Submersed Vegetation as Habitat for Invertebrates in the Hudson River Estuary

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ABSTRACT: We sampled epiphytic and benthic macroinvertebrates in 20 beds of submersed vegetation throughout the Hudson River estuary to assess the importance of plant beds in providing habitat for macroinvertebrates and to determine which characteristics of plant beds affected the density and composition of macroinvertebrates. Macroinvertebrate densities in plant beds were 4–5 times higher, on average, than densities in unvegetated sediments in the Hudson. The macroinvertebrate community in plant beds was dominated by chironomid midges, oligochaete worms, hydroids, gastropods, and amphipods. Many species of macroinvertebrates were found chiefly on submersed plants, showing that plant beds are important in supporting biodiversity in the Hudson. Macroinvertebrates were most numerous in beds with high plant biomass and in the interiors of beds, whereas neither bed size nor position along the length of the estuary affected macroinvertebrate density. Community composition varied strongly with position along the river (freshwater versus brackish), habitat (epiphytic versus benthic), and position within the bed (edge versus interior). Plant biomass also influenced macroinvertebrate community composition, but bed area had relatively little influence.

Introduction

Submersed vegetation plays important roles in aquatic ecosystems by producing organic matter (Hemminga and Duarte 2000; Wetzel 2001; Caffrey 2004), modulating the physical environment (Petticrew and Kalff 1992; Madsen et al. 2001), participating in biogeochemical cycles (Wetzel 2001; Pokorný and Květ 2004; Caraco et al. 2006), and providing habitat for algae and animals (Hemminga and Duarte 2000; Kalff 2002; Wetzel 2001; Heck et al. 2003; Pokorný and Květ 2004). Because submersed plants are vulnerable to such activities as nutrient loading (Sand-Jensen et al. 2000; Hauxwell et al. 2003; Hughes et al. 2004), filling, dredging, or other physical disturbance of shallow-water habitats (Short and Wyllie-Echeverria 1996; Sand-Jensen et al. 2000), and invasions of alien species (Madsen et al. 1991; Hauxwell et al. 2004; Rodriguez et al. 2005), there has been much recent concern about the loss of submersed vegetation and the ecological functions that it provides (Hemminga and Duarte 2000; Kemp et al. 2005).

Concern about the extensive beds of submersed vegetation in the Hudson River estuary led to a program to map the vegetation and assess its ecological functions. A mapping campaign based on aerial photography produced quantitative data on the extent, spatial distribution, and size distribution of patches of submersed vegetation over a 200-km section of the estuary (Nieder et al. 2004). These extensive mapping data provided us with two unusual opportunities to assess ecological functions of submersed vegetation over a broad scale. Because we had a complete inventory of plant beds in the Hudson, along with information on characteristics such as the size, shape, and location of each bed, we were able to include a statistically representative sample of plant beds in a study of how the functions of plant beds varied with the characteristics of the bed. We also were able to combine information on the function of individual plant beds with comprehensive information on the extent and characteristics of plant beds to assess the estuary-wide importance of plant beds in the Hudson estuary. Our goals were to both assess the system-wide importance of submersed vegetation in the Hudson and to determine the factors responsible for variation among beds in the intensity of various ecological functions. Findlay et al. (2006) described the effects of submersed plant beds on water quality, and the present paper describes how submersed vegetation in the Hudson serves as habitat for invertebrates.

Submersed plants support dense and distinctive communities of macroinvertebrates (Cogerino et al. 1995; Tolonen et al. 2001) and may be rich feeding grounds for fish (Crowder and Cooper 1982; Rozas and Odum 1988). Previous work has shown that plant density (Cyr and Downing 1988; Humphries 1996; Kurashov et al. 1996; Collier et al. 1999), plant species (Parker et al. 2001; Cheruvelil et al. 2002; Xie et al. 2006), water chemistry (Cyr and Downing 1988; France 1990; Wollheim and Lovvern 1996; Pieczynska et al. 1998), and position within the bed (Sloey et al. 1997; Cardinale et al. 1997, 1998;

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Bologna and Heck 2002) may affect the density and composition of invertebrate communities, although studies often have reached conflicting conclusions about the influence of these factors. Our study had three specific goals. We wanted to describe the invertebrate fauna of submersed macrophyte beds in the Hudson River estuary, a habitat that has not been well studied. We wanted to determine whether density and community structure varied with the longitudinal position and characteristics of the bed. We hypothesized that the area and density of plants in the plant bed would determine the number and kinds of invertebrates that it supported, and that the density and composition of the invertebrate community would vary from place to place (benthos versus epiphytes; edge versus interior of the plant bed) within plant beds. We also wanted to assess the importance of macrophyte beds as invertebrate habitat in the entire estuarine ecosystem.

Materials and Methods

STUDY AREA

The study area is the Hudson River estuary extending from Troy, New York, at rkm 248 (i.e., river kilometer 248, measured from The Battery in Manhattan) to Croton at rkm 50. The entire study area is tidal, with a daily tidal range of 0.8–1.6 m. Most of the study area is fresh water, but sea salt typically is present at least part of the year downriver from rkm 100. Salinities are very variable below rkm 100, depending on freshwater flow, but occasionally reach levels as high as 10 at the lower end of our study reach at rkm 50 (Cooper et al. 1988; Geyer and Chant 2006). This reach of the Hudson estuary averages 1 km wide and 11 m deep. The water is turbid (Secchi disk transparency = 0.5–1.5 m), moderately hard (calcium $\sim$ 27 mg l^{-1}), and nutrient-rich (Cole and Caraco 2006). Summer water temperatures usually reach 25–28°C (Wells and Young 1992).

STUDY DESIGN

The study was designed to encompass beds of submersed vegetation that spanned a wide range of sizes over the entire study area (rkm 50–248). We defined five classes of beds. The first three classes were based on the area of the bed: small (55–1,097 m² or roughly 10th–37th percentile in the size distribution of beds in the river), medium (1,098–8103 m² or 37th–63rd percentile), and large (8,104–59,874 m² or 63rd–90th percentile). We selected beds randomly within each size class for sampling. We rejected randomly chosen beds if they were near a site heavily used by humans (e.g., a marina) or if they were adjacent to a bed that had already been chosen for sampling. In 2000, we sampled two beds

in each size category between rkm 130 and 213. In 2001, we sampled two beds in each size category between rkm 50 and 130. In 2002, we sampled four linear beds between rkm 213 and 248. Linear beds are narrow beds lying along the shoreline in the upper riverine part of the estuary. They are so narrow that their width cannot be estimated from aerial photographs; where necessary to estimate bed area for statistical analyses, we assumed that they were 2 m wide. In addition to these randomly chosen beds, four beds of special significance were designated as keystone beds and sampled every year from 2000 or 2001 to 2003. The keystone beds were larger than the beds in the large size category, having areas of 88,592–250,747 m². Because our design was not randomized with respect to time, there is some potential for confounding of temporal and spatial variation. The repeated sampling of keystone beds should have reduced the likelihood that we misinterpreted temporal variation as spatial variation.

