the river in 1991 (Powell & Strayer, 1992), it was found in only three of our samples and in low numbers (4, 8 and 126 m^{-2}), so its impacts on unionids at the time of our study were negligible. A transect contained four or five stations located randomly across the width of the river. At each station, we took five replicate grabs with a standard (23 × 23 cm) PONAR grab.

About 5% of the river bottom, chiefly in deep water, was too hard to be sampled with a PONAR grab (D.L. Strayer, unpublished). If we could not obtain an adequate sample after between five and fifteen attempts, we moved on to the next random coordinate until four or five stations were successfully sampled. In making calculations in this paper, we have assumed that unionid density in hard-bottom

Table 1 Environmental characteristics of the eighty-nine stations sampled in the freshwater tidal Hudson River

Variable	$\bar{x}$ (range)
Depth (m)	6.54 (0.46–19.2)
Distance to nearer shore[a]	25.2 (1–50)
% loss on ignition	3.90 (0.53–18.0)
% coarse sand (>1 mm)	17.7 (0–96.0)
% medium sand (0.25–1 mm)	21.4 (0.8–92.4)
% fine sand (50–250 μm)	26.0 (0.2–95.0)
% silt (2–50 μm)	22.3 (0–78.8)
% clay (<2 μm)	11.3 (0.8–38.4)
Chlorophyll *a* (μg l^{-1})	13.0 (5.34–22.1)
Particulate organic carbon (mg l^{-1})	0.94 (0.50–1.23)

[a] As a percentage of the river width.

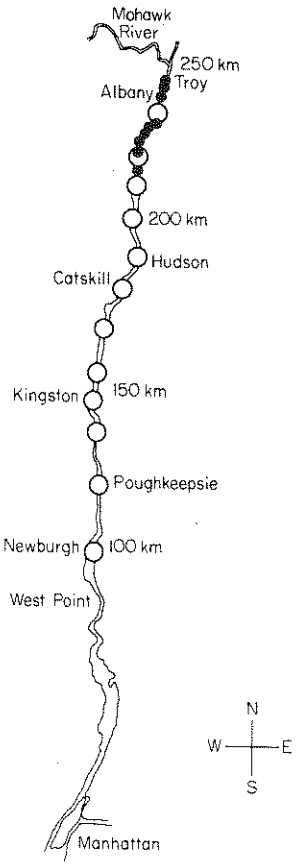

Fig. 1 The study area and sampling sites. White circles show sites sampled in 1991, black circles show sites sampled in 1992.

areas was identical to that in nearby soft-bottom areas.

Material collected by the grab was sieved (2.8 mm mesh) in the field. Unionids usually were removed from the sieve residue in the field, placed on ice and frozen upon return to the laboratory. When the sieve residue was voluminous, we froze the entire residue and sorted it in the laboratory. The length, width and height of unionid shells were measured with calipers, then the soft parts were removed, dried overnight at 60°C, and weighed. Unionid nomenclature follows Turgeon *et al.* (1988).

Variables tested as potential predictors of unionid distribution and abundance were water depth, distance from shore, grain size distribution and organic content of the sediment, the presence or absence of macrophytes, and the chlorophyll *a* and particulate organic carbon (POC) concentrations in the overlying water. We estimated water depth using sonar ('fishfinders'), and distance from the nearer shore (±18 m) with loran, which was expressed as a percentage of the river width. Grain size distribution was estimated by the hydrometer method, followed by dry sieving of the sand fraction (Gee & Bauder, 1986). Organic content of sediments was determined by loss on ignition after 16 h at 500°C. In 1991 (but not 1992), we recorded whether rooted macrophytes were present in the grabs that we collected. Chlorophyll *a* and POC data were supplied by colleagues at the Institute of Ecosystem Studies following methods described by Cole *et al.* (1991) and Findlay *et al.* (1991b). We used long-term means of these variables for the ice-free season, and interpolated linearly between stations where chlorophyll and POC were measured to derive estimates for our sampling sites.

