Freshwater Biology (2006) **51,** 25–38 doi:10.1111/j.1365-2427.2005.01472.x

Using geophysical information to define benthic habitats in a large river

DAVID L. STRAYER,* HEATHER M. MALCOM,* ROBIN E. BELL,† SUZANNE M. CARBOTTE† AND FRANK O. NITSCHE†
**Institute of Ecosystem Studies, Millbrook, NY, U.S.A.*
†Lamont-Doherty Earth Observatory of Columbia University, Palisades, NY, U.S.A.

SUMMARY

1. Most attempts to describe the distribution of benthic macroinvertebrates in large rivers have used local (grab-scale) assessments of environmental conditions, and have had limited ability to account for spatial variation in macroinvertebrate populations.
2. We tested the ability of a habitat classification system based on multibeam bathymetry, side-scan sonar, and chirp sub-bottom seismics to identify large-scale habitat units ('facies') and account for macroinvertebrate distribution in the Hudson River, a large tidal river in eastern New York.
3. Partial linear regression analysis showed that sediment facies were generally more effective than local or positional variables in explaining various aspects of the macroinvertebrate community (community structure, density of all invertebrates, density of fish forage, density of a pest species – *Dreissena polymorpha*).
4. Large-scale habitats may be effective at explaining macroinvertebrate distributions in large rivers because they are integrative and describe habitat at the spatial scales of dominant controlling processes.

Keywords: heterogeneity, Hudson River, patchiness, zoobenthos

Introduction

One of the central goals of ecology is to understand the characteristically patchy distribution of species. Describing and understanding the patchiness of benthic animals in large rivers has been especially difficult. This difficulty stems in part from the scarcity of studies on the benthos of large rivers (e.g. Hynes, 1989; Vinson & Hawkins, 1998), which are more difficult to study than smaller rivers and streams. However, the studies that have been carried out on the benthos of large rivers often have been ineffective at relating benthic animal distributions to such commonly measured environmental variables as sediment grain size and organic content (e.g. Haag & Thorp, 1991; Schönbauer, 1998; Seys, Vincx & Maire, 1999; Strayer & Smith, 2001). For instance, multiple regressions between population densities of benthic animal species and sediment grain size in the Hudson River typically have coefficients of determination (R^2) < 0.2 (Strayer & Smith, 2001).

One possible difficulty with these traditional approaches is that they rely solely on local (grab-scale) assessments of environmental conditions, without considering the broader environmental setting. In contrast, studies of benthic animals in smaller streams commonly consider the broad environmental setting (e.g. riffle, pool, run, point bar) as well as local conditions, which adds much to our understanding of benthic animal distributions in these habitats (e.g. Hawkins *et al.*, 1993; Thomson *et al.*, 2001; Rabeni, Doisy & Galat, 2002). Likewise, ecological studies in other habitats usually consider the setting from which the sample was taken (e.g. the slope, aspect, and vegetation in a forest). Because benthic samples in large rivers usually are taken remotely (with grabs or

Correspondence: David L. Strayer, Institute of Ecosystem Studies, PO Box AB, Millbrook, NY 12545, U.S.A.
E-mail: strayerd@ecostudies.org

cores), there has been little opportunity to observe the broad setting from which they are taken. As remote imaging technology improves, though, ecologists will have increased opportunities to describe the settings from which small samples are taken. Will this contextual information improve our ability to predict the distribution of benthic animals in large rivers? Here, we test whether sophisticated geophysical images of environments at the bottom of the Hudson River improve our ability to understand patchiness in benthic animal populations.

Methods

Study area

The study area was an 18.5 km reach of the freshwater tidal Hudson River between Kingston and Saugerties, New York State, corresponding to section A3 of Bell *et al.* (2000). Mean channel width is 1.3 km, and water depth and sediment type are highly variable (Fig. 1). During the growing season, the water is moderately turbid (Secchi disk, 1–2 m), hard (Ca, 27 mg L^{-1}), and nutrient-rich (NO^3-N, 0.5 mg L^{-1}; PO^4-P, 11 μg L^{-1}; Caraco *et al.*, 1997). Despite the strong tidal currents that reverse direction every 6 h, there is no trace of sea salt in the study reach. The organic carbon budget of the reach is dominated by allochthonous inputs (Howarth, Schneider & Swaney, 1996), but phytoplankton and macrophyte production are substantial and ecologically important (Cole & Caraco, in press). The zoobenthos of the freshwater tidal Hudson contains >200 species, and is numerically dominated by tubificid oligochaetes, amphipods, chironomid midges and bivalves (Simpson *et al.*, 1986; Strayer & Smith, 2001). Zebra mussels (*Dreissena polymorpha*) appeared in 1991, and are now abundant throughout the freshwater tidal Hudson (Strayer *et al.*, 1996).

Site selection

Bell *et al.* (2000) used multibeam bathymetry, side-scan sonar, chirp sub-bottom seismics, sediment cores and grabs during November 1998 to May 1999 to identify 14 major classes of sediments in the study reach (Fig. 1). These classes differ from one another in position in the channel (open channel versus margin), sediment grain size, surface relief, mobility and depositional or erosional status. We will refer to these classes of sediments as 'sediment facies.' Areas of two facies (coarse marginal deposits and bridge scour areas) were too small for us to sample using our criteria for site selection (see below). In addition to having small areas, three of the facies (bedrock, cable crossing and ship wrecks) could not be sampled using the gear chosen for unconsolidated sediments. Nine facies remained (Table 1), and we used a stratified random design to select five stations in each sediment facies, giving a total of 45 sampling sites. All sampling sites were chosen to be at least 50 m inside the edge of the patch of each sediment facies, as mapped by Bell *et al.* (2000).