We took invertebrate samples at six sites within each bed. In keystone beds, large beds, and medium beds, we took three samples widely spaced along the outer edge of the bed and three samples widely spaced through the interior of the bed. In small beds and linear beds, we simply spaced the six samples widely through the bed. Samples were taken in August to coincide with peak plant biomass.

MACROPHYTE SAMPLING

Macrophytes were sampled using a standard (23 × 23 cm) PONAR grab or by clipping quadrats. PONAR grabs were used for most sites. For each bed, we took eight PONAR samples dispersed along the outer edge of the bed and eight samples throughout the interior of the bed. In small beds, we took a total of eight PONAR samples scattered throughout the bed. We clipped vegetation in 0.25 or 0.79 m² quadrats in the linear beds and a few other beds, where the sediments were too hard for the PONAR grab or where the vegetation was sparse. We sampled 4–16 quadrats per site, depending on the size of the bed, plant density, and available time. For all samples, we included only aboveground parts of the plant. We put samples into a cooler in the field and returned them to the laboratory, where we separated the plants by species and dried them overnight at 60°C before weighing them to estimate dry mass (DM).

SEDIMENT SAMPLING

We took core samples for sediment analysis at each of the six sampling points where we collected macroinvertebrates in each macrophyte bed. If

sediments were too coarse to be sampled with the corer, we recorded the sediment texture as coarse and moved to the next sampling location. Cores 5–15 cm long were taken with a handheld corer of 20.2 cm^2, put into a cooler, and frozen upon return to the laboratory. Samples were later thawed and dried at 60°C for at least 24 h. Granulometry (percent sand, silt, and clay) was measured using the hydrometer method (Gee and Bauder 1986), and organic content was estimated by loss on ignition after 4 h at 500°C.

Macroinvertebrate Sampling

We sampled macroinvertebrates using two different methods. Animals living in the sediments were collected using a handheld coring tube of 20 cm^2. Three cores 5 cm long were taken from each sampling site and pooled in the field. No sample of sediment-dwelling invertebrates was taken if the sediments were too coarse to be sampled with the handheld core. This occurred throughout one bed and at a few sites in the linear beds. Invertebrates living on macrophytes were collected with a 30 × 21.2 × 11.5 cm Downing box sampler (Downing 1986). The plants and associated macroinvertebrates collected in Downing samples were preserved in the field and sorted in the laboratory (see below). We generally collected three Downing samples per site, which were pooled in the field. In the laboratory, we dried and weighed the plant material in the Downing samples, then calculated areal densities of invertebrates (m^{-2} of river bottom) by multiplying the density of invertebrates per gram of plant material in the Downing sample by the areal biomass of plants estimated from our macrophyte samples (see above).

All invertebrate samples were sieved through a 0.5-mm mesh sieve and preserved in buffered 10% formalin in the field. We sorted samples under 6–12× magnification, and placed invertebrates into 70% ethanol or 10% buffered formalin for long-term storage. Twenty-five percent of the samples were double-sorted; we estimated recovery efficiency from these samples using the removal method of Zippen (1958) and corrected all samples for these efficiencies. Random subsamples (10–20 individuals sample^{-1}) of oligochaetes, chironomids, and nematodes were slide mounted in CMC-10 on microscope slides prior to identification. Most invertebrates were identified to genus or species using Gosner (1971), Holsinger (1972), Bousfield (1973), Wiederholm (1983), Peckarsky et al. (1990), Smith (1995), and Kathman and Brinkhurst (1998). Dreissenids too small to be identified were assigned to *Dreissena polymorpha* for sites above rkm 109 and to *Mytilopsis leucophaeta* at sites below rkm 74 (no dreissenids were collected between rkm 74 and 109). Voucher specimens have been deposited in the American Museum of Natural History, New York City.

Statistical Analyses

We used (ANCOVA) to test for differences in invertebrate densities between the edges and interiors of plant beds as follows. We log$_{10}$-transformed data on plant biomass and invertebrate densities, then tested if the slopes of plant biomass-invertebrate density regressions were significantly different for samples taken in bed interiors and bed edges. Finding that none of these differences in slope were significant at p < 0.05, we used ANCOVA to test whether the regression intercepts differed significantly, and report these p values.

We used nonmetric multidimensional scaling (NMS), an ordination technique (McCune and Grace 2002), to express variation in macroinvertebrate community structure among sites. NMS uses information on the types of invertebrates found in each sample to order the samples according to the similarity of their macroinvertebrate communities. Sites with similar macroinvertebrate communities are placed close to one another in the ordination diagrams, and sites having very different macroinvertebrate communities are placed far apart in the ordination diagrams. We regressed ordination scores against environmental factors (e.g., location along the river, plant biomass) to identify which factors were related to variation in the overall composition of the macroinvertebrate community, and show the strongest of these relationships.

Various ordinations were based on either densities in individual samples or on mean densities of each macroinvertebrate taxon for each plant bed; for beds that were sampled in more than one year, we included each year separately. We treated benthic samples and epiphytic samples separately in some ordinations, and omitted species that occurred in fewer than three plant beds or five samples. Ordinations were done with PC-ORD using the autopilot mode. Statements about which taxa are characteristic of specific habitats in the Hudson or regions of ordination space are based on ordination scores of individual taxa or their population densities in specific habitats.