Except where indicated, statistical analyses were run using SAS (SAS Institute Inc., 1987). We tested relationships between environmental variables and clam distribution using stepwise multiple regression (PROC STEPWISE in SAS) and stepwise discriminant analysis (PROC STEPDISC in SAS), with $P = 0.15$ to enter or remove variables. To test for interspecific differences in habitat use, we used stepwise discriminant analysis, as modified by Salmon & Green (1983). The null association model of Schluter (1984) was used to test for associations among unionid species. Prior to statistical analyses, unionid densities were fourth-root transformed (Downing, 1979) and sediment grain size percentages were arcsin transformed.

Results

Unionids were abundant in the Hudson River estuary (Table 2). Of the seven species that have been reported from the estuary (Strayer, 1987), we found

Table 2 Estuary-wide mean densities (90% confidence limits in parentheses) of unionid clams in the freshwater tidal Hudson River

Species	Density (m^{-2})
Elliptio complanata	4.91 (±1.16)
Anodonta implicata	2.66 (±1.05)
Leptodea ochracea	0.38 (±0.15)
Ligumia nasuta	0.08 (±0.12)
Lampsilis radiata	0.006 (±0.007)
Total	8.03 (±1.57)

five, two of them represented by only a single specimen. Unionids constituted over half the biomass of macroinvertebrates in the freshwater tidal Hudson River (Table 3).

Unionids were distributed very unevenly in the estuary (Fig. 2), and were much more abundant in the upper estuary than elsewhere (Fig. 3). In addition to this longitudinal variation in clam population density, marked longitudinal differences in the size/age structure of the clam assemblage were found (Fig. 4). In the upper estuary, where clam populations were dense, the asssemblage was of mixed sizes and ages. Although our sample size was small, the size distribution appeared to be similar in the lower estuary. In contrast, our samples from the middle estuary contained only small animals, all of them apparently less than 1 year old. Larger animals do occur in the mid-estuary, but they were too sparse to be taken in our samples.

Table 3 Mean biomass of benthic macroinvertebrates in the freshwater tidal Hudson River, from this study (Unionidae) and Simpson *et al.* (1986) (all other taxa). Ninety per cent confidence limits on unionid biomass are shown in parentheses

Taxon	Biomass (g DM m^{-1})
Unionidae (shell-free)	6.2 (±1.7)
Oligochaeta	4.8
Chironomidae	0.1
Sphaeriidae	0.03
Amphipoda	0.02
Isopoda	0.02
Chaoborus	0.02
Others	0.08
Total	11.3

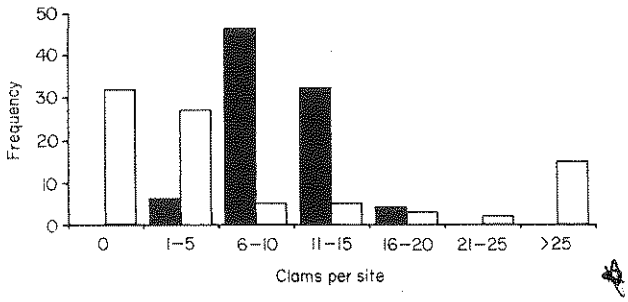

Fig. 2 Observed frequency distribution (□) of number of clams per site (i.e. per five PONAR grabs), compared with that expected from a Poisson distribution (■). The two distributions differ significantly ($P < 0.01$).

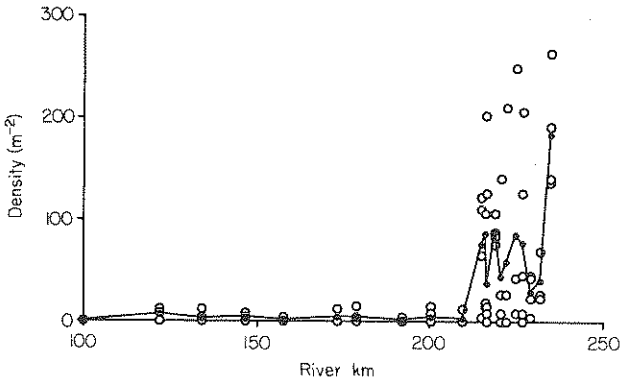

Fig. 3 Abundance of unionids in the Hudson River estuary as a function of longitudinal position along the river. Open circles show densities observed at each site, while the black line shows transect means.

