

Biodiversity in Hudson River shore zones: influence of shoreline type and physical structure

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Abstract The shore zones of the Hudson River, like those of many developed waterways, are highly varied, containing a mix of seminatural and highly engineered shores. Our goal was to document the biodiversity supported by different kinds of shore zones in the Hudson. We chose six common types of shore zones, three of them “natural” (sand, unconsolidated rock, and bedrock), and three of them engineered (riprap, cribbing, and bulkheads). We measured selected physical characteristics (shore zone width, exposure, substrate roughness and grain size, shoreline complexity) of three examples of each of these shore types, and also sampled communities of terrestrial plants, fishes, and aquatic and terrestrial invertebrates. Community composition of most taxa differed across shore types, and frequently differed between wide, sheltered shores and narrow, exposed shores. Alien plant species were especially well represented along engineered shores. Nevertheless, a great deal of variation in biological communities was not explained by our six-class categorization of shore zones or the physical variables that we measured. No single shore type supported the highest values of all kinds of biodiversity, but engineered shore zones (especially cribbing and bulkheads) tended to have

less desirable biodiversity characteristics than “natural” shore zones.

Keywords Shorelines · Littoral zone · Estuary · Fish · Macroinvertebrates · Riparian zone · Vegetation

Introduction

The shore zone of aquatic ecosystems (the region adjoining the shoreline in which direct interactions tightly link the terrestrial and aquatic ecosystems) is ecologically important, highly modified and understudied (e.g., Airoldi and Beck 2007; McLachlan and Brown 2006; National Research Council 2007; Strayer and Findlay 2010). As a consequence of the typically high heterogeneity and large inputs of organic matter to the shore zone, both aquatic and terrestrial biodiversity often are high in the shore zone, including many species not found in adjacent habitats (e.g., Ward et al. 1999; Sabo et al. 2005; Strayer and Findlay 2010; Kennedy and Turner 2011), and rates of primary production, respiration, and other biogeochemical processes can be very high (e.g., Wetzel 1990; Polis and Hurd 1996; Coupland et al. 2007; Strayer and Findlay 2010). However, human activities such as agriculture, urbanization, commercial navigation, and recreation have been focused on shore zones for millennia, so many shore zones have been highly modified (e.g., Tockner and Stanford 2002; Scholten et al. 2005; Strayer and Findlay 2010). In particular, many shore zones now contain structures such as walls and revetments designed to protect valuable waterfront property. Consequently, the biodiversity and ecological function of many shore zones has been greatly reduced (e.g., Strayer and Findlay 2010; Kennedy and Turner 2011).

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Despite their importance and imperiled condition, shore zones may be understudied because they are claimed by neither aquatic nor terrestrial ecologists. Further, the extremely high heterogeneity of the shore zone makes it difficult to design sampling schemes and apparatus that are efficient throughout the full range of conditions encountered. As a result, detailed information on the biodiversity and ecological functioning of shore zones often is lacking, especially along fresh waters.

Nevertheless, information about the biodiversity and ecological function of different kinds of shore zones is necessary for wise management of these important ecosystems. A challenge for shore zone management is to preserve human uses of the shore zone while retaining or improving ecological function. To reach this goal, we will have to understand what characteristics of shore zones determine their biodiversity and ecological functioning.

An extensive review of the literature led to the conclusion that shore zone biodiversity depends chiefly on the physical energy regime, geologic (or anthropogenic) structure, the hydrologic regime, nutrient inputs, and climate (Strayer and Findlay 2010). If we are thinking of managing a particular site, physical structure often will be the easiest of these factors to manipulate. In particular, high biodiversity often is associated with high physical heterogeneity, so it may be desirable to design sites or manage for high physical heterogeneity.

Here, we report on surveys of biodiversity in the shore zone of the freshwater tidal Hudson River. The goals of our study were to (1) describe the biological communities that occupy the shore zones of the freshwater tidal Hudson River; (2) test whether those biological communities differ among different types of shore zones, whether natural and engineered; and (3) test whether the physical characteristics of shore zones (e.g., roughness, slope, exposure) can be used to predict the attributes of their biological communities. Specifically, we hypothesized that high biodiversity would be associated with high physical complexity of shore zones, and that engineered shore zones would be physically simpler and therefore support lower biodiversity than natural shore zones. Instead of focusing on a single taxonomic group, we deliberately chose to study several taxa, both aquatic and terrestrial. We hope that this information will help to better manage shore zones along the Hudson and elsewhere.

Methods

The study area

The study area is the freshwater tidal portion of the Hudson River (Fig. 1), which extends from RKM 100 (i.e., river kilometer 100 as measured from the Battery at the southern

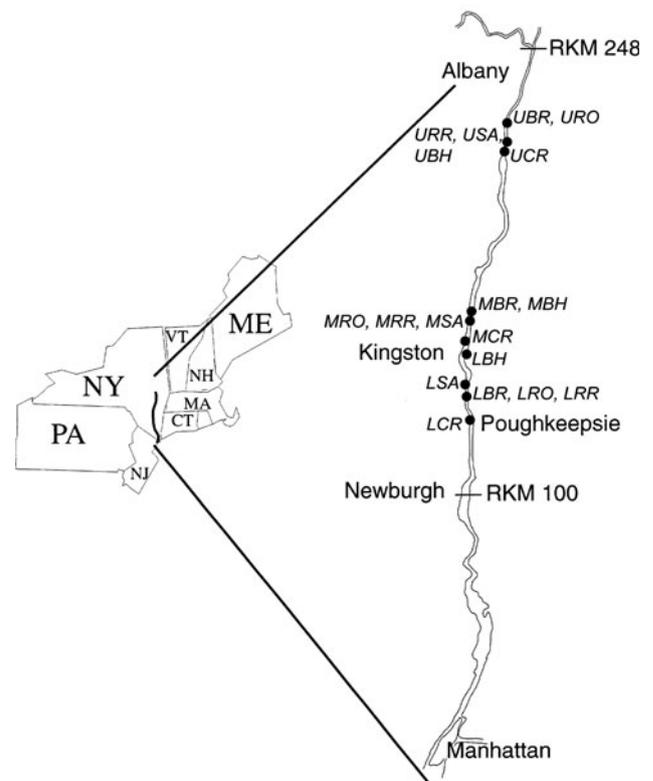


Fig. 1 Location of the study sites (black circles and italic labels) in the freshwater tidal Hudson River in eastern New York, USA. The first letter of the site code gives the section of river (*L* lower, *M* middle, *U* upper), and the last two letters give the shore type (*BH* bulkhead, *BR* bedrock, *CR* cribbing, *RO* natural rock, *RR* riprap, *SA* sand)

end of Manhattan in New York City) to the head of tide at RKM 248 in Troy. The entire study area is subject to twice-daily tides with an average range of 0.8–1.6 m; tidal range does not diminish upriver and is as large at Troy as at Manhattan (Geyer and Chant 2006). Because daily tidal flows are much greater than typical freshwater flows (Geyer and Chant 2006), water levels along the Hudson's shores are determined more by tides than by freshwater flows (Strayer and Findlay 2010; Fig. 17), and the Hudson does not have the large, well-defined floodplain characteristic of typical alluvial rivers. The average water depth is ~8 m and the average channel width is ~900 m. The Hudson is used by ocean-going ships as far as Albany (RKM 226), and smaller commercial ships all the way to Troy, and is heavily used by recreational boaters throughout the study area. Wakes from this traffic probably are important forces on shore zones throughout the study area.