Results

Sediment Characteristics

Sediments at the study sites were predominately sand and silt, but highly variable among beds. Both the texture and organic content of the sediments changed along the course of the river, from sandy, organic-poor sediments upriver to muddy, organic-rich sediments downriver (Fig. 1). Sediments in the
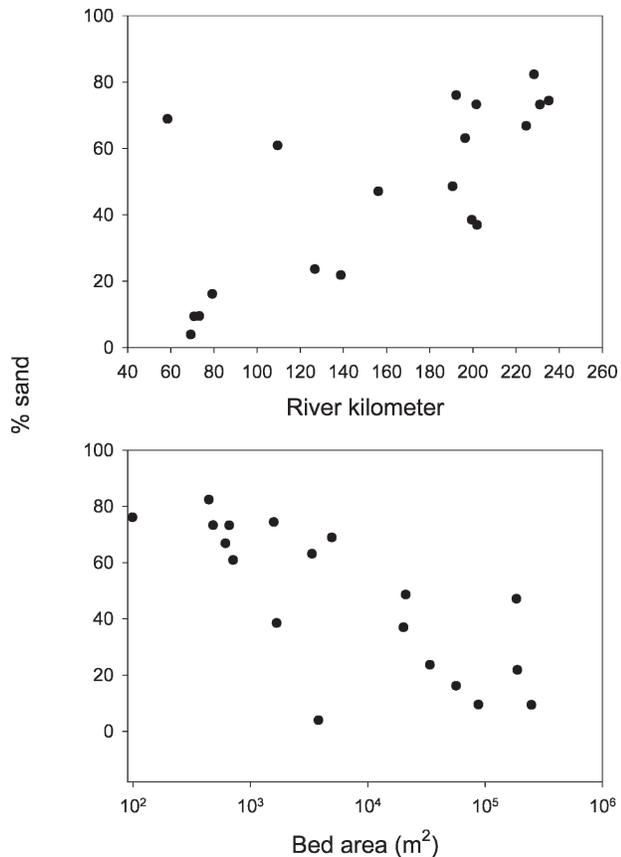
Fig. 1. Sediment texture as a function of position along the river and size of the macrophyte bed (which is scaled logarithmically). For the upper panel, $r^2 = 0.48$, p = 0.001; for the lower panel, $r^2 = 0.49$, p = 0.004.

linear beds upriver were sometimes too coarse to core, containing cobbles, boulders, and riprap. Bed area also was strongly associated with sediment characteristics – sediments in large beds were finer and richer in organic matter than sediments in small beds. This effect was stronger than and independent of the long-river changes (bed area and river kilometer were only weakly correlated; r^2 = 0.09, p = 0.27, excluding linear beds). Neither organic content nor sediment texture (percent sand) was significantly correlated with plant biomass ($r^2 < 0.1$ in both cases). There was no difference (p > 0.25) between edge and interior samples in percent sand or organic content.

MACROPHYTE BIOMASS AND COMPOSITION

Macrophyte biomass was highly variable among beds, ranging from 2.5 to 479 g DM m^{-2}. This variation was not closely related to position along the river or bed area, although there was a weak tendency for small beds to have higher macrophyte biomass than large beds (r^2 = 0.15, p = 0.09).
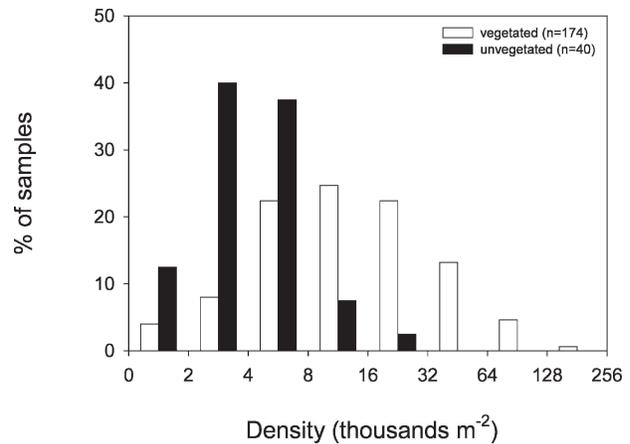

Fig. 2. Frequency distribution of invertebrate densities (epiphytic + benthic) in vegetated (this study) and unvegetated habitats in the Hudson estuary. Data for unvegetated habitats are taken from a study of 40 sites in the freshwater tidal Hudson (Strayer et al. 2006).

Macrophyte biomass tended to be higher in bed interiors than along their edges, but this difference was not consistent among beds and was only marginally significant (p = 0.14, paired t-test). Biomass also varied considerably among beds that were sampled in more than 1 yr. For instance, macrophyte biomass at one bed ranged from 6 to 268 g DM m^{-2} over the 4 yr of our study. *Vallisneria americana* strongly dominated submersed macrophyte beds in the Hudson, constituting > 90% of plant biomass overall; no other macrophyte species accounted for > 2% of submersed plant biomass riverwide.

INVERTEBRATE COMMUNITIES

Macroinvertebrates were abundant and diverse in plant beds. Macroinvertebrate density nearly always exceeded typical values for unvegetated sediments (5,805 m^{-2} for the freshwater tidal Hudson: Strayer and Smith 2001; 3,138 m^{-2} for the oligohaline and freshwater estuary: Llanso et al. 2003; 4,576 m^{-2} for sites in the midestuary: Strayer et al. 2006; Figs. 2 and 3), and sometimes surpassed 100,000 m^{-2} in individual samples. The mean density of macroinvertebrates over all beds and years was 20,600 m^{-2}, considerably higher than the mean density in unvegetated sediments. We estimate that 27% of the macroinvertebrates in the Hudson live in beds of submersed plants beds, with an additional 10% in *Trapa natans* beds (based on Strayer et al. 2003).