None of the environmental predictor variables that we examined was effective in explaining much of the substantial spatial variation in clam densities. Concentrations of chlorophyll *a* and particulate organic carbon in the water column were strongly correlated with clam densities ($r = -0.49$, -0.59, respectively, $P < 0.001$), but the signs of these correlations were inconsistent with the hypothesis that clam density is controlled by food concentrations. After removing chlorophyll *a* and POC, our best regression model accounted for only about 20% of the variation in clam densities (Table 4, Fig. 5). Likewise, a discriminant analysis of areas with and without clams, while highly significant statistically ($F = 10.2$, $P = 0.002$), was based on only one environmental attribute (% fine sand) and had little power (average squared canonical correlation = 0.11) to identify areas with clams (Fig. 5).

According to the null association model of Schluter (1984), the three common species of unionids in the Hudson estuary were significantly positively associated ($P < 0.01$). In fact, neither canonical nor stepwise discriminant analysis could identify any significant differences ($P < 0.15$) in the distributions of these three species with respect to the environmental variables that we measured.

To estimate the filtering rate of the clam community in the Hudson, we applied the regression of Kryger & Riisgard (1988) to observed body sizes and densities of clams. On average, unionids filter $0.14\,m^3\,m^{-2}$ day^{-1}, which translates to $2 \times 10^7\,m^3\,day^{-1}$ at the scale of the entire freshwater estuary. This is roughly