Sediment profile imaging

Sediment profile imaging (SPI) is widely used in marine ecology to characterise conditions at the sediment-water interface (e.g. Nilsson & Rosenberg, 2000), but has not been used widely in fresh water. In SPI photography, a weighted camera is lowered a few cm into the sediment to take a picture of the sediment-water interface. Such pictures can show sediment grain size, sediment redox conditions, surface microtopography, and biogenic features such as tubes, burrows or shells. SPI images were taken at the sampling locations on 13 September 2001 by Science Applications International Corporation (SAIC) (2001). Global positioning system (GPS) readings and water depths were taken at the actual locations of the SPI photography. SPI images were not taken at the five 'marginal flats' sites because the water was too shallow to allow safe access by the ship. SAIC (2001) carried out a preliminary analysis of the images, and we then analysed them further.

Animal and sediment sampling

Sites were sampled for animals and sediments in September 2001 and again in May 2002. Using a Trimble TSC1 Asset Surveyor GPS unit, sampling stations were matched as closely as possible (<18 m) to the actual sites of SPI photography. At each station, we took three samples with a petite PONAR grab (15 × 15 cm), lowering the grab slowly (<1 m s^{-1}) to the sediment surface to avoid creating a pressure wave. We pooled the three samples, and in May we removed a small subsample (approximately 10 mL) for sediment analysis. This subsample was refrigerated immediately, and frozen upon return to the

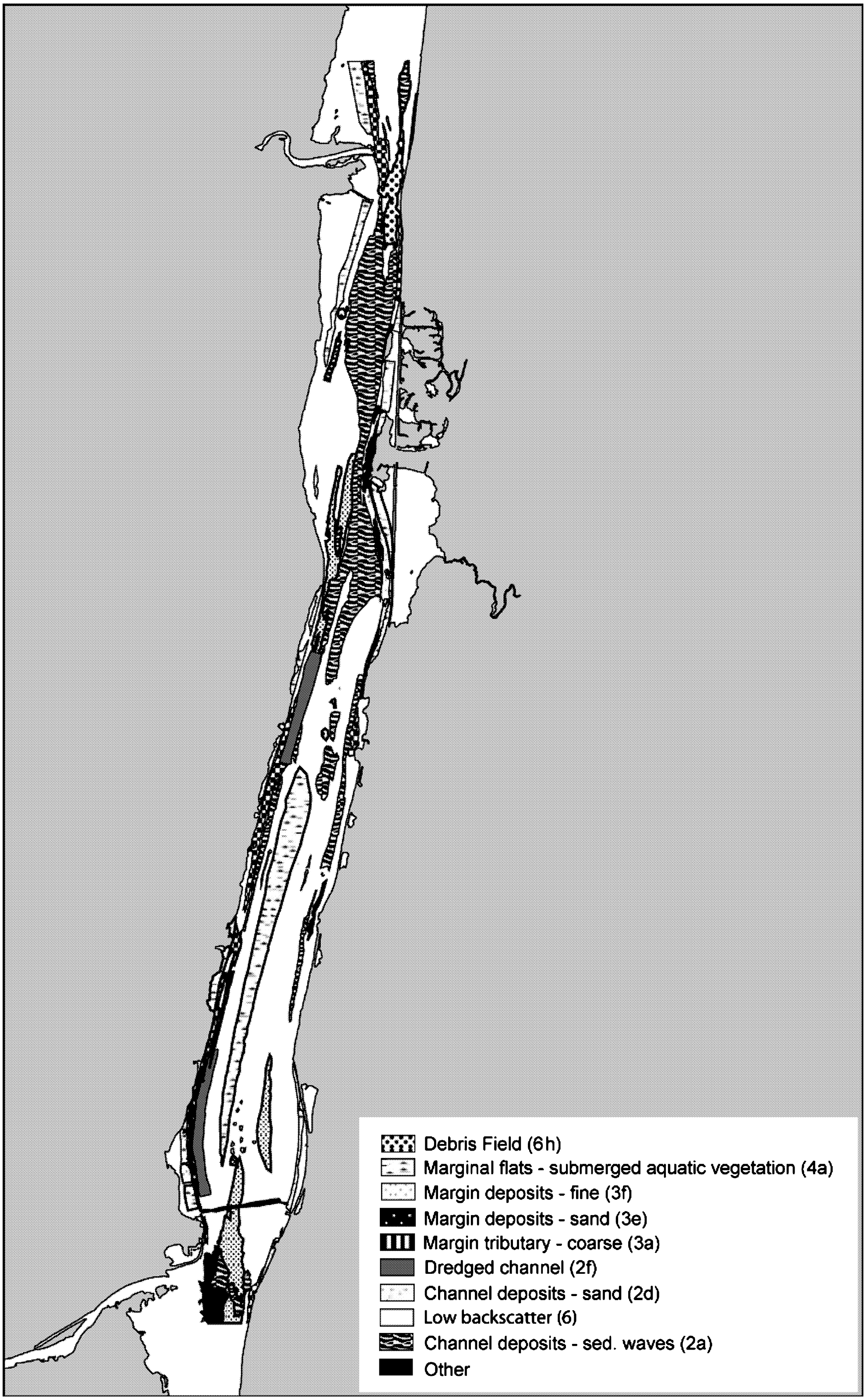

Fig. 1 Map of the study area showing sediment facies and bathymetry.