Macroinvertebrate density was strongly related to plant biomass in the beds (Fig. 3). Position within the plant bed also strongly affected macroinvertebrate density, with total densities in the interiors of plant beds 2.2 times higher than along their edges. This difference was highly significant (p =
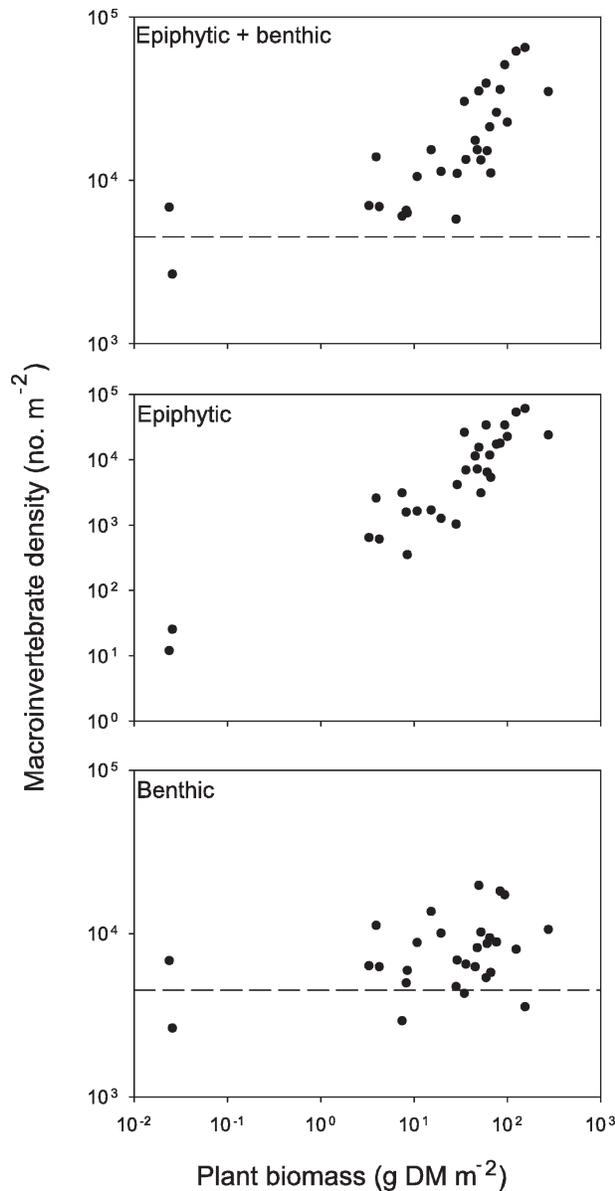
Fig. 3.   Density of macroinvertebrates as a function of plant biomass in each bed. Total (epiphytic + benthic) macroinvertebrates; $\log_{10}$ density = 3.83 + 0.27 ($\log_{10}$ plant biomass); r^2 = 0.54, p < 0.0001. Epiphytic macroinvertebrates; $\log_{10}$ density = 2.46 + 0.87 ($\log_{10}$ plant biomass); r^2 = 0.85, p < 0.0001. Benthic macroinvertebrates; $\log_{10}$ density = 3.76 + 0.087 ($\log_{10}$ plant biomass); r^2 = 0.14, p = 0.05. The dashed horizontal line shows the approximate mean density of macroinvertebrates on unvegetated sediments in the freshwater and oligohaline tidal Hudson after the zebra mussel invasion (Strayer and Smith 2001; Llanso et al. 2003; Strayer et al. 2006).
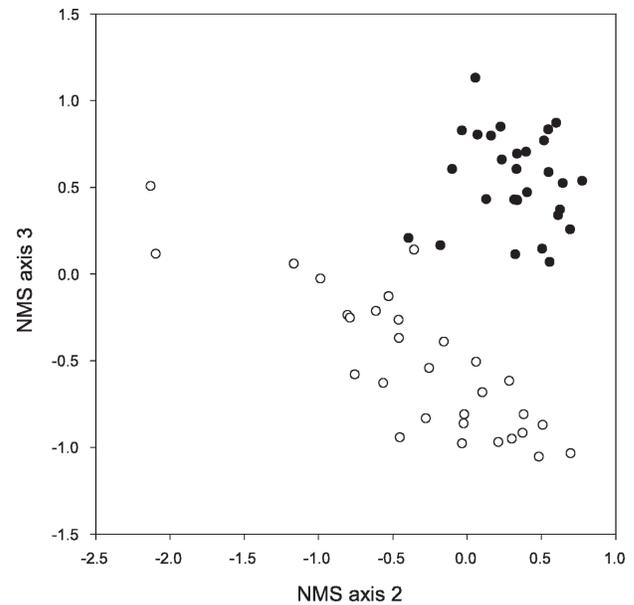

Fig. 4.   Ordination results, based on mean densities for each plant bed. Benthic samples (black circles) are clearly separated from epiphytic samples (white circles). Each year's data from keystone beds are treated separately; i.e., each keystone bed is represented by three or four points. Species occurring in fewer than three plant beds are omitted.

We identified > 100 taxa of macroinvertebrates from plant beds, even though we did not identify some animals (e.g., nematodes) to the genus or species level (unpublished data; available from the author). Dominant groups (in terms of density) included chironomid midges, oligochaete worms, hydroids, gastropods, and amphipods. Nematodes, cladocerans, bivalves, mites, barnacles, polychaetes, flatworms, and caddisflies also were often abundant, and many other kinds of invertebrates were taken less frequently.

Ordinations successfully summarized spatial variation in macroinvertebrate community structure. NMS ordinations based on the 71 most widespread macroinvertebrates (i.e., those present in at least three plant beds) was 3-dimensional and had a stress value of 11.9, indicating a satisfactory ordination (McCune and Grace 2002). Community composition depended chiefly on whether the samples were benthic or epiphytic (Fig. 4) and position along the river (Fig. 5). In particular, community composition was relatively constant above rkm 100, then changed sharply through the transition into brackish water between rkm 96 and 59. Sites in the middle estuary (rkm 110–202) were always dominated by chironomids and oligochaetes, while sites further downriver often contained large numbers of such typically brackish-water invertebrates as the hydroid *Cordylophora caspia*, the amphipods *Corophium lacustre* and *Leptocheirus plumulosus*, the barnacle *Balanus impro-*