The water is moderately hard, turbid, and fertile (typical growing-season values: calcium = 25 mg/L, NO₃-N = 0.5 mg/L, PO₄-P = 28 µg/L, Secchi transparency = 1 m; Caraco et al. 1997; Simpson et al. 2006). Large beds of the

macrophytes *Vallisneria americana* (submersed) and *Trapa natans* (floating-leaved) are common (Nieder et al. 2004). The fauna is dominated by species typical of warm fresh waters, although diadromous fishes (e.g., *Alosa* spp.) and several typically brackish-water fishes and invertebrates are common in the freshwater estuary (e.g., Simpson et al. 1985).

We defined the shore zone as the region extending from 1 m vertically below mean low water to 1 m vertically above mean high water. Although admittedly arbitrary, this definition is consistent with previous definitions (reviewed by Strayer and Findlay 2010) that delimit the shore zone as a region of strong interactions between land and water, and was practical to apply in the field. Note that this definition of the shore zone includes areas that are usually under water, areas that are usually exposed to the air, and areas that are intermittently inundated.

Study design

We studied six types of shore zones, three of them engineered (riprap, cribbing, and steel or concrete bulkheads) and three of them without obvious signs of human engineering (bedrock, natural unconsolidated rock, and sand). Even these “natural” shore zones often showed some signs of past human activity. Definition of shore types was based on predominant conditions at and just above the high water mark. Riprap shores are revetments constructed of large stone (typically >50 cm in diameter), cribbing shores consist of wooden pilings (typically ~25 cm diameter) back-filled on the land side with crushed stone 15–25 cm in diameter, and bulkheads are vertical walls or revetments made of steel or concrete. These engineered structures typically extend from well below mean low water to well above mean high water, although some parts of the cribbing are overtopped at mean high water. Designation of shore types and their locations were based on a complete GIS inventory of both shores of RKM 50–248 of the Hudson in 2006 (D. Miller, unpublished).

We selected one example of each type of shore zone in three reaches of the Hudson (Fig. 1): upper (RKM 213–247), middle (RKM 151–213), and lower (RKM 100–151). Blocking by reach was intended to control for north–south differences in biota along the length of the river. We selected a random point in each river reach, then chose the closest example of each shore type to that random point that met the following criteria: it was at least 130 m long (i.e., 100 m of shore to be studied plus at least a 15 m buffer on each end) and was not interrupted by a tributary mouth or any major human structure (e.g., a marina). In two cases where a particular shore type was rare in a section of the river, we had to relax these standards and choose a slightly shorter reach of shore (the shortest reach was 75 m long).

Physical variables

We measured several physical properties of each site: shore zone width, sediment grain size, exposure, substrate roughness, and shoreline complexity. We measured shore zone width as the distance along a line perpendicular to the shoreline from 1 m vertically above the high-water mark to 1 m vertically below the low-water mark. At a few sites with very shallow slopes, we measured the underwater slope only to a point 60 m from the shoreline, where the water was less than 1 m deep and extrapolated the slope from the low water mark to the 1 m depth contour. We repeated this procedure three times at each site: at the upriver end, middle, and downriver end of the site. These estimates were then combined into a single estimate of shore zone width for each site.

We used the modified pebble count method of Lazorchak et al. (1998) to estimate sediment grain size in the intertidal zone. Briefly, we laid out a 100-m long tape along the low-water line, the mean-water line, and the high-water line, and categorized the sediment at 1 m intervals along the line as 0 = silt or clay, 1 = sand, 2 = sand to the size of a marble (16 mm), 3 = size of a marble to a tennis ball (64 mm), 4 = size of a tennis ball to a basketball (250 mm), 5 = size of a basketball to 1 m diameter, 6 = 1–4 m diameter, and 7 = larger than 4 m diameter. We averaged these 300 measurements to get a single estimate of average sediment grain size for each site.

Sediment grain size of subtidal sediments was estimated from handheld cores (5 cm diameter) taken at depths of 0.33 and 0.67 m below the low-water mark. Three cores were taken at each depth at each site. We dried each sample, weighed it, then wet-sieved the sample through brass soil sieves of 0.25, 1, and 4 mm mesh, and measured the dry mass of sediment retained on each sieve. We then calculated an index of grain size as $[\text{mass retained on } 0.25\text{-mm mesh sieve} + 2 \times (\text{mass retained on } 1\text{-mm mesh sieve}) + 3 \times (\text{mass retained on } 4\text{-mm mesh sieve})] / (\text{total mass of sample})$. If the sediment was too coarse to core, we assigned it a value of 4. We then calculated a mean value for each site. This index ranged from 0 (if all of the sediment was finer than 0.25 mm) to 4 (if the sediment was too coarse to core).

We used three methods to estimate exposure to waves and currents. First, we deployed a modified version (using a weaker spring to accommodate lower wave forces) of the dynamometer of Bell and Denny (1994), which is designed to measure peak wave forces. Second, we set out clod cards (Petticrew and Kalff 1991) to get a general estimate of the intensity of water movement at each site. Clod cards were ~600 g masses of plaster-of-paris molded in beverage cups and attached to cement blocks. After they were retrieved from the field, they were oven-dried and

reweighed to calculate mass loss, which is roughly proportional to water movement. We set out three dynamometers and six clod cards at each site for ~10 days. Because we had only a few dynamometers, we deployed dynamometers and clod cards at the six sites in one reach of river, then later moved on to the other reaches. Third, we assumed that sediment grain size would reflect peak physical forces at a site, and used our estimates of sediment grain size as one measure of exposure. For the sites in each reach of river (the reaches were treated individually because dynamometers and clod cards were deployed at different times in different reaches), we ranked the dynamometer readings from 1 (most exposed) to 6 (least exposed), mass loss of clod cards from 1 to 6, and sediment grain size from 1 to 6. We then summed these three estimates of exposure for each site, and ranked them for all sites in the river from 1 (most exposed site) to 18 (least exposed site).

We measured local substratum roughness (rugosity) using the chain technique of Frost et al. (2005). In this method, a 1-m long chain is placed to conform as closely as possible to the contours of the bottom and the distance covered by the chain is measured with a taut tape. Roughness is the ratio of the chain length (1 m) to the tape-measured distance. We measured rugosity parallel and perpendicular to the shoreline at nine places using a chain with a 12-mm link (low water, mean water, and high water at upriver end, center, and downriver end of each site).

We estimated the complexity of the shoreline in plan view by stepping off the length of the 100-m stretch of shoreline at mean low water level using a pair of 1-m wide calipers. Complexity is estimated as the ratio of shoreline length measured using calipers to that measured using a taut line (i.e., 100 m). Values for complexity range from one for perfectly straight shorelines to higher values for complex shorelines.

In addition, we tested the effect of nearby beds of submersed aquatic vegetation (SAV) (chiefly *Vallisneria americana*). SAV beds could serve as a source of wrack, which is important to shore zone invertebrates and plants (e.g., Backlund 1945; Minchinton 2002), as well as serving directly as a source of fish and invertebrate colonists to nearby shore zones. We constructed an SAV index as the area of the nearest mapped bed of SAV (in m²) divided by the squared distance to the bed (in m), using data described by Nieder et al. (2004).