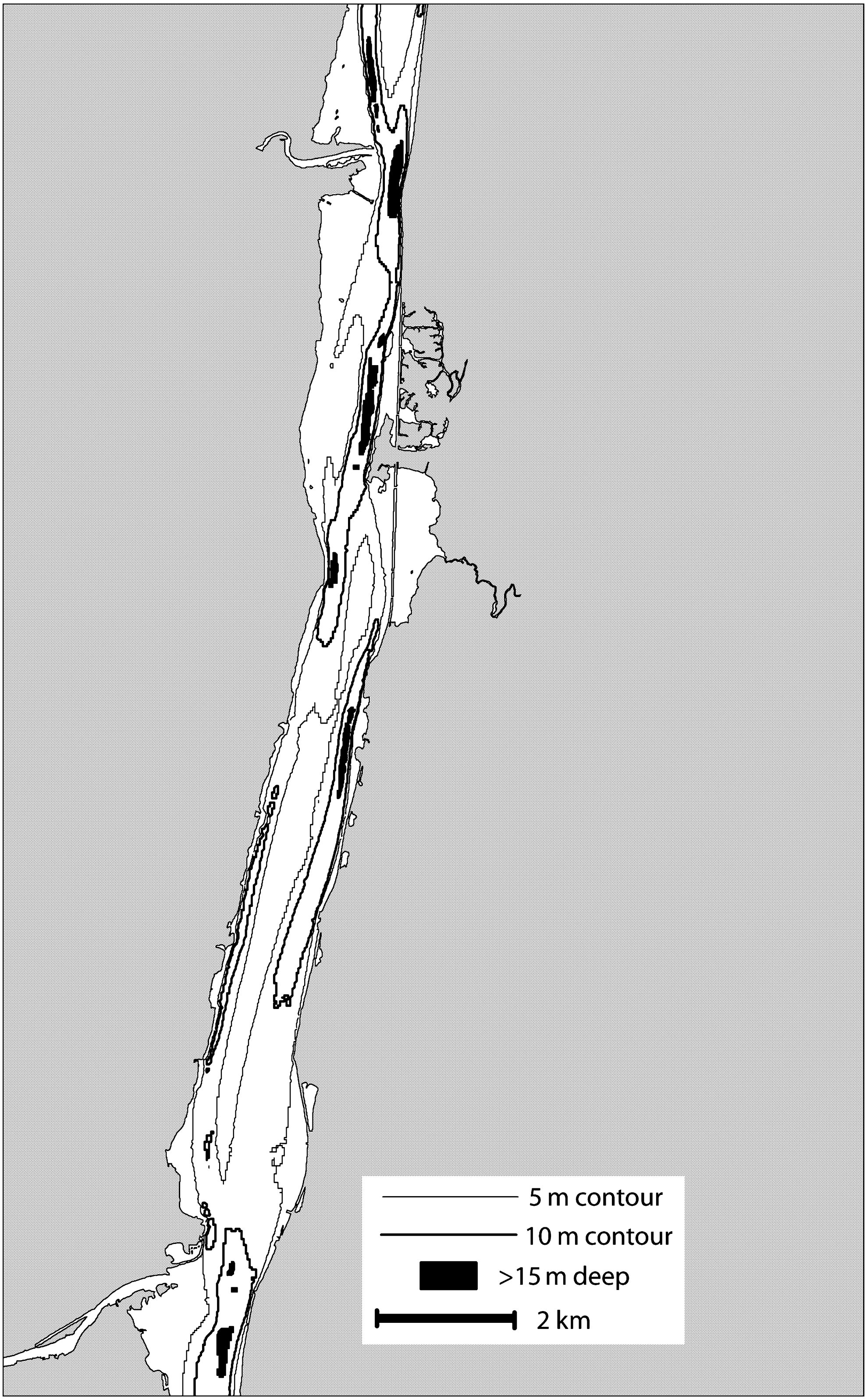

Fig. 1 *(Continued)*

Table 1 Major sediment facies sampled in the present study, as identified by Bell *et al.* (2000)

Channel sediment waves (2a, 'wave')
Channel deposits – sand (2d, 'sand')
Dredged channel (2f, 'dredge')
Margin tributary – coarse (3a, 'trib')
Margin – sand (3e, 'msand')
Margin – fine (3f, 'mfine')
Marginal flats (4a, 'mflats')
Low backscatter (6, 'low')
Debris fields (6h, 'debris')

laboratory. The remaining sample was sieved in the field through a 0.5-mm mesh sieve and preserved in 10% buffered formalin.

In the laboratory, faunal samples were sorted under 6× magnification, sometimes after staining overnight in Rose Bengal. Animals were counted, removed from the samples, and placed into 10% formalin, 70% ethanol, or Koenike's fluid (Peckarsky *et al.*, 1990) for long-term storage. At least 20% of the samples were picked twice to allow for calculation of sorting efficiency using the removal method (Zippin, 1958). Subsamples of preserved animals (20 animals per sample for chironomids and oligochaetes, 10 animals per sample for nematodes) were slide-mounted and identified to genus or species; the proportion of each species in the full sample was assumed to be the same as in the subsamples. To account for fragmentation of oligochaetes, we counted only specimens that had a head. Sources used for identification and nomenclature include Thorne & Swanger (1936), Hyman (1959), Gosner (1971), Bousfield (1973), Andrassy (1981, 1988), Wiederholm (1983), Pennak (1989), Peckarsky *et al.* (1990), Smith (1995), Merritt & Cummins (1996), Wiggins (1996), Kathman & Brinkhurst (1998), Thorp & Covich (2001) and Epler (2001). Because this study does not focus on seasonal variation in macroinvertebrate communities, we pooled the data from the two sampling times, and ran all of our analyses on the average of spring and autumn samples.

Sediment samples were thawed, then analysed for grain size distribution by the hydrometer method (Gee & Bauder, 1986). Organic content was estimated by loss on ignition after at least 4 h at 500 °C.