0.0004, ANCOVA of $\log_{10}$-transformed data) even when the effects of plant biomass were taken into consideration. Macroinvertebrate density was unrelated to position along the river or area of the plant bed.
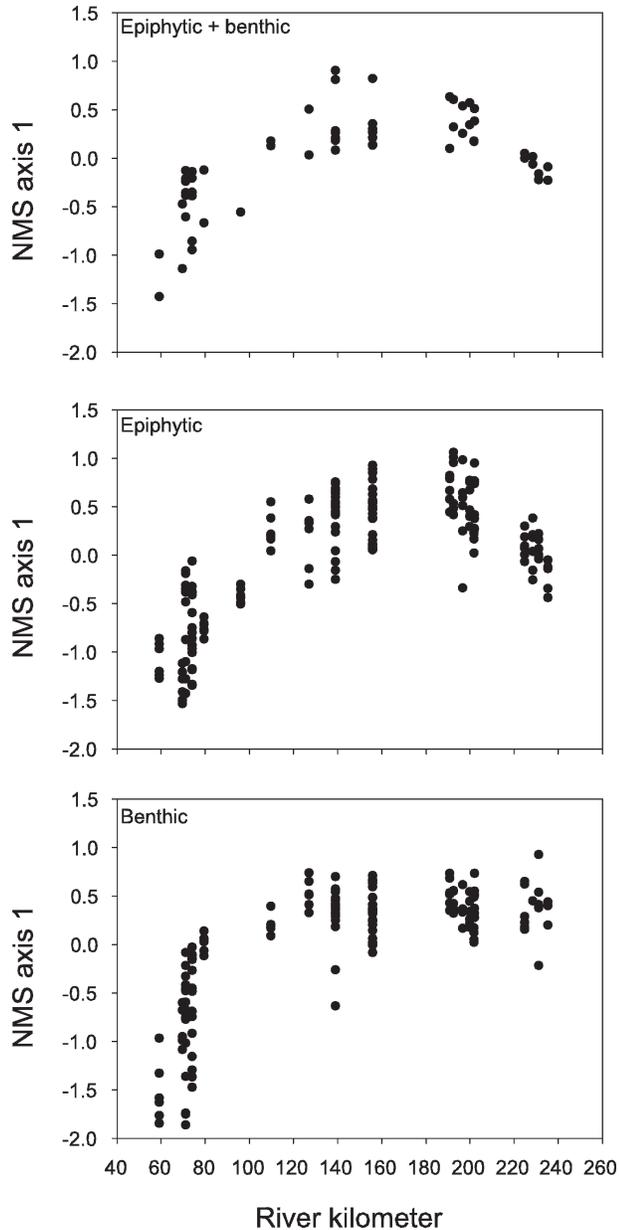
Fig. 5.   Relationship between community structure, expressed as ordination results, and position along the river. All samples combined, based on bed means ($r^2 = 0.32$, $p < 0.0001$). Epiphytic samples ($r^2 = 0.42$, $p < 0.0001$). Benthic samples ($r^2 = 0.51$, $p < 0.0001$).

visus, the bivalve *Rangia cuneata*, and polychaetes. Communities of linear beds in the upper estuary (rkm 225–235) also were distinctive, with large numbers of gastropods and the amphipod *Gammarus* sp.

The fauna is clearly differentiated into benthic and epiphytic (plant-dwelling) forms (Fig. 4); very few taxa are abundant both on the plants and in the
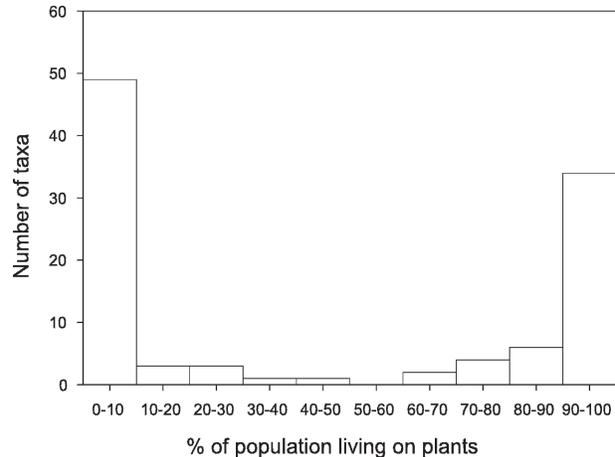

Fig. 6.   Frequency distribution of the percentage of the population of each invertebrate taxon that lives on vegetation.

sediments (Fig. 6). Hydroids, most gastropods, cladocerans, mites, odonates, most naidid oligochaetes, the nudibranch *Tenellia fuscata*, the flatworm *Dugesia* spp., and many chironomids live on the plants themselves, whereas tubificid oligochaetes, polychaetes, isopods, bivalves other than dreissenids, nematodes, ostracods, the amphipod *L. plumulosus*, the flatworm *Hydrolimax grisea*, and many other chironomids live in the sediments beneath the plants. Only two of the amphipods, two of the genera of chironomids, barnacles, and zebra mussels were really common on both sediments and plants.

EPIPHYTIC FAUNA

The average density of plant-dwelling invertebrates was 12,500 m^{-2} or 61% of the macroinvertebrates in the plant beds. The density of epiphytic macroinvertebrates, not surprisingly, was correlated with plant biomass (Fig. 3), but not with bed area ($p = 0.71$) or position along the river ($p = 0.26$). Densities of epiphytic invertebrates were 3.6 times higher in the interiors of beds than along their edges; this difference was highly significant ($p = 0.003$, ANCOVA of log$_{10}$-transformed data) after plant biomass was taken into account. The degree to which macroinvertebrate species preferred bed interiors or edges seemed to depend on the functional attributes of the species (Fig. 7). Suspension feeders, which presumably benefit from rapid movement of fresh river water, were less likely than other epiphytic species to be found in bed interiors. Large, active invertebrates (the amphipod *Gammarus* spp. and odonates) were especially likely to be found in bed interiors.

The epiphytic fauna was dominated by the suspension-feeding chironomid *Rheotanytarsus* sp.,
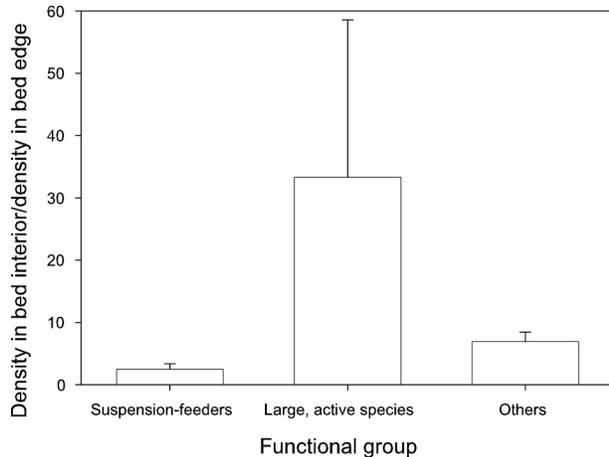
Fig. 7. Ratio (mean ± SE) of population density in bed interior to population density in bed edge for all epiphytic species having a mean density > 10 m^{-2}. Suspension feeders include *Rheotanytarsus* sp., *Sida crystallina*, *Balanus improvisus*, Dreissenidae, and *Corophium lacustre*; large, active animals are *Gammarus* spp. and *Enallagma* sp.