Biological sampling

We sampled fishes, plants, aquatic invertebrates, terrestrial invertebrates, and snails living in each shore zone site. We sampled fishes by electrofishing using a Smith-Root Type VI-A electrofisher mounted in a 6.4-m long john boat. Sites

were continuously shocked until we had covered the length of the study site or 5 min total of shocking time had elapsed, whichever occurred first. Sampling occurred within 3 h of high tide. Fishes were dipped and placed in an onboard live well. After we finished sampling, we identified, measured, and counted fish. If more than 25 individuals of a species were collected at a site, the first 25 individuals were measured. We sampled fish three times: spring, summer, and autumn of 2008.

We sampled terrestrial plants using timed searches on 4–20 August 2008. Timed searches are an efficient way to locate rare species (cf. Strayer and Smith 2003). We walked each site for three consecutive 10-min periods (a total of 30 min searching) and recorded as many plant species as possible between the low water mark and 1 m above the mean high water mark. This search was not sufficient to detect all plant species, especially at high-diversity sites. As a result, our data probably underestimate differences between high- and low-diversity sites. Nevertheless, inspection of the species-accumulation curves suggested that this method detected >75% of the vascular plant species at each site.

We sampled aquatic invertebrates using two methods. We took kick samples at all sites, using a 0.5-mm mesh D-net for 10 min/site, deliberately attempting to sample the full range of available habitats. We also sampled benthic invertebrates using 5-cm diameter hand-held cores. We tried to take samples at the upriver end, middle, and downriver end of each site at depths of 0.33 and 0.67 m below the low-water mark. Substrata were too coarse to allow such core samples to be taken at all sampling locations. These core samples were sieved in the field through a 0.5-mm mesh sieve. All aquatic invertebrate samples were preserved in the field in 10% buffered formalin and sorted in the laboratory under 6× magnification, and identified to the lowest practical taxonomic level (usually classes or orders). We took samples of aquatic invertebrates between 5 May–6 June and again in 4–20 August 2008.

We sampled terrestrial invertebrates using a backpack aspirator. We spent 10 min at each site taking a sample from the ground and an additional 10 min sampling the air and vegetation, again attempting to cover the full range of microhabitats available at each site. Invertebrates were killed in the field using a killing jar with ethyl acetate, then stored in the freezer until they were identified to the lowest practical taxonomic level (usually orders or families). We took samples of terrestrial invertebrates in early June and again in early September 2008.

We examined land and aquatic gastropod communities in detail, identifying all specimens to genus or species. We sampled aquatic gastropods by taking a 30 s sweep of 1 m² of substrate at a depth of 1 m below the low tide mark with a 1.2-mm mesh D-net. Intertidal gastropods were sampled

by handpicking and washing substrate from a 1 m² plot at mid-tide level through a 1.4-mm mesh sieve. Upland gastropods were collected within 10 m (horizontally) inland of the high tide mark, by handpicking and sieving soil through a 1.4-mm mesh sieve. Each type of sample was repeated three times, near the upriver end, middle, and downriver end of each site. We collected gastropods twice at all sites, on 1–3 June and 29 June–2 July 2008. All gastropods collected were preserved in the field in 95% ethanol, and identified in the laboratory using Pilsbry (1939–1948); Burch (1962, 1989); Harman and Berg (1971); Strayer (1990); and Jokinen (1992).

Statistical analyses

We conducted four statistical analyses for most taxonomic groups. First, we used one-way ANOVA (following data transformation, where needed) to test for differences in abundance or diversity across the six types of shore zones. We used Gini diversity as a measure of taxonomic diversity because it is relatively insensitive to sample size (Gotelli and Ellison 2004). Second, we ran two-dimensional nonmetric multidimensional scaling ordinations (NMS, PC-ORD 5.10) to display variation in community composition across sampling sites (McCune and Grace 2002). We transformed the data using a $\log_{10}(X + 1)$ transformation and removed taxa present at fewer than three sites prior to ordination. Plant ordinations were based on presence-absence data, because we did not collect data on relative abundance of plants. We then used multi-response permutation procedures (MRPP) to test for significant differences in community composition among shore types. Third, we used multiple regression using Pearson correlations (Table 4) and best subset regression in Statistix 9.0 to identify associations between biodiversity (abundance and species richness of each taxon, scores on ordination axes) and the physical characteristics of the study sites. We transformed shore zone width using a $\log_{10}(X + 0.1)$ transformation and the SAV index using a log transformation prior to statistical analyses.

Table 1 Environmental characteristics (mean, with range in parentheses) of Hudson River shore zones

Shore type	Shore zone width* (m)	Pebble count*	Diversity of pebble count	Shoreline complexity	Roughness*	Exposure*	Sediment organic matter (%)	Subtidal sediment index
Sand	124 (55–257)	1.0 (0.96–1.1)	0.25 (0.03–0.65)	1.03 (1.00–1.06)	1.06 (1.02–1.10)	16 (14–18)	2.2 (1.5–2.8)	0.47 (0.14–0.79)
Rock	24 (8.9–52)	3.4 (1.6–4.8)	0.68 (0.63–0.76)	1.08 (1.00–1.12)	1.27 (1.12–1.40)	12 (7–17)	3.7 (2.3–5.3)	2.0 (0.06–3.3)
Bedrock	30 (8.3–72)	4.7 (3.6–6.2)	0.66 (0.33–0.85)	1.11 (1.03–1.20)	1.19 (1.17–1.21)	9.8 (4–14)	3.2 (3.0–3.5)	2.4 (1.0–3.4)
Riprap	8.4 (6.2–11)	5.0 (4.5–5.6)	0.59 (0.45–0.73)	1.23 (1.11–1.44)	1.45 (1.30–1.54)	8 (6–10)	2.9 (0.64–4.2)	2.5 (1.2–3.8)
Cribbing	20 (0–52)	4.2 (2.7–5.7)	0.71 (0.65–0.77)	1.06 (1.00–1.11)	1.37 (1.18–1.58)	10 (7–14)	2.7 (2.3–3.2)	1.6 (0.52–2.6)
Bulkhead	0.8 (0–2.4)	6.4 (5.3–7)	0 (0–0.45)	1 (1.00–1.00)	1.15 (1.00–1.24)	2.7 (1–5)	2.7 (2.7–2.7)	1.3 (0.83–1.7)

Variables marked with asterisks differed significantly (ANOVA, $p < 0.05$) among shore types

Results

Physical properties of Hudson River shore zones

The shore zones that we studied were highly varied, both within and among shore types (Table 1). Important environmental characteristics differed significantly among shore types, as well as between natural and engineered shores (Table 2). The primary axis of variation in the physical characteristics of shore zones, which accounted for 61% of variance in a principal components analysis (Fig. 2), distinguished flat, sheltered, fine-grained shores (e.g., sand) from steep, exposed, coarse-grained shores (e.g., bulkheads). A secondary axis (accounting for an additional 28% of variance) separated sites with complex shorelines and rough surfaces from those with simple shorelines and smooth surfaces.