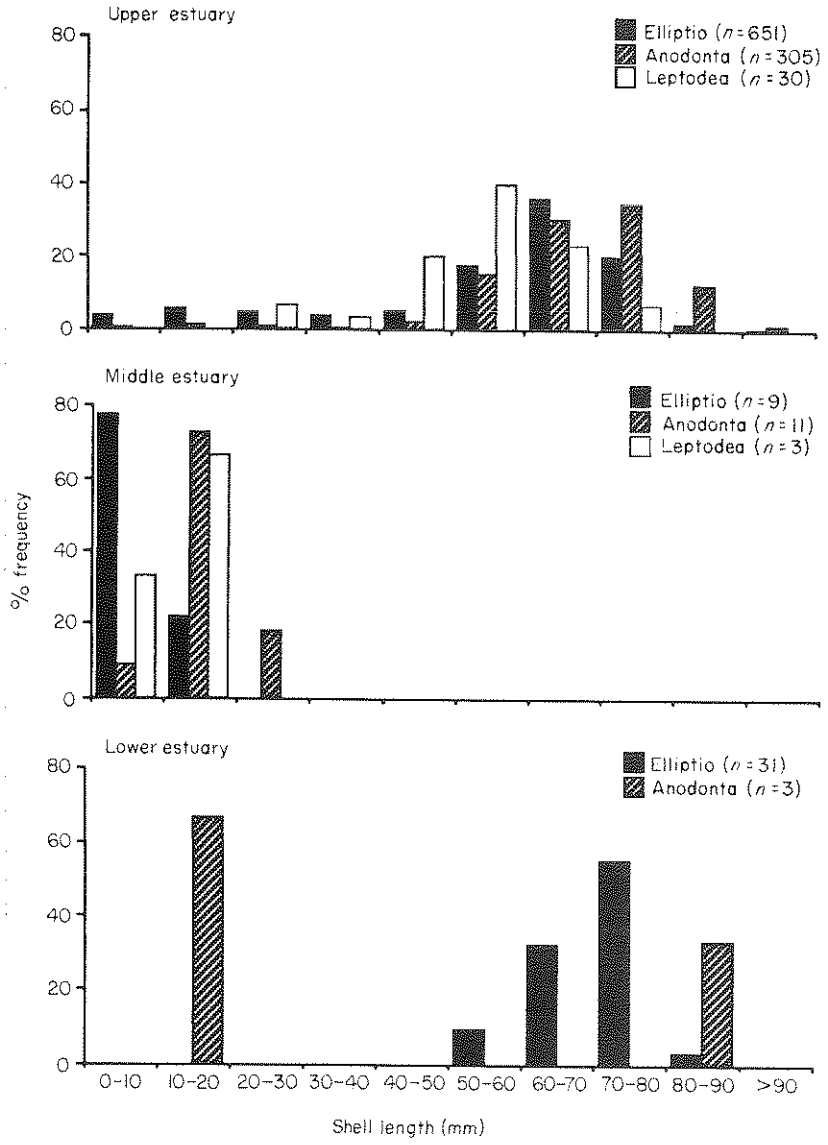

Fig. 4 Size distribution of unionids in three reaches of the Hudson Estuary: upper (RKM 213–248), middle (RKM 151–213) and lower (RKM 99–151).

Table 4 Multiple regression model to predict numbers of clams per station (i.e. in five replicate grabs) in the Hudson River estuary. Variables listed in order of entry. Clam numbers fourth-root transformed prior to analysis

Variable	Parameter	Partial F	P (F)	model r^2	P (model)
Intercept	1.189	34.7	<0.0001	0.19	<0.0001
Arcsin (% fine sand)	−1.260	16.2	<0.0001		
Distance from shore	0.012	3.4	0.07		

equal to the mean freshwater discharge through the estuary in summer (approximately 2×10^7 m^3 day^{-1}), suggesting that, on the scale of the entire estuary, downstream flushing and filtration by unionids could be of about the same importance in particle removal.

Because both flushing rates and clam densities varied greatly from point to point along the river, a river-wide estimate of filtering impacts obscures some interesting details. The impact of unionids was highest in the upper estuary (Fig. 6), where unionid populations were most dense, even though flushing rates also were highest in this reach. In the upper estuary during summer, an amount of water equivalent to freshwater flow through the reach was

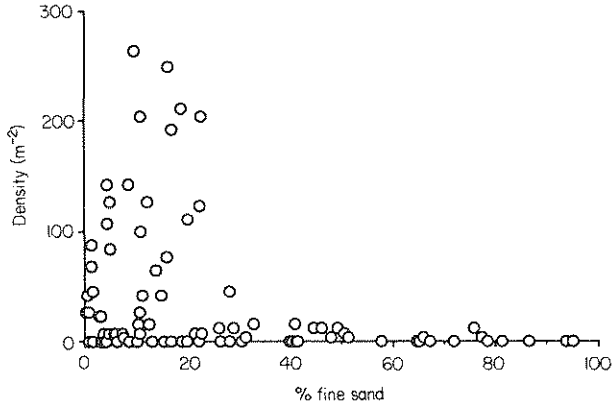

Fig. 5 Abundance of unionids (per five PONAR grabs) as a function of the fine sand (0.05–0.25 mm) content of the sediments. $r = -0.30$, $P < 0.01$.

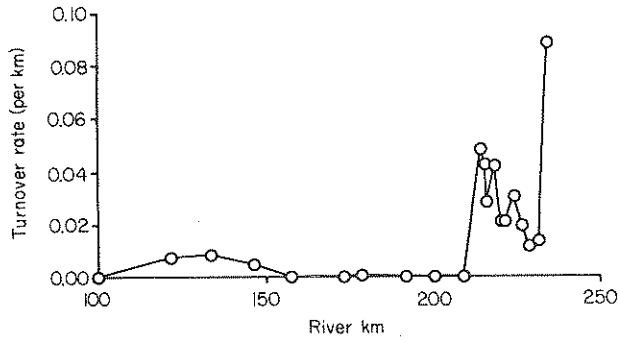

Fig. 6 Estimated filtration rate of the unionid community compared with net summertime (June–September) freshwater discharge as a function of longitudinal position along the river.

estimated to be filtered by unionids in a 10–50 km long reach of river.