Fig. 8. Relationship between the third NMS ordination axis for epiphytic samples and plant biomass (r^2 = 0.63, p < 0.0001).

several taxa of browsing chironomids (especially *Cricotopus bicinctus*, *Dicrotendipes* sp., and *Polypedilum* spp.), the cnidarians *C. caspia* and *Hydra* sp., naidid oligochaetes (especially *Nais variabilis* and *Stylaria lacustris*), and the suspension-feeding cladoceran *Sida crystallina*.

The NMS ordination of epiphytic samples was satisfactory, yielding a 3-dimensional solution with a stress value of 14.95. Epiphytic community composition was strongly related to local plant biomass (Fig. 8) and position along the river (Fig. 5). The barnacle *B. improvisus*, the bivalve *M. leucophaeta*, the oligochaete *Nais* spp., and the amphipod *C. lacustre* all were typically found in sparse macrophyte beds. It is perhaps notable that all of these but *Nais* spp. are suspension feeders, and may be disadvantaged by slow water movement in dense macrophyte beds. Abundant epiphytic invertebrates typical of dense macrophyte beds included several species of insects (*Orthocladius annectens*, *Nectopsyche* sp., *Enallagma* sp., *Thienemanniella* sp., *Hydroptila* sp., *Polypedilum* spp., and other Diptera), the gastropods *Elimia virginica*, *Micromenetus dilatatus*, and *Physella* sp., and the cladoceran *Chydorus* sp., Microturbellaria, and the flatworm *Dugesia* spp. Many of these invertebrates are large and presumably susceptible to fish predation. The ordination axes were more weakly but significantly related to bed area and position within the bed (i.e., interior versus edge).

BENTHIC FAUNA

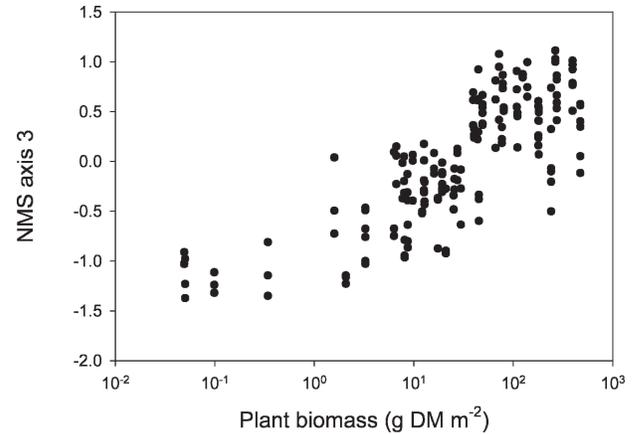The average density of benthic (sediment-dwelling) invertebrates was 8,060 m^{-2} or 39% of the macroinvertebrates in the plant beds. This number is about 80% higher than the average density of benthic macroinvertebrates in unvegetated sediments in the Hudson after the zebra mussel invasion (Fig. 3). The density of benthic macroinvertebrates was not strongly correlated with any environmental factor that we measured. Densities tended to be higher where plant biomass was greatest (r^2 = 0.14, p = 0.05), upriver (r^2 = 0.19, p = 0.02), and sediments were poor in organic matter (r^2 = 0.17, p = 0.03). Density of benthic macroinvertebrates tended to be higher in the interior of plant beds than along their edges, but this difference was much weaker (11%) than that seen for epiphytic macroinvertebrates and was not statistically significant (p = 0.25, ANCOVA of log$_{10}$-transformed data).

Numerically dominant benthic invertebrates in plant beds include tubificid oligochaetes (especially *Limnodrilus hoffmeisteri*), nematodes, several chironomid midges, the amphipods *Gammarus* spp. and (in brackish water) *L. plumulosus*, and bivalves.

The NMS ordination of benthic samples was adequate, giving a 3-dimensional solution with a stress value of 16.0. Community composition was strongly related to position along the river, especially below rkm 100 (Fig. 5). There was a weak indication that the size of the plant bed also affected benthic community composition (Fig. 9). Populations of the chironomids *Paralauterborniella* sp., *Thienemanniella* sp., and *Rheotanytarsus* sp., and the oligochaete *Nais* spp. were highest in small plant beds, whereas those of the bivalve *D. polymorpha*, the oligochaetes *S. lacustris* and *Tubificoides heterochaetus*, mites, the cumacean *Almyracuma proximoculi*, ostracods, the chironomid *Cryptotendipes* sp., the poly-
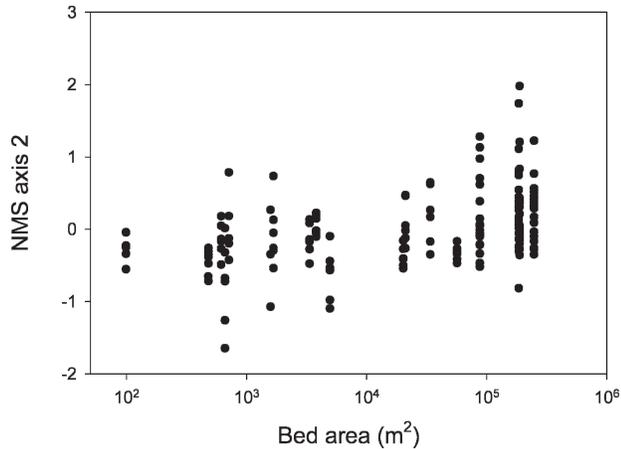
Fig. 9.   Relationship between the second NMS ordination axis for benthic samples and size of the plant bed ($r^2 = 0.16$, $p < 0.0001$).

chaete *Neanthes succinea*, and the snail *Littoridinops tenuipes* were highest in large beds.

Several of the dominant species living in plant beds in the Hudson are aliens. It is not possible to give a full accounting of alien species in the Hudson's plant beds without better information on the taxonomy and origins of all of the species. At least *C. caspia, T. heterochaetus, D. polymorpha, M. leucophaeta*, and *R. cuneata* probably are alien to the Hudson (Mills et al. 1996; Erséus personal communication); at least one of these species occurred in every bed that we sampled. These species accounted for 7% of macroinvertebrates in the Hudson's plant beds, reaching values as high as 68% in brackish sites.