Terrestrial plants

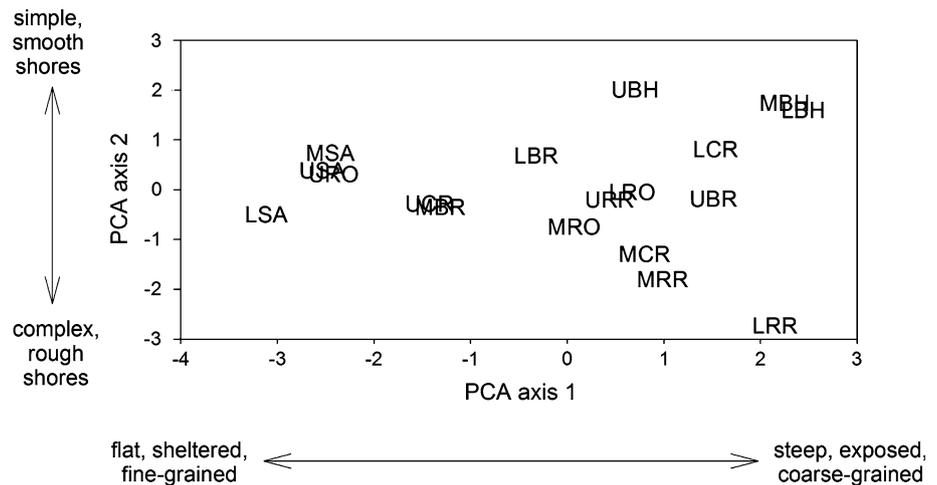
We identified 190 taxa of plants in Hudson River shore zones, 46 of which are alien to the region. Plants that were especially frequent (detected at >50% of sites) included bush honeysuckles (*Lonicera* spp.), false indigo (*Amorpha*

Table 2 Differences between natural and engineered shore zones along the Hudson River ($n = 9$ for each kind of shore zone)

Variable	Natural	Engineered	p
Log (shore zone width) (m)	1.51	0.68	0.006
Exposure	12.6	6.9	0.01
Rugosity	1.17	1.32	0.07
Pebble count	3.1	5.2	0.02
Native plant richness	30.8	14.8	0.0005
Total plant richness	49.7	34.2	0.01
% alien plants	14.9	27.1	0.002
Abundance of small fish (square-root transformed)	8.2	3.4	0.04

We show only variables for which significant ($p < 0.1$) differences exist between natural and engineered shore zones

Fig. 2 PCA analysis of Hudson Valley shore zones on the basis of physical characteristics (shore zone width, pebble count, shoreline complexity, roughness, and exposure). Axes are scaled according to the % variance explained (these two axes account for 90% of total variance). The *first letter* of the site code gives the section of river (*L* lower, *M* middle, *U* upper), and the *last two letters* give the shore type (*BH* bulkhead, *BR* natural rock, *CR* cribbing, *RO* natural rock, *RR* riprap, *SA* sand)



fruticosa), Virginia creeper (*Parthenocissus quinquefolia*), wild grapes (*Vitis* spp.), dogwoods (*Cornus* spp.), ashes (*Fraxinus* spp.), cottonwood (*Populus deltoides*), goldenrods (*Solidago* spp.), sugar maple (*Acer saccharum*), poison ivy (*Toxicodendron radicans*), bedstraw (*Galium* spp.), roses (*Rosa* spp.), and elms (*Ulmus* spp.).

Total taxonomic richness of plants did not vary significantly among shore types ($p = 0.55$), but was higher along natural than engineered shores (Table 2). Species richness of alien plant species tended to be higher along engineered shores than natural shores (Fig. 3), but this difference was not significant ($p = 0.43$). Species richness of native plants differed marginally among shore types (Fig. 3, $p = 0.05$), and was higher along natural than engineered shores (Table 2). As a consequence of opposing trends in native and alien plant species, the percentage of shore zone plants that are aliens differed significantly among shore types (Fig. 3, $p = 0.0003$) and was significantly higher along engineered shores than natural shores (Table 2).

The ordination (Fig. 5) shows some clustering by shore type (e.g., the mowed bulkhead sites grouping in the lower left), but with considerable overlap among shore types, so that overall this clustering was not statistically significant ($p = 0.18$, MRPP). Axis 2 was significantly ($p < 0.05$) correlated with exposure ($r^2 = 0.45$). Sites near the bottom end of axis 2 were exposed, narrow shore zones with coarse sediments, while sites near the top end of the axis were sheltered, wide, and fine-grained. Typical plants of sites near the lower left of the ordination were lawn weeds such as butter-and-eggs (*Linaria vulgaris*), English plantain (*Plantago lanceolata*), chicory (*Cichorium intybus*), and bedstraw (*Galium* spp.), while shrubs such as willows (*Salix* spp.), witch hazel (*Hamamelis virginiana*), and ninebark (*Physocarpus opulifolius*) were typical of sites near upper right. Axis 1 was not significantly correlated with any of the environmental variables that we measured.

Attempts to predict other characteristics of the shore zone plant community from the physical variables we measured were only partly successful. Models to predict native, alien, or total species richness from physical variables had $R^2 < 0.25$. Echoing the differences we saw across shore types, the percentage of shore zone plants that were aliens was strongly ($r^2 = 0.50$) and positively correlated with exposure (Fig. 4).

Fishes

We collected 1121 individual fishes, representing 24 species. Numerical dominants included spottail shiner (*Notropis hudsonius*, 41%), banded killifish (*Fundulus diaphanus*, 25%), pumpkinseed (*Lepomis gibbosus*, 7%), blueback herring (*Alosa aestivalis*, 5%), white perch (*Morone americana*, 5%), and alewife (*Alosa pseudoharengus*, 4%). The abundance, but not the Gini diversity ($p = 0.39$) of fishes varied significantly among shore types (Fig. 3). Natural shore zones had higher numbers of small fishes than did engineered shore zones (Table 2). Sand shores supported dense communities dominated by small fishes such as spottail shiners and banded killifish, whereas riprap and rock shores supported communities of moderately high density. Bulkheads and cribbing supported low numbers of fishes, and especially low numbers of small fishes.

The physical properties of shore zones that we measured were significantly correlated with fish communities. Gini diversity was positively related ($R^2 = 0.43$) to high roughness ($p = 0.005$) and low shoreline complexity ($p = 0.06$), with roughness having by far the largest influence (Fig. 4; Table 4). Density of small fishes (total length < 20 cm) was positively correlated ($R^2 = 0.63$) and high shoreline complexity, or nearly as well ($R^2 = 0.52$) with wide shore zones (Fig. 4; Table 4). The density of large fishes was somewhat correlated ($R^2 = 0.37$, $p = 0.013$) with coarse underwater sediments.