Statistical analyses

Our statistical analyses were designed to test the relative effectiveness of different explanatory variables (especially sediment facies) in explaining sample-to-sample variation in characteristics of the macroinvertebrate community. We used partial linear regression (Legendre & Legendre, 1998, pp. 528–533) to quantify the strength of relationships between explanatory variables and selected characteristics of the macroinvertebrate community. Partial linear regression is useful in cases where there are multiple predictor variables, to separate out the unique and shared effects of each predictor variable. Here, we used partial linear regression to identify the unique and shared effects of three major classes of predictor variables: local environmental conditions (sediment grain size and organic content, and water depth at the sampling site; i.e. variables traditionally used to explain macroinvertebrate distribution in large rivers), sediment facies and sampling position. Partial linear regression is especially appropriate here because the predictor variables are correlated with one another through their spatial structures.

An additional complication that arises when testing these ideas is that the spatial structure of benthic animal communities must be taken into account. Both local environmental conditions and sediment facies are spatially structured; i.e. two sites near to one another are likely to have similar local environmental conditions and belong to the same sediment facies. Many other factors are similarly likely to produce spatially structured benthic animal communities as well. Any analysis of the ability of local environmental variables or sediment facies to explain benthic animal communities must take into account spatial structuring in benthic animal communities that is unrelated to local environmental conditions and sediment facies. The 'position' variable in the partial linear regressions and partial canonical analysis represents such spatial variation.

We modelled spatial variation in response variables using trend surface analysis (Legendre & Legendre, 1998, pp. 739–746). We expressed sampling locations in decimal latitude and longitude and centred them on their mean values, then calculated all possible first-, second- and third-order combinations of these centred positional variables. Each response variable was regressed against all possible combinations of these nine positional variables; we selected the regression model with the lowest value of the corrected Akaike Information Criterion (AIC^c). The positional variables appearing in this selected regression model were then used in subsequent analyses.

The characteristics of the macroinvertebrate community that we modelled using this approach were the total density of macroinvertebrates; macroinvertebrate community structure (as measured by ordination scores – see below); the density of an important pest species (the zebra mussel, *D. polymorpha*); and the density of valuable 'fish forage.' We defined fish forage as the summed densities of all insects and macrocrustaceans, which are important fish food (Strayer & Smith, 2001). There is relatively little difference in body mass among common crustacean and insect species in the Hudson (Strayer, unpublished), so forage density is proportional to forage biomass. We chose these four attributes because they are of ecological interest and provide a diverse set of response variables against which to test the utility of geophysically defined sediment facies.

We used non-metric multidimensional scaling to summarise community structure, following the recommendations of McCune & Grace (2002). Macroinvertebrate densities were fourth-root transformed, and taxa present in fewer than three samples were omitted prior to analysis. We used the autopilot mode in PC-ORD, which recommended a two-dimensional description of community structure.

Results

General description of invertebrate communities

We identified 58 taxa of macroinvertebrates in the samples. Because a few animals were not identified to species, true species richness in our samples was probably a little higher than this. As has been reported previously for the freshwater tidal Hudson (Simpson *et al.*, 1986; Strayer & Smith, 2001), the community was numerically dominated by tubificid oligochaetes, amphipods, chironomid midges and bivalves (especially *D. polymorpha*). Overall macroinvertebrate density in the study area (4830 m^{-2}) was low, reflecting the generally sparse macroinvertebrate communities of unvegetated sediments in the Hudson after the zebra mussel invasion (Strayer & Smith, 2001).

Invertebrate communities differed conspicuously among the different sediment types. Overall density of macroinvertebrates was 2.5 times as high in the marginal flats as in the marginal fine deposits (Fig. 2).

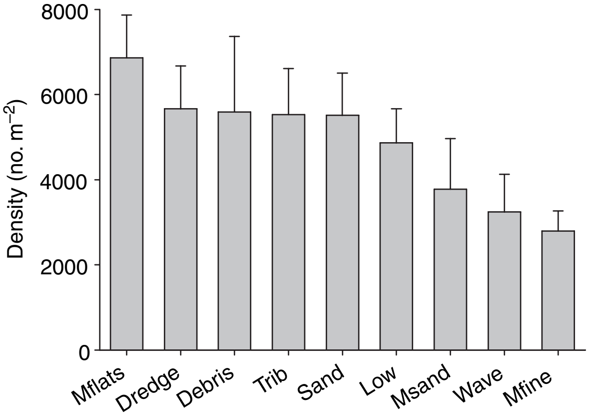

Fig. 2 Density of macroinvertebrates (±SE) in the different sediment facies (mean of two sampling periods). See Table 1 for abbreviations.

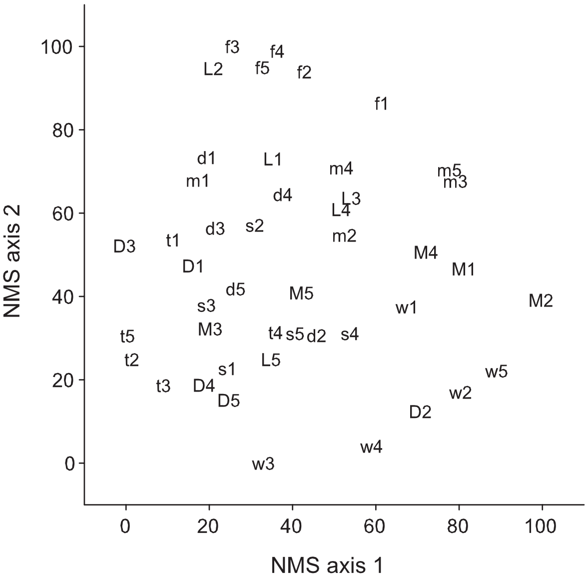

Fig. 3 Non-metric multidimensional scaling ordination of the mean data from the two sampling periods. Species found in fewer than three sites were omitted from the ordination. Final stress = 15.98 ($P < 0.01$). The five samples from each facies are labelled as follows: D, debris fields; d, dredged channel; f, marginal flats; L, low backscatter; M, margin – fine; m, margin – sand; s, channel deposits – sand; t, margin tributary – coarse; w, channel sediment waves.