Discussion

Beds of submersed vegetation are an important habitat for macroinvertebrates in the Hudson. Densities of macroinvertebrates are much (4–5 times, on average) higher in plant beds than in unvegetated sediments (Fig. 3), as observed in many other bodies of water (Soszka 1975; Mittelbach 1981; Cogerino et al. 1995). Essentially all of the sites in the Hudson that support very high macroinvertebrate densities ($> 16{,}000$ m^{-2}) are in submersed vegetation (Fig. 2). This suggests that the richest feeding grounds for fish are in plant beds (cf., Rozas and Odum 1988), although the reduced foraging efficiency caused by the structural complexity of these beds may diminish their value to fish (Crowder and Cooper 1982; Hershey 1985; Zhao et al. 2006).

Dozens of species of macroinvertebrates live on plants but not in the sediments of the Hudson (Fig. 6). Beds of submersed vegetation also play an important role in supporting biodiversity of macroinvertebrates in the Hudson, as in other aquatic ecosystems (Cogerino et al. 1995; James et al. 1998; Tolonen et al. 2001); but see Asmus and Asmus (2000) and van Houtes-Howes et al. (2004) for counterexamples.

It is worth noting how many of the invertebrates living in plant beds depend directly on food that is brought into the beds by tidal currents. The suspension feeders, which are among the most abundant invertebrates in plant beds (summed density > 5000 m^{-2}), strip edible particles from the water as it moves through plant beds. Cnidarians, which were extraordinarily numerous in many plant beds (riverwide mean density = $1{,}700$ m^{-2}), are predators that capture prey from the surrounding water. The abundance of suspension feeders and cnidarians, which together account for more than one-third of the macroinvertebrates in plant beds, suggests that edible particles and planktonic prey may decline in density as water moves through large plant beds.

The wide range in macroinvertebrate density and species composition among and within plant beds in the Hudson is related in part to the geographic location of the plant bed, the density of the plants in the bed, the size of the bed, and location within the bed. Geographic location probably affects macroinvertebrates in the Hudson chiefly as a result of variation in salinity below rkm 100. Water chemistry is well known to affect macroinvertebrates in plant beds, either through the direct physiological effects of variables, such as salinity (Wollheim and Lovvorn 1996) and pH (France 1990), or indirect effects of variables like nutrients, which presumably affect macroinvertebrates through their effects on periphyton and phytoplankton (Cyr and Downing 1988; Kornijow 1989; Pieczynska et al. 1998). In the Hudson, position along the length of the river (and by inference, salinity) has strong effects on the composition of both epiphytic and benthic macroinvertebrates (Fig. 5); macroinvertebrate density does not vary across the course of the Hudson estuary.

There can be multiple, complex links between plant density (or biomass) and macroinvertebrate communities, probably preventing any simple correlations between these variables that apply across a wide range of plant densities and ecosystem types. High plant density increases the surface area for colonization by periphyton and invertebrates. High plant density should generally lead to high primary production and increase shelter from fish predation, which appears generally to be important in structuring macroinvertebrate communities in plant beds (Marklund et al. 2002). All of these factors should lead macroinvertebrate density to increase

with plant density. Many studies have reported such a positive correlation between plant density and macroinvertebrate density (Cyr and Downing 1988; Humphries 1996; Kurashov et al. 1996; Collier et al. 1999). High plant density reduces water velocity through plant bed (Madsen and Warncke 1983; Madsen et al. 2001; Green 2005), which might be expected to reduce densities of suspension feeders. Especially if current speeds are slow, nighttime concentrations of dissolved oxygen in dense plant beds may be very low (Miranda et al. 2000), leading to negative correlations between plant density and macroinvertebrate density, at least over some range of plant density.

In the Hudson, we found positive correlations between plant density and densities of both epiphytic and benthic macroinvertebrates (Fig. 3). We also found that plant density affected community composition of macroinvertebrates (Fig. 8). Dense beds harbored more large insects and gastropods, possibly because such dense beds offer protection from fish predation. Suspension feeders were especially characteristic of sparse plant beds, perhaps because of better water movement.

Patch area may be important in determining biodiversity and ecosystem function in heterogeneous landscapes (Turner et al. 2001), especially through its influence on immigration and extinction rates (MacArthur and Wilson 1967). A previous study of seagrass beds found that patch area had only a modest influence on the diversity and composition of macroinvertebrate communities (Bowden et al. 2001). Bed area had only a weak influence on macroinvertebrate communities in the Hudson, despite the fact that our sampling design deliberately encompassed a very wide range in bed areas. We did not detect any effect of bed area on macroinvertebrate density and only weak effects on species composition (Fig. 9 shows the strongest example). It seems likely that patch area is relatively unimportant to macroinvertebrates in plant beds because even small patches are large relative to macroinvertebrates and contain large enough populations that extinction rates are not strongly area-dependent. The smallest plant beds that we studied in the Hudson supported ca. 10^6 macroinvertebrates, in contrast to the small numbers of terrestrial vertebrates that typically occur in the patches studied by most landscape ecologists. Alternatively, there may be high rates of immigration of invertebrates through current-driven drift.

We investigated two aspects of location within plant beds: the edges versus the interiors of the beds and the sediments versus the plants themselves. Several recent studies (Sloey et al. 1997; Cardinale et al. 1997, 1998; Bologna and Heck 2002) have explored differences in macroinvertebrate communities between the edges and interiors of plant beds, with conflicting results. Some studies have reported higher densities of invertebrates along bed edges (Bologna and Heck 2002), whereas others have found higher densities in bed interiors (Sloey et al. 1997). These inconclusive results can perhaps be understood as a result of multiple processes that differ between the edges and interiors of plant beds. Plant density often is higher in the interiors of plant beds (Sloey et al. 1997), although not in the Hudson. Generally, the bed interiors are more isolated from the surrounding water mass than bed edges, potentially leading to lower fish predation, lower current velocities, and lower nighttime dissolved oxygen. Species with planktonic larvae may settle chiefly at bed edges (Bologna and Heck 2002), as may suspension feeders (Cardinale et al. 1997) and mobile species seeking shelter from predators (Bologna and Heck 2002), whereas invertebrates susceptible to fish predation may be most abundant in bed interiors (Cardinale et al. 1998; Tolonen et al. 2001, 2003). This mixture of processes operating with different strengths in different environments should lead to differences in relationships between bed edges and interiors and complicate attempts to reach simple generalities.