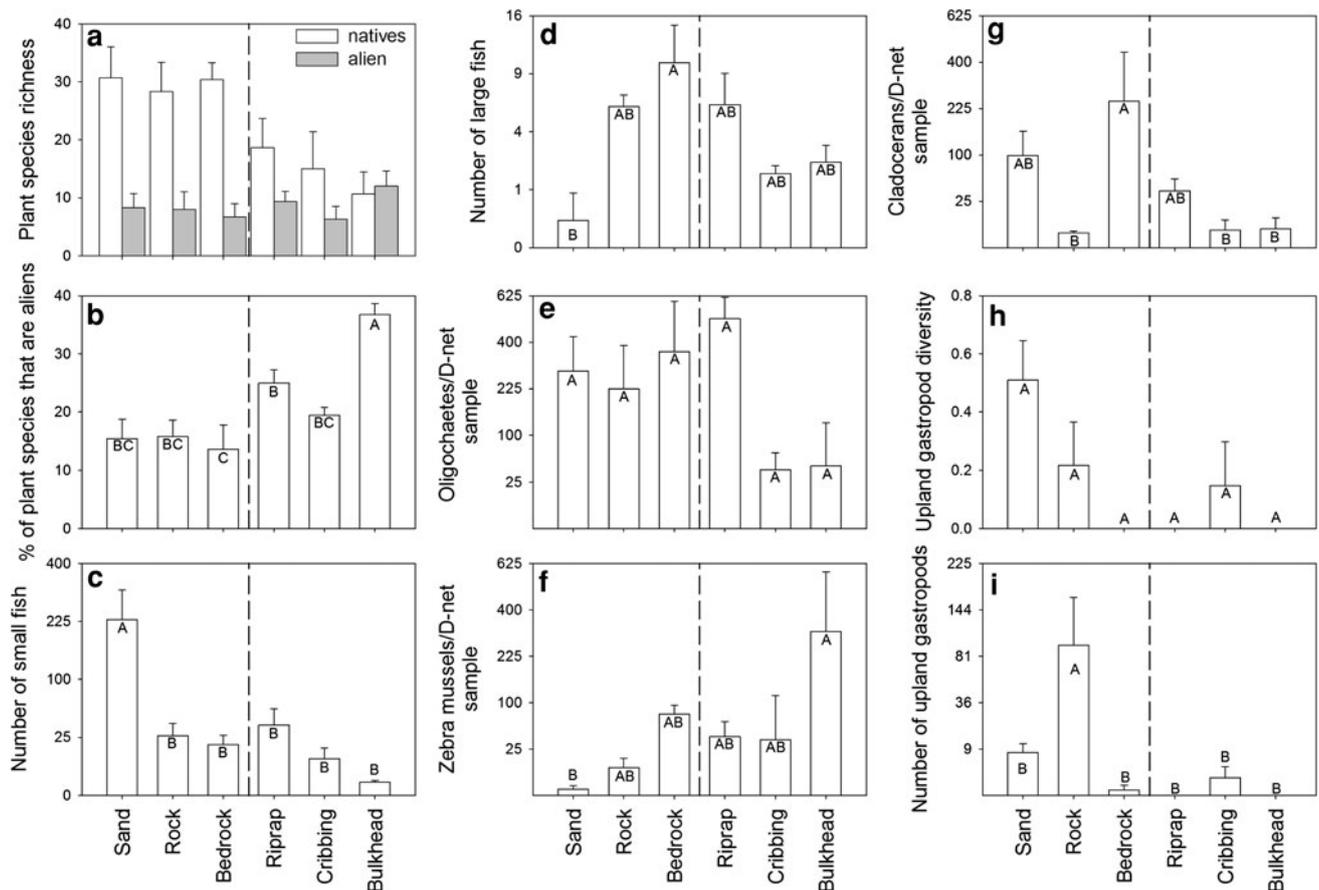


Fig. 3 Summary of differences in biodiversity across types of shore zones in the Hudson River: **a** species richness of native and alien plants, **b** percentage of plant species found at each site that are alien, **c** number of small (<20 cm long) fish caught at each site, **d** number of large (>20 cm long) fish caught at each site, **e** number of oligochaetes caught per D-net sample, **f** number of zebra mussels caught per D-net sample, **g** number of cladocerans caught per D-net sample, **h**

diversity of upland gastropods, **i** number of upland gastropods collected. Error bars show 1 SE, letters in or above bars show differences between shore types according to Tukey's Studentized Range (HSD) test at $p = 0.05$; the vertical dashed line separates "natural" shore zones on the left from engineered shore zones on the right. Note the differences in scaling on different y-axes

The ordination (Fig. 5) confirmed the existence of clear differences in fish communities among shore types. The first ordination axis was significantly ($p < 0.05$) correlated with sediment grain size (pebble count), exposure, and slope, and separated steep, high-energy shores (bulkheads and cribbing) on the left end of the axis from flat, low-energy shores (sand) on the right end of the axis. The second axis was not significantly correlated with any of the physical variables that we measured, nor did we see any evidence of consistent differences in physical attributes among the different geographic sections of the river.

Aquatic macroinvertebrates

The D-net samples were dominated by oligochaetes (overall mean = 275/sample), chironomids (163/sample), zebra mussels (102/sample), cladocerans (79/sample),

amphipods (59/sample), gastropods (53/sample), and mites (44/sample). Neither the overall abundance nor diversity of D-net invertebrates was related to shore type ($p = 0.15$ and 0.37 , respectively), or differed between natural and engineered shore zones ($p > 0.4$). Of the dominant groups just listed, only the abundance of oligochaetes, zebra mussels, and cladocerans was related to shore type (Fig. 3). Oligochaetes tended to be less abundant off of high-energy shorelines (bulkheads and cribbing), zebra mussels were most abundant on coarse-grained shores (bulkheads, bedrock, riprap, and cribbing), and cladocerans were most abundant on bedrock, sand, and riprap.

Community structure of D-net invertebrates varied across shore types (Fig. 5). Axis 2 was clearly related to site exposure, with highly exposed sites having coarse-grained substrates near the upper end of the axis, and sheltered sites with fine-grained substrates near the lower