Although it is difficult to make a precise estimate, we expect living unionids in the Hudson to be a major substratum for the invading zebra mussel, *Dreissena polymorpha*. As a first-order estimate, we assume that living adult unionids will support a *Dreissena* population equivalent to 0.02 m^2 of hard substratum (Lewandowski, 1976; Strayer, 1991; Schloesser & Kovalak, 1991; MacIsaac *et al.*, 1992). Combining this assumption with our estimate of 12 km^2 of available hard substratum in the study area (revised from Strayer & Smith, 1993), we calculate that about 50–60% of the *Dreissena* in the study reach will be attached to living unionids. Such an estimate of course underestimates the actual importance of unionids to *Dreissena* because it ignores the potential for *Dreissena* to settle on spent unionid shells or to proliferate into mats, using living or dead unionids as nuclei (Hunter & Bailey, 1992). The relative importance of unionids as substrata for *Dreissena* should vary greatly from site to site in the estuary, depending on both their density and the availability of alternative hard substrata.

Discussion

Quantitative studies of freshwater clams in large rivers are so few that it is difficult to make any firm generalizations about the abundance of clams in such habitats. Estimates of abundance range from 8 to 58 m^{-2} (this study; Negus, 1966; Duncan & Thiel, 1983; Holland-Bartels, 1990; Miller & Payne, 1993); however, it is clear that the sites to which these estimates apply were selected for study because of their high clam densities. Such densities, although most frequently reported, probably therefore represent the upper bound to unionid densities over large areas in big rivers. These densities probably correspond to a shell-free biomass of 5–100 g DM m^{-2}, almost certainly making clams the dominant part of zoobenthic biomass in such systems. Unionids turn over much more slowly than other macrobenthic animals, so concluding that unionid biomass can dwarf the biomass of other macroinvertebrates in large rivers overstates the energetic importance of unionids. To evaluate the energetic importance of unionids, it would be more appropriate to compare the production of unionids with that of other macroinvertebrates. The recent work of Downing *et al.* (1992) and Downing & Downing (1993) casts doubt on the accuracy of previous estimates of unionid productivity. Nevertheless, if the annual production/biomass ratio of unionids is roughly 0.2 (Nalepa & Gauvin, 1988), then production of unionids may be 1–20 g DM m^{-2} yr^{-1} in rivers where clams are dense, probably comparable with rates of production of the remainder of the macrobenthos (e.g. Mann *et al.*, 1972; Benke *et al.*, 1984).

Although it has been suggested for a long time that unionid beds in large rivers might filter enough water to control phytoplankton and other suspended particles, we are not aware of any previous attempts to estimate quantitatively the filtering impacts of unionid clams in rivers. Our admittedly crude estimates (e.g. Fig. 6) confirm the speculation that unionids can play

a significant role in particle dynamics in rivers, at least locally, although downstream transport plays a dominant role even where clam populations are dense. In general, downstream flushing may limit the impact of consumers in rivers, by washing out populations of planktonic grazers (e.g. Pace, Findlay & Lints, 1992) as well as the particles upon which grazers feed. We might therefore expect that the importance of consumers in particle dynamics varies inversely with flushing rate and is usually less in rivers than in lakes of similar mixed depth.