Bed interiors supported more and different kinds of epiphytic invertebrates than bed edges in the Hudson. Large, mobile invertebrates tended to be especially abundant in bed interiors, whereas suspension feeders showed a much less pronounced difference between bed edges and interiors (Fig. 7). This pattern suggests that fish predation and water movement may be important factors structuring macroinvertebrate communities in the Hudson.

There are profound differences in physical structure, chemical conditions, predation intensity, and other ecological interactions between the sediments and the plants themselves as microhabitats for invertebrates. Not surprisingly, almost every study that has sampled both benthic and epiphytic invertebrates in plant beds has reported large differences between these two communities (Soszka 1975; Menzie 1980; Wollheim and Lovvern 1996; but see Asmus and Asmus 2000). We found such large differences in the Hudson (Fig. 4), with few species abundant both in the sediment and on the plants (Fig. 6).

Several attributes of plant beds in the Hudson estuary affected the density and composition of the macroinvertebrates that they contained. The local setting (particularly salinity), plant biomass, and position within the bed all had strong effects on the macroinvertebrate community, whereas bed size had relatively weak effects. Different attributes of

the plant beds affected different attributes of the macroinvertebrate community. Because multiple mechanisms link the attributes of plant beds to their macroinvertebrate communities, it probably is naïve to expect simple correlations between the characteristics of submersed plant beds and macro-invertebrate communities to apply universally across all aquatic ecosystems. Instead, attempts to predict the roles of specific beds of submersed vegetation from their attributes will probably need to consider the extent to which processes like fish predation, larval transport, nighttime hypoxia, and food supply for suspension feeders are important in the ecosystem under consideration.

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SOURCE OF UNPUBLISHED MATERIALS

Table 1. Densities of macroinvertebrates in plant beds, averaged over all sampling sites and dates, along with the percentage of the population that lives on the vegetation.

	Mean density (no. m^{-2})	% epiphytic
Turbellaria (flatworms)		
Dugesia spp.	85	99
Hydrolimax grisea	59	1
Microturbellaria	13	92
Polycladida	1	100
Cnidaria (hydroids)		
Cordylophora caspia	1020	99
Hydra sp.	660	100
Jellyfish	2	37
Nematoda (roundworms)	771	3
Oligochaetes (earthworms)		
Arcteonais lomondi	4	0
Aulodrilus americanus	5	0
Aulodrilus limnobius	35	0
Aulodrilus pauciseta	34	0
Aulodrilus pigueti	24	0

Chaetogaster sp.	0.03	100
Enchytraeidae	1	0
Ilyodrilus templetoni	9	0
Limnodrilus hoffmeisteri	469	0
Limnodrilus udekemianus	69	1
Lumbriculidae	3	0
Nais communis/variabilis	625	97
Nais simplex	0.8	100
Stylaria lacustris	534	88
Tubificidae w/hairs	176	1
Tubificidae w/o hairs	2635	0.2
Tubificoides heterochaetus	21	0
Polychaetes		
Hobsonia florida	3	0
Marenzellaria viridis	92	0.01
Neanthes succinea	15	17
Polydora sp.	1	0.01
Sabellidae	4	0
Hirudinea (leeches)	2	100
Bivalvia (clams, mussels)		

Dreissena polymorpha	140	46
Mytilopsis leucophaeta	36	84
Pisidium sp.	169	0.2
Rangia cuneata	224	0.5

Gastropoda (snails, nudibranchs)

Amnicola limosa	107	80
Elimia virginica	12	91
Ferrissia fragilis	878	97
Gyraulus parvus	67	95
Littoridinops tenuipes	105	7
Micromenetus dilatatus	14	100
Physella sp.	49	98
Pyrgulopsis lustrica?	0.05	100
Stagnicola catascopium	1	0
Tenellia fuscata	6	100

Mysidacea (opossum shrimps)

Neomysis americana	1	21

Cirripedia (barnacles)

Balanus improvisus	129	73

Amphipoda (scuds)

Corophium lacustre.	89	67
Gammarus spp.	549	32
Hyallela sp.	4	100
Leptocheirus plumulosus	250	0

Isopoda (sow bugs)

Chiridotea almyra	1	0
Cyathura polita	58	0

Decapoda (crabs)

Rhithropanopeus harrissi	6	79

Cumacea

Almyracuma proximoculi	10	0

Copepoda	38	25

Ostracoda	73	4

Cladocera (water fleas)

Chydorus sp.	190	99
Eurycercus sp.	8	100

Sida crystalline	521	83
Simocephalus sp.	1	100
Acari (mites)	179	75
Collembola (springtails)	1	0
Ephemeroptera (mayflies)	3	19
Plecoptera (stoneflies)		
Shipsa rotunda	1	0
Odonata (damselflies)		
Enallagma sp.	54	94
Hemiptera (true bugs)		
Neoplea sp.	0.2	100
Other Hemiptera	2	0
Lepidoptera (moths, butterflies)		
Petrophila sp.	1	100
Trichoptera (caddisflies)		

Hydroptila sp.	53	96
Nectopsyche sp.	15	92
Oecetis sp.	13	12
Oxyethria sp.	2	100
Phylocentropus sp.	8	1
Trianodes sp.	0.4	100

Coleoptera (beetles)

Dubiraphia sp.	1	0
Oulimnius sp.	6	21
Pyrrhalta sp.	0.02	100

Diptera (true flies)

Ceratopogonidae	17	0
Other Diptera	11	100
Ablabesmyia sp.	6	80
Chironomus sp.	98	0
Cladopelma sp.	4	0
Clinotanypus sp.	1	0
Coelotanypus sp.	153	0
Cricotopus bicinctus	1467	92
Cricotopus not *bicinctus*	1	1
Cryptochironomus sp.	43	0

Cryptotendipes sp.	69	0
Dicrotendipes sp.	1033	91
Harnischia sp.	65	0
Hayesomyia seneta	2	3
Orthocladius annectens	24	100
Paralauterborniella sp.	9	0
Phaenopsectra s.l. sp.	43	0
Polypedilum spp.	941	71
Procladius sp.	295	0
Rheotanytarsus sp.	3752	93
Stichtochironomus sp.	3	0
Synorthocladius sp.	5	100
Tanytarsus sp.	324	1
Thienemanniella sp.	78	68
Chironomid pupae	676	96
Total	**20587**	**61**