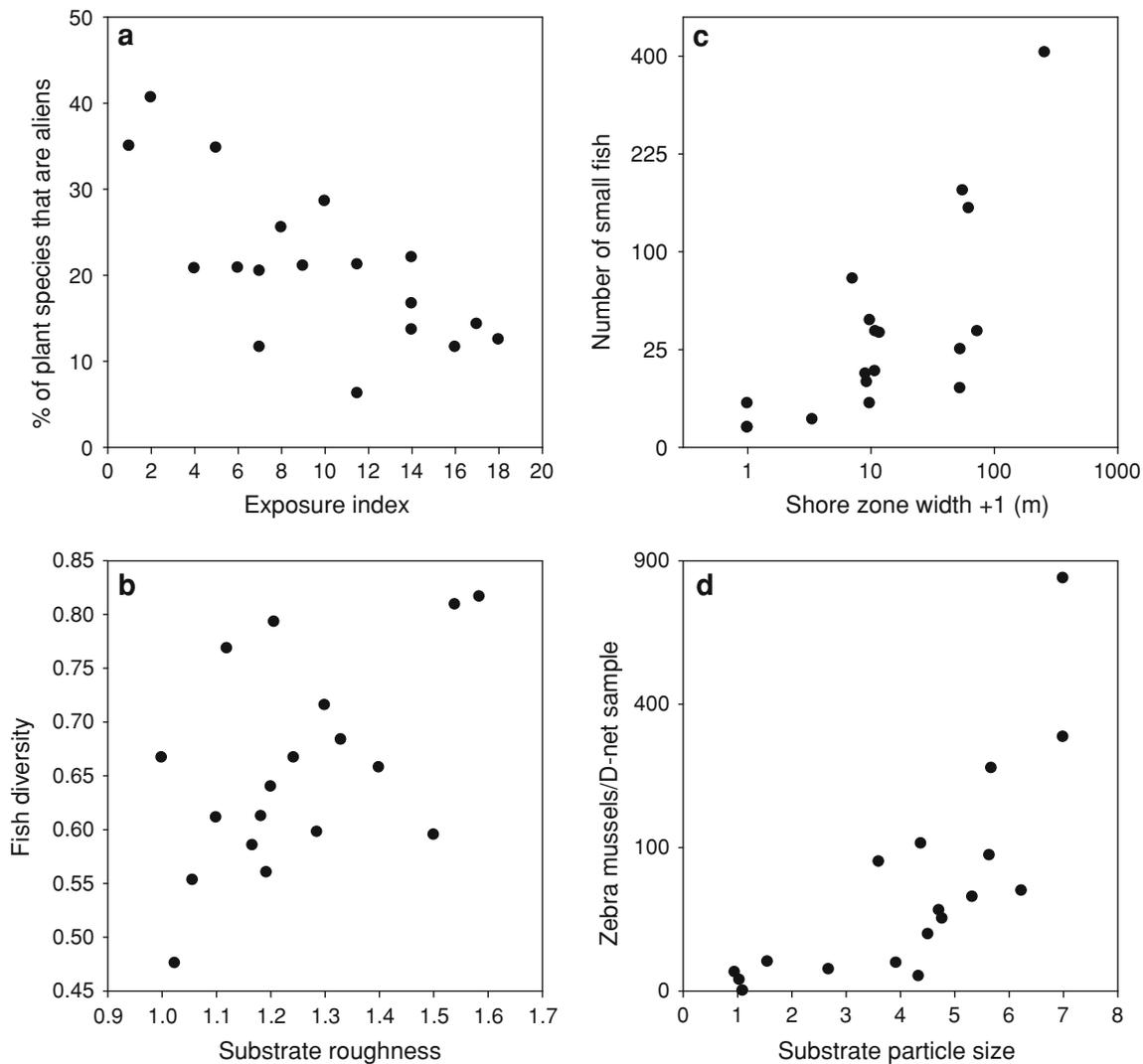


Fig. 4 Examples of relationships between physical characteristics and biodiversity of Hudson River shore zones: **a** percentage of plant species found at each site that are alien as a function of site exposure (low values indicate high exposure; $r^2 = 0.56$, $p < 0.001$), **b** fish diversity (Gini index) as a function of substrate roughness ($r^2 = 0.25$,

$p = 0.03$), **c** number of small (<20 cm long) fish caught at each site as a function of shore zone width ($r^2 = 0.55$, $p < 0.001$), **d** number of zebra mussels caught per D-net sample as a function of substrate particle size (larger numbers indicate coarser sediments; $r^2 = 0.56$, $p < 0.001$)

end of the axis. Axis 1 scores were not closely correlated with any of the environmental variables that we measured.

Gini diversity of D-net invertebrates was weakly correlated with shore zone width (i.e., slope) ($r = -0.47$, $p = 0.05$). Generally, abundance of dominant taxa (or of all taxa combined) and diversity of D-net invertebrates were poorly correlated with environmental variables (R^2 of models with the lowest AIC usually were <0.2). Exceptions were models for the abundance of zebra mussels ($R^2 = 0.66$, positively correlated with pebble count (Fig. 4) and surprisingly negatively correlated with roughness), oligochaetes ($R^2 = 0.36$, positively correlated with SAV index and exposure), amphipods ($R^2 = 0.32$, positively correlated with SAV index and pebble count), and gastropods ($R^2 = 0.29$, positively correlated with pebble count).

We were able to obtain cores at both depths and months at only 10 of the 18 study sites, so the statistical analyses of densities and diversity are based on this subset of 10 sites. Mean invertebrate density was $20,500/m^2$; dominant groups were oligochaetes ($10,400/m^2$), chironomids ($3,400/m^2$), nematodes ($1,900/m^2$), zebra mussels ($1,200/m^2$), amphipods ($660/m^2$), and sphaeriids ($610/m^2$). Neither total macroinvertebrate density nor the density of any of the dominant groups just mentioned varied significantly among shore types or between natural and engineered shores, possibly because of the small, unbalanced data set. Furthermore, density of all macroinvertebrates and most groups taken individually was statistically unrelated to the environmental characteristics that we measured. The exception was oligochaetes, whose density was negatively

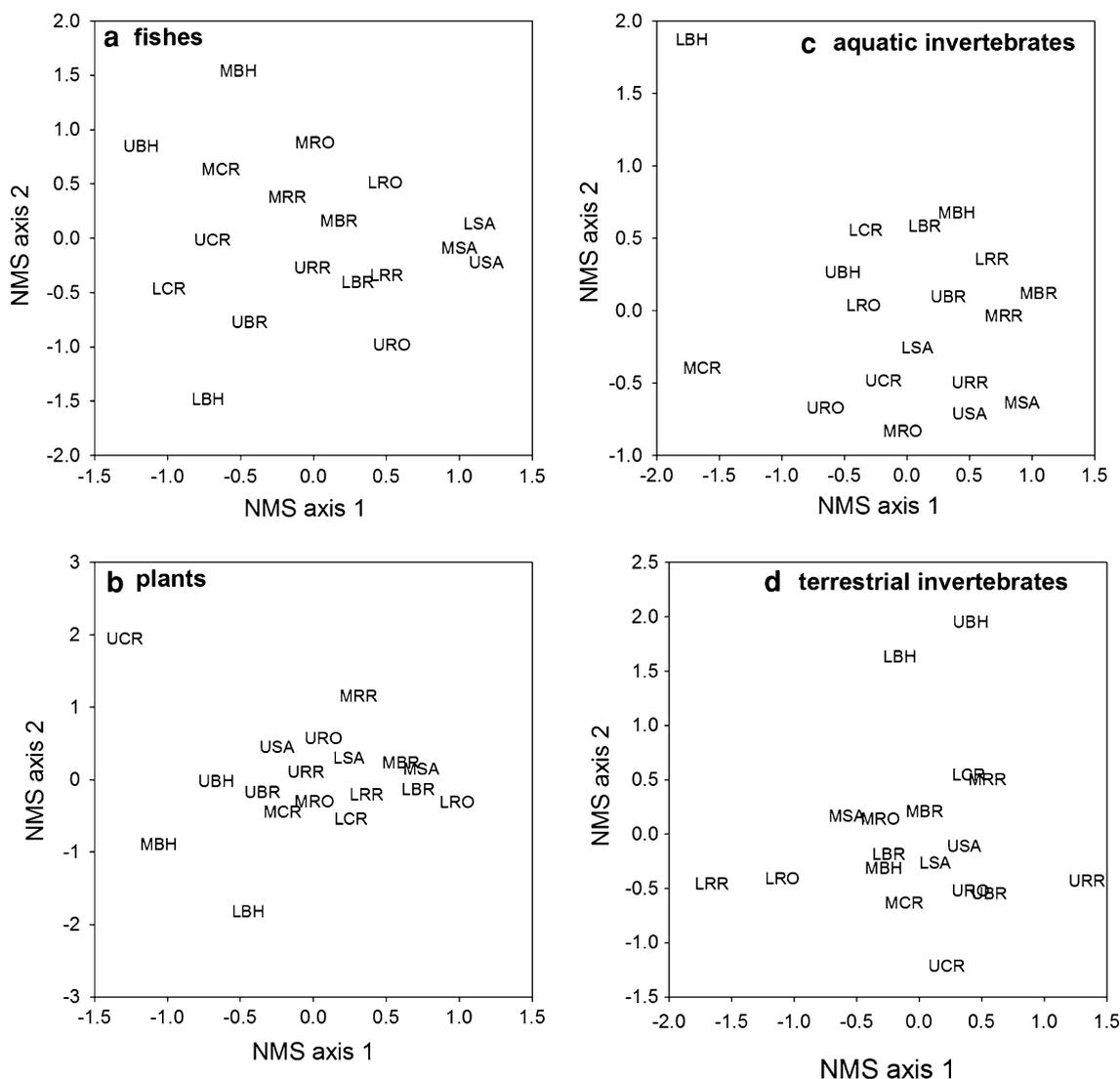


Fig. 5 Ordinations of community structure of **a** fishes, **b** plants, **c** aquatic invertebrates (D-net samples), **d** terrestrial invertebrates. The first letter of the site code gives the section of river (*L* lower, *M* middle, *U* upper), and the last two letters give the shore type (*BH* bulkhead, *BR* bedrock, *CR* cribbing, *RO* natural rock, *RR* riprap,