Further, different kinds of invertebrates inhabited the different sediment types. An ordination of the species data showed that samples taken from the same sediment type tended to cluster together (Fig. 3). Differences among the different sediment types were apparent even from inspection of a simple table

Table 2 Mean density (no. m^{-2}) of common invertebrates (those with a mean density >10 m^{-2}) in each of the sediment types. Sediment types are listed in the same order as in Fig. 2 (highest to lowest total macroinvertebrate density). Note the generally diagonal arrangement of numbers in the table, showing that community structure shifts along this density gradient.

Species	Flats	Dredge	Debris	Tributary	Sand	Low	Marginal sand	Wave	Marginal fine
Idiodorylaimus novazealandiae (Cobb)	218	0	0	0	0	0	0	0	2
Aulodrilus americanus Brinkhurst & Cook	407	9	0	0	0	0	20	0	0
Chironomus decorus gr. sp.	455	0	0	3	0	0	11	0	0
Pisidium sp.	458	52	0	17	6	40	77	0	2
Dorylaimus cf. *stagnalis* Dujardin	151	1	0	6	2	0	27	0	4
Coelotanypus scapularis (Loew)	399	30	0	58	6	20	61	0	8
Procladius (*Holotanypus*) sp.	65	0	0	6	0	22	0	0	10
Ilyodrilus templetoni (Southern)	61	10	0	4	13	0	7	0	0
Limnodrilus hoffmeisteri Claparède	1019	728	81	211	390	409	483	15	130
Immature Tubificidae without hairs	2939	2270	928	548	979	2617	1312	348	458
Paralauterborniella nigrohalterale (Malloch)	12	19	0	3	5	31	32	0	32
Harnischia curtilamellata (Malloch)	5	4	0	16	5	8	44	0	9
Immature Tubificidae with hairs	113	10	7	12	56	23	29	0	17
Limnodrilus udekemianus Claparède	0	33	34	7	55	166	62	0	55
Hydrolimax grisea Haldeman	43	76	37	37	13	53	49	37	24
Cryptochironomus sp.	44	49	3	9	13	90	58	33	61
Ceratopogonidae	20	5	4	13	3	11	36	1	24
Tanytarsus sp.	94	21	5	21	26	30	50	11	131
Potamothrix moldaviensis Vejdovsky & Mrazek	0	10	0	0	11	54	0	11	0
Oecetis inconspicua (Walker)	0	5	6	26	0	3	59	0	68
Dreissena polymorpha (Pallas)	27	12	113	1099	481	283	747	2	26
Gammarus tigrinus Sexton	64	1906	3313	3085	1898	587	489	576	1128
Cyathura polita (Stimpson)	1	111	158	66	216	41	35	11	393
Isochaetides freyi (Brinkhurst)	0	0	0	4	22	14	27	18	94
Potamothrix vejdovskyi (Hrabě)	0	0	4	0	7	0	0	0	38
Dicrotendipes neomodestus (Malloch)	0	0	16	78	13	6	6	0	5
Chiridotea almyra Bowman	2	14	6	9	41	13	2	24	4
Polypedilum halterale gr. sp.	94	269	816	116	886	309	18	2066	22
Piguetiella michiganensis Hiltunen	0	0	2	2	0	0	0	103	0

giving the dominant species found in the samples (Table 2). For example, *Idiodorylaimus novazealandiae* (Nematoda), *Aulodrilus americanus* (Oligochaeta), and *Chironomus decorus* group species (Diptera) were abundant in the marginal flats but scarce elsewhere, whereas *Polypedilum halterale* group species (Diptera) and *Piguetiella michiganensis* (Oligochaeta) were especially abundant in samples from sediment waves.

The sediment types and their animal communities

Although there was a 3-year gap between the geophysical mapping and the biological sampling, there was no indication of major shifts in the distribution of sediment facies in the study reach during that time. The SPI images and sediment samples taken in 2001 and 2002 showed sediments consistent with the descriptions of Bell *et al.* (2000), and two transects (bathymetry and side-scan sonar) run in 2000–2002 did not show any evidence for major changes in facies distribution (Bell *et al.*, unpublished data). The facies and their animal communities are described briefly below.

Marginal flats. These are very shallow-water areas that support submersed vegetation (chiefly *Vallisneria americana* Michx.) during the growing season. The largest such area is in mid-channel beneath the Kingston-Rhinecliff Bridge, but scattered areas occur elsewhere in the study area (Fig. 1). Sediments have the highest content of silt and organic matter of any of the sediment types that we sampled (Table 3).

Previous studies have shown that shallow-water, vegetated areas in the Hudson support dense and species-rich communities of benthic invertebrates (Strayer & Smith, 2001; Strayer *et al.*, 2003). Not

Table 3 Environmental characteristics at the sample sites. Values are means, with ranges in parentheses.