So far, this assessment of the importance of unionid clams in river ecosystems has had the conventional focus on energetics and the food web. Nevertheless, our projection that unionids will serve as the major substratum for zebra mussel settlement in the Hudson emphasizes that unionids might play important non-trophic roles in freshwater ecosystems. Where unionids are abundant, they can alter the physical structure of the benthic habitat. Most obviously, living unionids and their spent shells, which can persist for decades, may be a significant source of large particles in lakes or rivers with otherwise fine-grained sediments (sands or silts). As we have suggested for *Dreissena*, unionids can thereby extend the range of organisms that depend on coarse-grained sediments into otherwise unsuitable habitats. Living unionids and spent shells also might serve as substrata for other organisms if they are more stable than the surrounding sediments, in a manner similar to snags, which support much of the macroinvertebrate productivity in rivers with unstable sand bottoms (e.g. Benke *et al.*, 1984). In addition, on fine-grained sediments, living unionids probably alter the hydraulic roughness of the bottom, with consequent effects on the near-bottom hydrologic environment and sediment dynamics. Finally, McCall, Tevesz & Schwelgien (1979) showed that the movements of unionids can be important in mixing sediments. At this point any discussion of the non-trophic roles of unionids is necessarily sketchy, but we believe it is important to emphasize that the most important roles of unionids in river ecosystems may well arise from their physical alteration of the benthic habitat, rather than from their place in the food web.

In addition to evaluating the role of unionids in the freshwater tidal Hudson River, our goal was to investigate unionid patchiness and its causes in a large river. As in many other systems (e.g. Downing & Downing, 1992; Strayer & Ralley, 1993), the distribution of unionids in the Hudson was highly aggregated (Fig. 2). Traditional habitat descriptors (sediment grain size, water depth, etc.) had almost no power to explain this patchiness (Table 4, Fig. 5). The chief environmental correlate of unionid distribution and abundance in the Hudson was sediment grain size: unionids were more abundant on clay and silt than on medium to coarse sands (Fig. 5). Although some authors have reported a similar scarcity of unionids on sandy sediments (Tudorancea, 1972), others have found peak densities on such sediments (Holland-Bartels, 1990). There clearly is no simple, general correlation between unionid density and sediment grain size.

Furthermore, we believe that we can rule out pollution and the distribution of host fishes as causes for the observed distributional patterns. Historically, most of the pollution in the study reach came from the Albany area (Boyle, 1979), where clam densities are highest today. We know of no major sources of pollution in RKM 99–213 that might affect the unionids, and Simpson *et al.* (1986) found no major discontinuities in macroinverebrate community structure suggestive of pollution. The fish hosts of the larvae of *Anodonta implicata* and *Leptodea ochracea* are thought to be *Alosa* spp. (Johnson, 1946, 1947; Davenport & Warmuth, 1965), but *Elliptio complanata* uses *Perca flavescens* and *Fundulus diaphanus* (Matteson, 1948; Wiles, 1975). Even if *E. complanata* uses *Alosa* as well, it would not be expected to have the same distribution as the other unionid species. *E. complanata* breeds at a different time of the year than *A. implicata* and *L. ochracea*, so it would be unlikely to encounter a similar number and distribution of the migratory *Alosa* (cf. Schmidt, Klauda & Bartels, 1988). Therefore, it is unlikely that a patchy distribution of fish hosts causes the distributional patterns that we observed.

Numerous published studies have shown that traditional habitat descriptors (water depth, current speed, sediment granulometry, etc.) are unable to satisfactorily explain unionid distributions in running waters (e.g. Strayer, 1981; Holland-Bartels, 1990; Strayer & Ralley, 1993). Consequently, we seriously doubt whether it is worthwhile to focus on such variables in future studies of unionid ecology. As we have argued elsewhere (Strayer & Ralley, 1993), it may be time to try entirely new approaches towards

understanding the distribution of unionids in streams and rivers. For example, studies have focused on static properties of the sediments (e.g. grain size), whereas dynamic properties (e.g. disturbance regime) of the riverbed might be of considerably more importance to unionids. Another area that might merit further investigation is the behaviour and ecological requirements of juvenile clams, which are almost entirely unknown, but which could influence adult distribution and abundance. We hope that these and other innovative approaches will yield better explanations of unionid distribution than the traditional habitat-based approach.

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