SA sand). The community structure of different shore types differed significantly (according to MRPP) for fish ($p = 0.001$) and aquatic invertebrates ($p = 0.008$), but not for plants ($p = 0.18$) or terrestrial invertebrates ($p = 0.15$)

related to sediment grain size and positively related to the SAV index ($R^2 = 0.81$, $p = 0.003$). Gini diversity of sediment macroinvertebrates in cores did not differ significantly across shore types, but was positively correlated with both shore zone width and site exposure ($R^2 = 0.67$, $p = 0.02$; data not shown).

We ordinated samples from each site, depth, and time separately (we had at least one sample from 14 of the 18 sites). Inspection of this ordination showed that samples from the two sampling times (May and August) fell out separately, so we re-analyzed samples from each month separately. There were no clear relationships between shore type and the ordination axes for either month (data not shown), but community structure was clearly related to

environmental characteristics, especially sediment grain size. In May, axis 1 was significantly related to exposure, the SAV index, and sediment organic content ($R^2 = 0.65$, $p = 0.0001$), while axis 2 was related to sediment grain size and organic content ($R^2 = 0.65$, $p = 0.0001$). In August, axis 2 was unrelated to measured environmental characteristics, but axis 1 was related to sediment grain size and organic content, log (shore zone width), and exposure ($R^2 = 0.61$, $p = 0.0009$).

Terrestrial invertebrates

Our samples of terrestrial invertebrates were strongly dominated by dipterans (79% of animals collected, on

average) and hemipterans (8%). Other taxa that constituted >1% of the catch included gastropods, collembolans, spiders, mites, ants, and beetles. There were no significant differences among shore types, or between natural and engineered shores, in densities of total invertebrates or of any of the taxa just named, except for mites ($p = 0.01$), or in Gini diversity of terrestrial invertebrates.

Density of terrestrial invertebrates was positively related to the SAV index ($R^2 = 0.31$, $p = 0.02$), perhaps reflecting inputs of wrack from nearby SAV beds. Densities of specific invertebrate groups were related to environmental characteristics as follows (data not shown): mites (complexity[+], logSAV[+], $R^2 = 0.44$, $p = 0.01$); beetles (log-shore zone width[-], pebble count[-], $R^2 = 0.48$, $p = 0.008$); collembolans (logSAV[+], $R^2 = 0.31$, $p = 0.02$); dipterans (logSAV[+], rugosity[-], $R^2 = 0.45$, $p = 0.01$). Densities of spiders, ants, gastropods, and hemipterans, and Gini diversity were not significantly correlated with any of the environmental features that we measured.

The ordination results separated the sampling sites partly on the basis of environmental characteristics (the two bulkhead sites near the top of Fig. 5 both are mowed lawns) and partly on the basis of geography (note the cluster of upper-river sites in the lower-right corner of the figure). Axis 1 scores were weakly related to log SAV index ($R^2 = 0.18$, $p = 0.08$), whereas axis 2 scores were not related to the environmental variables that we measured.

Gastropods

We found 20 species of freshwater and land gastropods along the Hudson's shores. The amphibious *Fossaria* sp. was most abundant, with the freshwater *Physella* sp. and *Littoridinops tenuipes* also being common and widespread. Gastropod communities were highly variable across sites, and neither abundance nor diversity (Gini index) differed significantly among shore types for subtidal or intertidal gastropods. There were significant differences across shore types for upland gastropods, however, with higher densities and diversities along sandy and rocky shores (Fig. 3). Ordinations of gastropod communities (not shown) did not clearly distinguish among shore types, although communities of flat slopes were weakly separated from those of steep slopes.

Although there were few clear differences in gastropod communities among the pre-defined shore types, high density and diversity of gastropods were consistently associated with high structural complexity of the shore zone. Abundance of subtidal gastropods was significantly correlated ($R^2 = 0.53$, $p = 0.005$) with high shoreline complexity, and abundance of intertidal gastropods was significantly correlated with high roughness ($R^2 = 0.36$,

$p = 0.009$). Gini diversity of both subtidal and intertidal gastropods was positively correlated with rugosity ($R^2 = 0.24$, $p = 0.04$; $R^2 = 0.23$, $p = 0.05$, respectively). In the upland zone, gastropod abundance was not significantly correlated with any of the environmental variables that we measured, but Gini diversity was correlated ($R^2 = 0.53$, $p = 0.004$) with pebble count (-) and exposure (+).

Discussion

Hudson River shore zones support rich biological communities. Even in a cursory survey, we found hundreds of taxa of plants and dozens of species of fishes, as well as diverse communities of terrestrial and freshwater invertebrates. The densities of aquatic invertebrates are at least twice as high as those in the rest of the river (Strayer and Smith 2001).

The Hudson's shore zones are enormously varied in terms of their physical characteristics (Table 1) and the biodiversity they support (Table 3). Much of this variation was associated with our classification of shore type, even though this classification was very simple and based only on conditions around the high-water line. Presumably, a more sophisticated classification that considered adjoining land use (e.g., forest, railroad, lawn) and intertidal and subtidal conditions (depth, particle size, submersed vegetation) more thoroughly would be even more successful in explaining variation in biodiversity.

As a class, engineered shore zones differed from "natural" shore zones (Tables 1, 2). Engineered shores were narrower (and therefore steeper), coarser-grained, and more exposed than natural shore zones. Engineered sites may have been more exposed prior to human activity (i.e., defenses were built on the most naturally exposed sites, so the engineering is a result of the naturally high exposure) or often because the shoreline was built out into deeper water or more exposed locations (i.e., the high exposure is a result of the engineering activity). Surprisingly, some of the engineered shore zones (riprap and cribbing) were rougher than many natural shores, at the scale of our roughness measurements.