Sediment type	Water depth (m)	Loss on ignition (%)	% sand	% silt	% clay
Marginal flats	1.3 (1.1–1.6)	5.3 (4.6–6.5)	21 (17–24)	58 (46–67)	21 (17–24)
Dredged channel	12.1 (11.5–12.5)	3.7 (2.3–6.4)	79 (28–95)	14 (2–50)	7 (2–22)
Debris field	19.6 (17.4–21.9)	2.4 (0.9–4.0)	94 (86–98)	4 (0–10)	2 (0–4)
Margin tributary – coarse	14.2 (10.5–16.8)	2.7 (0.8–6.0)	71 (19–94)	20 (4–52)	9 (1–29)
Channel deposits – sand	14.3 (12.7–15.8)	2.0 (1.2–2.6)	93 (89–98)	4 (0–6)	3 (1–6)
Low backscatter	5.9 (3.7–9.0)	3.2 (1.2–6.3)	64 (31–93)	28 (4–50)	9 (2–19)
Margin – sand	5.1 (3.5–7.6)	2.4 (1.8–2.8)	61 (40–74)	27 (19–41)	12 (7–19)
Channel sediment waves	8.2 (4.8–11.8)	0.8 (0.6–1.3)	96 (91–100)	3 (1–7)	1 (0–2)
Margin – fine	6.8 (4.1–8.9)	4.2 (3.8–5.0)	28 (14–44)	50 (38–56)	22 (18–30)

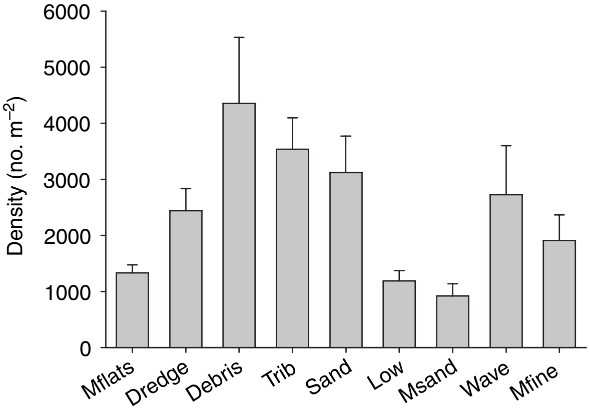

Fig. 4 Density of forage invertebrates (insects plus macrocrustaceans) (±SE) in the different sediment facies (mean of two sampling periods). See Table 1 for abbreviations.

surprisingly, we found the highest density of benthic invertebrates in this sediment type (Fig. 2), including many species that were scarce or absent from other sediment types (e.g. the first eight species in Table 2). Despite the high overall abundance of invertebrates, taxa important as fish food were relatively scarce in the marginal flats (Fig. 4).

Dredged channel. Small areas of the navigational channel are maintained by periodic dredging (Fig. 1). The sediments in this area are mostly very sandy, but vary from site to site (Table 3). The SPI images show coarse, oxidised sand overlying finer reduced sediments; some images show surface features a few centimetres high. Samples taken from this sediment type had surprisingly dense and diverse communities of benthic animals (Fig. 2; Table 2). No animal species was especially closely associated with the dredged channel, however.

Debris fields. These sediments are thought to contain coarse material from human activities, and occur chiefly in very deep water just south of Esopus Creek (Fig. 1). We could not recover the coarsest material in our grab samples, but the sediments we were able to collect were very sandy (Table 3). SPI images show muddy sand containing various amounts of small stones, clinkers, coal and zebra mussel shells. Samples taken from debris fields contained moderately dense invertebrate populations, including high numbers of the crustaceans *Gammarus tigrinus* and *Cyathura polita* (Table 2), which are valuable food for many fish in the Hudson (Strayer & Smith, 2001). In fact, this facies had the highest density of forage invertebrates of any part of the study area (Fig. 4).

Margin tributary – coarse. These sediments are arrayed in narrow bands off the mouths of major tributaries (Fig. 1; Bell *et al.*, 2000). Granulometry and organic content are very variable within this sediment type, and the SPI images show sediments ranging from mud to muddy sand with pebbles and zebra mussel shells. This sediment type contained very high densities of the zebra mussel (*D. polymorpha*) and the amphipod *G. tigrinus* (Fig. 5; Table 2), presumably as a result of the availability of relatively coarse sediments for shelter and settlement (e.g. Mellina & Rasmussen, 1994).

Channel deposits – sand. These are sandy sediments of low organic content (Table 3), but without obvious bedforms. SPI images do show some low (<10 cm high) waves, as well as shells of zebra mussels and unionids embedded in sand. This sediment type is widespread in the study area (Fig. 1). Channel sands supported moderately dense invertebrate communi-

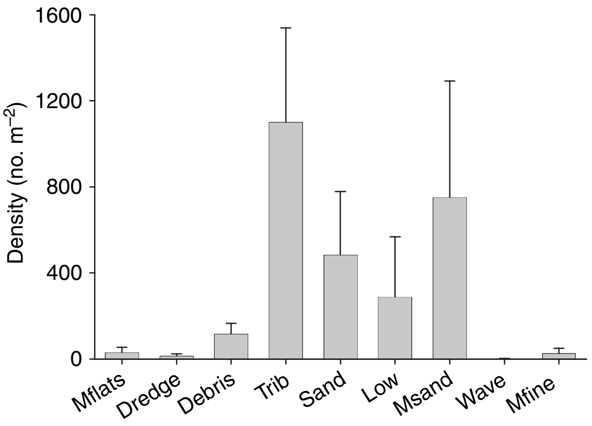

Fig. 5 Density of zebra mussels (±SE) in the different sediment facies (mean of two sampling periods). See Table 1 for abbreviations.

ties, especially zebra mussels and crustaceans (Fig. 5; Table 2).

Low backscatter. This sediment type, which was defined by Bell *et al.* (2000) as an area of low sidescan sonar backscatter with no distinctive bedform or grain size, covers most of the southern half of the study area (Fig. 1). Water depth, sediment grain size and organic content all vary widely within this sediment type (Table 3). SPI photos show fine-grained sediments, sometimes with gas bubbles, usually without shells or surface features. Areas of low backscatter supported animal communities of average density and composition (Figs 2 and 3), with tubificid oligochaetes perhaps more abundant than in other sediment types (Table 2). Forage invertebrates were scarce (Fig. 4).

Margin – sand. Small bands of this sediment type occur along the river margins (Fig. 1). Water depth is moderate, and sediments have a fairly high content of silt and clay (Table 3). SPI photos show muddy sands, occasionally with a few shell fragments. Marginal sands support a diverse but somewhat sparse invertebrate community, including some species that are typical of vegetated, shallow-water sediments (Table 2). Zebra mussels were relatively abundant in this facies (Fig. 5), but forage invertebrates were scarce (Fig. 4).

Channel sediment waves. These sediments are nearly pure sand with very low organic content (Table 3) with waves up to 3 m high (Bell *et al.*, 2000). The waves are thought to be moving (Bell *et al.*, 2000), so this is an unstable environment for long-lived sediment-dwelling animals. SPI photos of these sediments show coarse sand with a few shells, and obvious surface waves. This sediment type covers much of the northern part of the study area (Fig. 1). The invertebrate community of this sediment type was sparse and strongly dominated by a single species of chironomid (*P. halterale* group species), which constituted 64% of all macroinvertebrates in our samples from sediment waves (Table 2). *Piguetiella michiganensis*, a naidid oligochaete, was also strongly associated with this sediment type.

Margin – fine. A narrow band of this sediment type occurs along and just south of Tivoli South Bay in water of moderate depth (Fig. 1). The sediments are predominately silty, but contain substantial clay, sand and organic matter. The SPI photos show fine-grained sediments, sometimes veneered with sand, and sometimes containing gas bubbles. Unlike other shallow-water, marginal habitats, macroinvertebrate density was low in this sediment type (Fig. 2). No animal species was closely associated with this sediment type, although the chironomid *Tanytarsus* sp., the isopod *C. polita*, and the caddisfly *Oecetis inconspicua* were relatively abundant there (Table 2).

Are geophysical data useful in explaining patchiness in benthic animal communities?

For geophysical data to be useful to benthic ecologists, they must either replace or supplement the traditionally used data on local environmental conditions. That is, geophysically defined facies could be used *in place of* variables like grain size to define the habitats in which benthic invertebrates live. Such a replacement will be useful if geophysical data are less expensive or more readily available than local environmental data, or if the relationships between the benthos and sediment facies are stronger than those between benthic animals and local (i.e. sample-scale) environmental conditions. Alternatively, benthic ecologists could *add* geophysical data to local data to improve our understanding of benthic animal communities. The test of the utility of geophysical data in this case is the extent to which our understanding (say model R^2) improves when geophysical information is added to local environmental data as predictors of benthic animal communities.

Density of macroinvertebrates. Local environmental conditions (sediment grain size and organic content, water depth) were only modestly successful in explaining macroinvertebrate density ($r^2 = 0.24$, $P = 0.024$ for 4th-root transformed density). The only effective local environmental variable was sediment organic content, which was weakly and positively related to macroinvertebrate density. Sediment facies alone explained about the same amount of variation in macroinvertebrate density ($r^2 = 0.26$, $P = 0.17$). All variables considered together accounted for 51% of the variation in macroinvertebrate density (Table 4). Adding sediment facies to models already containing local environmental variables and sampling position accounted for an additional 14% of variation in macroinvertebrate density.

Macroinvertebrate community composition. Models of community structure based on local environmental variables, specifically water depth and sediment organic content, had high R^2 (Table 4). As suggested by Fig. 3, sediment facies was also closely related to variation in macroinvertebrate community structure. Correlations between sediment facies alone and the ordination axes had R^2 of 0.6–0.8 (Table 4). Much of the explained variation in macroinvertebrate community structure was shared among local, facies and positional variables (Table 4). Nevertheless, adding sediment facies to models based on sampling position and local environmental conditions increased R^2 by 0.11–0.17.

Zebra mussel density. Local environmental variables (grain size, organic content, water depth) were ineffective at predicting zebra mussel density (after fourth-root transformation; $r^2 = 0.10$, $P = 0.38$). In contrast, sediment facies was strongly related to zebra mussel density (Fig. 5; $r^2 = 0.51$, $P = 0.0005$). In the full model, sediment facies increased the explained amount of variation in zebra mussel density by 42%, far more than other classes of variables (Table 4).

Density of forage invertebrates. Local environmental conditions were fairly effective in predicting the density of forage invertebrates ($r^2 = 0.47$, $P = 0.00004$, after fourth-root transformation), almost entirely as a result of a strong positive correlation between forage density and water depth. Sediment facies also were a good predictor of forage density. When used by itself as a predictor, sediment facies accounted for 50% ($P = 0.0008$) of the variation (after fourth-root transformation) in the density of forage invertebrates. A combined model using local environmental conditions, position within the study area, and sediment facies accounted for 74% of the variation in forage invertebrate density (Table 4), about half of which was explained jointly by all three classes of variables. Sediment facies uniquely accoun-

Table 4 Proportion of variance in different attributes of the Hudson River macroinvertebrate community (total macroinvertebrate density after fourth-root transformation, macroinvertebrate community structure as expressed by NMS axes, zebra mussel density after fourth-root transformation, and forage invertebrates after fourth-root transformation) explained by sediment facies, local environmental conditions (sediment grain size and organic content), and position

	Total density	NMS axis 1	NMS axis 2	Zebra	Forage
Full model R^2	0.51	0.87	0.78	0.62	0.74
Facies (total)	0.26	0.79	0.60	0.51	0.50
Facies alone	0.14	0.11	0.17	0.42	0.14
Shared facies + local	−0.08	0.12	0.01	−0.06	−0.04
Shared facies + position	0.07	0.13	0.04	0.10	0.05
Shared facies + local + position	0.12	0.43	0.39	0.05	0.35
Local (total)	0.24	0.61	0.48	0.10	0.47
Local alone	0.10	0.03	0.05	0.11	0.12
Shared local + facies	−0.08	0.12	0.01	−0.06	−0.04
Shared local + position	0.09	0.02	0.03	0	0.04
Shared local + facies + position	0.12	0.43	0.39	0.05	0.35
Position (total)	0.35	0.60	0.55	0.15	0.52
Position alone	0.06	0.02	0.09	0	0.08
Shared position + facies	0.07	0.13	0.04	0.10	0.05
Shared position + local	0.09	0.02	0.03	0	0.04
Shared position + facies + local	0.12	0.43	0.39	0.05	0.35

ted for a fairly large fraction (14%) of the total variation in forage density.