Community composition of most taxonomic groups differed across shore types (Fig. 5). For the majority (13/18) of our biological attributes, there was some relationship with a physical variable that we measured (Table 4). Because we identified invertebrates only to a coarse taxonomic level, we probably underestimated the importance of shore type in determining the composition of the invertebrate community. If we had identified all of the invertebrates to species or genus, we might have seen clearer separations among the invertebrate communities of

Table 3 Summary of differences in major ecological characteristics of different types of shores along the Hudson River

	Sand	Rock	Bedrock	Riprap	Cribbing	Bulkhead	<i>p</i>
Fish diversity	77	95	95	100	100	89	0.32
Abundance of large (>20 cm long) fish	6	55	100	61	15	21	0.01
Abundance of small (<20 cm long) fish	100	12	8	17	5	1	0.0003
Species richness of native plants	100	84	90	55	45	32	0.05
Species richness of alien plants	69	67	56	78	53	100	0.64
% of plant species that are not native	42	43	37	68	53	100	0.0003
Aquatic invertebrate diversity	92	74	100	95	100	78	0.40
Aquatic invertebrate abundance	54	32	100	74	24	50	0.22
Terrestrial invertebrate diversity	58	80	40	100	48	87	0.23
Terrestrial invertebrate abundance	44	27	59	53	37	100	0.48

All variables are scaled to a maximum of 100, based on untransformed data to allow comparisons across variables (note that statistical tests usually were based on transformed data). For example, a value of 61 means that the mean value of a variable on a particular shore type was 61% of that of the maximum for any shore type. Boldface indicates variables that differed significantly among shore types. Aquatic invertebrate data are from D-net samples

Table 4 Summary of simple Pearson correlations between environmental variables and major aspects of shore zone biodiversity along the Hudson River

	Exposure	Log (shore zone width)	Pebble count	Shoreline complexity	Rugosity	Log (SAV index)	Sediment grain size	Sediment organic matter
Fish diversity				–	++			NA
Abundance of large fish			+				++	NA
Abundance of small fish	----	+++	----					NA
Fish ordination axis 1	----	+++	----					NA
Fish ordination axis 2								NA
Native plant richness						NA	NA	NA
Alien plant richness	+					NA	NA	NA
% alien plant species	+++	----	+++			NA	NA	NA
Plant ordination axis 1						NA	NA	NA
Plant ordination axis 2	----	+++	----			NA	NA	NA
Aquatic invertebrate diversity							+	--
Aquatic invertebrate abundance								
Aquatic invertebrate ordination axis 1						+		
Aquatic invertebrate ordination axis 2	+++	----	+++					
Terrestrial invertebrate diversity	+	--	+					
Terrestrial invertebrate abundance					–			
Terrestrial invertebrate ordination axis 1								
Terrestrial invertebrate ordination axis 2		–						

“Aquatic invertebrate” results are based on D-net samples

NA not applicable (i.e., the environmental variable was not included in the statistical model for that biodiversity variable)

Symbols show the direction of the relationship; the number of symbols indicates statistical significance (+++ *p* < 0.01, ++ *p* < 0.05, + *p* < 0.1)

different shore types (e.g., Lenat and Resh 2001; but see Bailey et al. 2001). Overall, we found that shore zone types supported quite different biological communities and often these could be traced to relationships between specific taxa and some physical attribute of the shore zone. For the biodiversity variables that differed significantly across

shore types (Table 3), engineered shore zones tended to have less desirable characteristics than natural shore zones: fewer fishes, fewer species of native plants, and a higher percentage of alien plants. It is worth noting that riprapped shore tended to have more desirable values for biodiversity variables than the other engineered shore types,

presumably a result of its higher physical complexity and lower wave reflectivity (cf. Pister 2009).

Nevertheless, there was a great deal of variation in biodiversity among our study sites that was not related to shore type. Even our relatively small sample (18 sites or 1.8 km out of ~300 km of shoreline) revealed large variation in both shore zone character (several to 100-fold differences) and associated biota. Some of this variation surely arose from unmeasured physical variables and a host of biotic interactions. Moreover, while it may be tempting to view relationships between shore zone attributes and biota as causal the patterns may be driven by indirect interactions or covariation with other factors. Our findings have important implications for management or design of shore zones capable of supporting higher biodiversity but in our desire to encompass as much of the range in shore zone function as possible we could not explore these mechanistic linkages.

Not surprisingly, no single shore type provides high values of all ecological functions (Table 3). Wide, sandy, dissipative shores support many small fishes and a high proportion of native plant species, but few large fishes. Thus, no shore zone maximizes all kinds of biodiversity.

Our study sites can be broadly arranged according to their physical characteristics along the two axes of exposure and complexity (Fig. 2). Both of these dominant physical axes appear to affect shore zone biodiversity. Community composition varies along the first axis (defined by the related variables of exposure, sediment grain size, shore zone slope, and shore zone width), as shown both by the ordinations and the responses of individual taxa such as small fishes (which avoid highly exposed shores) and zebra mussels (which favor highly exposed shores). The association between alien plants and high exposure and engineered shorelines may result from the ability of alien plants to exploit disturbed sites (e.g., Davis et al. 2000). The second axis of physical complexity (expressed by variables such as substrate roughness or shoreline complexity) may generally favor high biodiversity (Fig. 4; Barwick 2004; Brauns et al. 2007; Paetzold et al. 2008; Pollock et al. 1998; Sass et al. 2006; Strayer and Findlay 2010). We suggest that these two physical axes (exposure and complexity) may generally be useful in explaining variation in predicting the species composition, diversity, and dominant ecological traits of shore zone communities.

Although we were able to point to the importance of exposure to shore zone communities, scientists and managers will need to develop faster, easier, more reliable, and more standardized ways of measuring “exposure”, which up to this point has often been treated as a narrative variable or simply assumed to be related to fetch (e.g., Keddy 1982; Brodersen 1995; Ekeboom et al. 2003). When we say “exposure”, do we mean average wave force, peak wave

force, peak forces of any kind (whether wave or ice-push), or all of the preceding? How do we reliably measure these forces so we can compare across studies?

Clearly, our results present only a broad and preliminary assessment of how the biological communities of shore zones vary according to their physical characteristics and human engineering. Nevertheless, even at this early stage in our investigations, we can offer the following suggestions for shore zone management. Because biotic communities consistently vary along the gradient between wide, sheltered, fine-grained shore zones and narrow, exposed, coarse-grained shore zones, it seems important to preserve or restore a mix of shore types all along this gradient, at least to the extent that they occurred naturally. In particular, the common trend to replace wide, sheltered shore zones with narrow, exposed shore zones (Strayer and Findlay 2010) may require special protection for the former to preserve biodiversity in intensively developed waterways. At a finer scale, biodiversity often is enhanced by local roughness and heterogeneity (e.g., Barwick 2004; Brauns et al. 2007; Paetzold et al. 2008; Pollock et al. 1998; Strayer and Findlay 2010). Thus, the common tendency to destroy such local heterogeneity by using uniform building materials, smooth grades, and straight-line designs may have strongly negative consequences for shore zone biodiversity, and should be avoided.

We suggest two lines of future research that should be useful in achieving the level of understanding needed to manage shore zone biodiversity well. First, comparative field investigations like our study might be focused more tightly on a particular type of shore zones (e.g., riprapped shores) or a particular taxonomic or functional group. This tighter focus would allow for use of sampling techniques that are especially well-suited to that shoreline type or taxonomic group, sampling designs well-matched to the taxonomic group (e.g., seasonal or diurnal sampling), and finer levels of identification or analysis (e.g., body size or condition). Ultimately, this tighter focus should lead to higher resolution, lower variance, and increased statistical power to detect differences among shore types or along environmental gradients of interest.

Second, it would be very valuable to conduct large-scale field experiments to test how factors that we have identified as potentially important might affect shore zone biodiversity. An experimental approach would allow a much stronger test of the effects of characteristics that are especially amenable to management intervention (e.g., size of riprap, slope of revetments, roughness of bulkheads). As others have suggested (e.g., Doyle et al. 2008), it may be possible to include such experiments in the construction of new shore zone defenses or the repair of aging shore zone infrastructure.

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