Discussion

Geophysically defined sediment facies are promising as descriptors of benthic animal habitat in large rivers. Models based on sediment facies alone always had higher R^2 than those based solely on local environmental conditions; in some cases this difference in explanatory power was large (Table 4). The predictive power of models based on sediment facies alone (Figs 2, 4 and 5) may even be high enough that it is not necessary to add further independent variables.

Further, adding information on sediment facies to combined models using all classes of predictor variables always produced a larger increase to model R^2 than adding information on local environmental conditions or sampling position (Table 4). These increases in model R^2 were large enough (0.14–0.42) to justify the addition of data on sediment facies, if that information were readily available at a reasonable cost.

More generally, our results suggest that information on the environmental setting around the sampling point, whether obtained from remotely sensed geophysical data or from other means, has much promise for improving our currently poor ability to describe habitats of animals living in large rivers. Other recent papers in large rivers (e.g. Hildrew, 1996; Kynard *et al*., 2000; Brunke, Hoffmann & Pusch, 2002) and other environments also have emphasised the importance of the broad environmental setting in defining habitat suitability for species. Given the logistic difficulties of working in large rivers and rapidly evolving technological capabilities to sense underwater environments, the challenge now is to determine which large-scale geophysical variables are most effective in describing biological distributions in large rivers, and the most effective ways to collect this information.

The sole response variable that sediment facies did not predict well was summed macroinvertebrate density (Table 4), which includes the aggregated responses of >50 species to the environment. Other response variables (community composition, zebra mussel density, density of forage invertebrates) depend more on the individual responses of one or a few species to the environment. A possible interpretation of these results (assuming they are robust) is that sediment facies affect conditions for individual species more than they constrain the whole community. It will be interesting to see if this idea holds up through testing with other response variables and other sites.

This leads finally to the mechanisms by which sediment facies affect the distribution and abundance of benthic invertebrates. It seems likely that sediment facies are effective descriptors of macroinvertebrate habitat because they integrate several environmental factors that affect macroinvertebrates: sediment grain size and compaction; sediment mobility; bedform features; and current regime. The different sediment facies differ in their grain size distributions, a factor often thought to affect macroinvertebrate communities (e.g. Allan, 1995; Beisel *et al*., 1998; Seys *et al*., 1999; De Drago, Marchese & Wantzen, 2004). Further, because organic content is often related to grain size, compaction, and dynamics, assigning sampling sites to sediment facies provides information about sediment organic content (Table 3), another factor often related to macroinvertebrate communities (Corkum, 1992; Allan, 1995). Nevertheless, direct measurements of local sediment grain size and organic content were of limited use in explaining the characteristics of the macroinvertebrate community, so sediment facies must have some additional value. The sediment facies defined by Bell *et al*. (2000) include information about sediment mobility by identifying erosional and depositional areas through the use of chirp sub-bottom seismics and by identifying mobile bedforms (e.g. sand waves). Although difficult to measure, sediment mobility is increasingly shown to be of key importance to macroinvertebrates (e.g. Rempel, Richardson & Healey, 1999, 2000; Strayer, 1999; Howard & Cuffey, 2003). Large-river sediments often have bedforms that could be important to the biota, although they have not often been studied by biologists. Recent work on the Missouri River (Wildhaber, Lamberson & Galat, 2003) has shown that sediment bedforms may be important to benthic fish, and it is easy to imagine that they might be important to benthic invertebrates, by affecting local flow environments (and thereby food delivery) and patterns of sedimentation. In addition, grain size distribution, bedform and erosional status of the sediments are all related to the current regime, another factor classically known to affect the riverine biota (e.g. Allan, 1995; Poff & Allan, 1995; Doisy & Rabeni, 2001; Hart & Finelli, 2001).

Further, physical patchiness may be coarser in large rivers than in small streams (Hildrew, 1996), so that the mismatch between the size of the sampling device and the scale of ecologically important patchiness may be especially severe in large rivers. Thus, a facies-level approach may be particularly effective in large rivers.

Finally, facies-scale predictors may be more effective than grab-scale variables for predicting benthic animal abundance because the scale of important ecological interactions is larger than the size of a benthic grab. The spatial scale of the processes that control benthic animal populations is not well known, but is it clear that important processes operate at distances much beyond the local environment (e.g. Hildrew, 1996; Finlay, Khandwala & Power, 2002). Geophysically defined sediment facies may be useful predictors of benthic animal communities because they come closer to the ideal of matching the spatial scale of predictor variables to the scale of dominant controlling processes.

Acknowledgments

New York State Department of Environmental Conservation provided funding for this project from the Environmental Protection Fund through the Hudson River Estuary Program. We thank Carolyn Klocker, Colleen Lutz and Krista Munger for technical help, Betsy Blair, Bob Cerrato, Roger Flood, John Ladd, Nicole Maher, William Ryan and Chuck Nieder for encouragement and ideas, and Alan Hildrew and two reviewers for helpful suggestions. Nicole Maher was especially helpful in helping to obtain the SPI images. This is a contribution to the programme of the Institute of Ecosystem Studies.

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(Manuscript accepted 6 September 2005)