Ecology of Hudson River Submerged Aquatic Vegetation

Final Report to the
New York State Department
of Environmental Conservation

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TABLE OF CONTENTS

FIGURES AND TABLES

I. EXECUTIVE SUMMARY

A. Introduction

Submerged aquatic vegetation (SAV) includes rooted plants living primarily beneath the water surface and is an important part of the Hudson River Estuary ecosystem. SAV has been extensively researched in many aquatic systems, and declining SAV is an important conservation concern in many rivers and estuaries. SAV is spatially extensive in the freshwater tidal portion of the estuary, but even where its distribution is limited it contributes to primary production and provides habitat for invertebrates and fishes. In the Hudson River, ecological and management questions related to SAV prompted a concerted effort by a team of researchers, educators, and managers to monitor its distribution, change in extent, and ecological role. Since the early biological inventories it has been clear that SAV occupies major portions of some reaches of the River, and we now know that SAV can cover as much as 25% of the river bottom. Additionally, water clarity has improved moderately since the arrival of the zebra mussel, potentially allowing these light-limited plants to spread.

New York State has been studying the SAV in the Hudson River estuary from Troy south to Yonkers (125 miles) since 1995. A partnership of Cornell University's Institute for Resource Information Sciences (IRIS), Cornell's Department of Natural Resources, the Institute of Ecosystem Studies (IES), and New York Sea Grant Extension inventoried the spatial extent of the SAV and Eurasian water chestnut (*Trapa natans*) beds from 1995, 1997, and 2002 true color aerial photography (stereo coverage, 1:14,400 scale). Vegetated area constitutes roughly 8% of total river surface area with the SAV three times as abundant as the exotic *T. natans* (4046 vs. 1521 acres in 2002).

This report summarizes the results of an ecological assessment of SAV habitats conducted on the tidal Hudson River from Hastings-on-Hudson to the federal dam at Troy between 2000 and 2004. The SAV habitat characteristics studied include water quality, invertebrates, and fishes.

B. Findings

1. SAV in the Hudson River Estuary

There are two predominant species of rooted aquatic plants in the Hudson River, the native submerged *Vallisneria americana* and the exotic floating-leafed water chestnut, *Trapa natans*. Plant coverage averaged over the entire study reach is about 6% of the river bottom area for *V. americana* and 2% for *T. natans* although the distribution of both plants varies greatly among reaches of the tidal freshwater Hudson River (Nieder et al. 2004). *T. natans*, an introduced plant, is not considered part of the SAV community since much of its biomass floats on the water surface. It has likely displaced *V. americana* in portions of the freshwater tidal Hudson. There is information available for water chestnut habitat characteristics in Caraco and Cole (2002), Hummel and Findlay (2006), and Findlay et al. (2006).

Vallisneria americana strongly dominates SAV beds in the Hudson, constituting more than 90% of SAV plant biomass. Due to light limitation, *V. americana* plants are generally found in water shallower than 3 m, although beds can be deeper in sections near Albany. Other species that make up the majority of biomass in a few locations include *Potamogeton crispus*, *Myriophyllum spicatum*, and *Najas flexilis*.

SAV bed area varies broadly from 100 to 360,000 m^2 (0.03 to 90 acres). SAV biomass was highly variable across beds also, ranging from 2.5 to 479 g dry mass/m^2. This variation was

not significantly related to position along the river or bed area. SAV biomass tended to be higher in bed interiors than along their edges, but this difference was not consistent across beds. Plant biomass also varied considerably across years in beds that were sampled in more than one year of the four-year study.

2. SAV Influence on Water Quality

Dissolved oxygen in the Hudson River is generally undersaturated (below approximately 8.0 mg/L) and SAV beds clearly have the potential to raise local oxygen concentrations. SAV beds larger than about 50,000 m^2 (12 acres) can spend as much as twelve hours out of a 24 hr period supersaturated with oxygen. Beds greater than 100,000 m^2 (24 acres) will often have supersaturated dissolved oxygen for greater than twelve hours of a 24 hr period. The cumulative area of SAV beds 400,000 m^2 or greater is 720 ha (1580 acres) or about 40% of the total SAV area. Therefore, 40% of the vegetated area represents locations of high oxygen, which may be significant for animals and may influence a variety of redox-sensitive biogeochemical processes.

For turbidity, the relationship between the proportion of time a site was highly turbid (greater than 40 NTU) and bed area was not significant. Turbidity showed extreme variability across the course of a day, with peak values of several hundred NTU. The median turbidity did not differ between SAV and open water and the highest medians observed were practically identical. The degree of turbidity at a point within a SAV bed was affected by the area of SAV in a 300 m radius neighborhood suggesting a cumulative rather than patch-specific control on local suspended sediment concentration.

3. Aquatic Invertebrate Dependency

SAV beds in the Hudson support dense and diverse macroinvertebrate communities. Densities of macroinvertebrates in SAV beds were more than three times as high as densities on

unvegetated sediments; sometimes surpassing 100,000 individuals/m^2. This strongly indicates that SAV beds may be the richest feeding grounds in the Hudson River estuary for fish. Further, many species of macroinvertebrates that are common in plant beds are rare or absent from unvegetated sites. Thus, SAV beds play important roles in maintaining high population densities and high biodiversity of macroinvertebrates in the Hudson.

The macroinvertebrate community of plant beds in the Hudson includes a long list of species from seven phyla. Chironomid midges, oligochaete worms, hydroids, gastropods, and amphipods are especially abundant and widespread. In fact, if SAV beds were to be removed from the Hudson, and macroinvertebrate populations fell to those typical of unvegetated sediments, 13% of the macroinvertebrates in the river would be lost.

Macroinvertebrate density was strongly related to plant biomass in the beds; the higher the plant biomass, the more the invertebrates. Position within the plant bed also strongly affected macroinvertebrate density, with densities in the interiors of plant beds more than two times higher than along their edges. Macroinvertebrate density was unrelated to position along the river or area of the plant bed, which indicates that all SAV beds are equally important for supporting macroinvertebrates regardless of bed size or position along the estuary.

Perhaps more importantly, SAV beds are "hotspots" for populations of prey items for fish. Dozens of species of invertebrates are specialized for life among SAV beds and are rare or absent elsewhere. Thus, SAV beds play an essential role in supporting the biodiversity of invertebrates in the Hudson.

4. Fish Dependency

SAV in the Hudson River estuary supports more fish, a greater diversity of species, and provides a greater food supply as compared to unvegetated substrates. The dominant food items

consumed by fish are also the dominant species found in SAV and these invertebrates were significantly reduced on artificial substrates placed in SAV that were exposed to fish predation. While SAV provides valuable habitat for fish, the precise benefits and fish responses vary by location and by fish community composition. We identified three distinct fish assemblages in SAV beds along the estuarine gradient from Troy to Yonkers. The upper freshwater estuarine fish community was largely composed of resident freshwater fishes (e.g., spottail shiner, American eel, and common carp). The lower freshwater zone fish community includes resident freshwater fishes combined with abundant anadromous species (dominant species were white perch, spottail shiner, and banded killifish). SAV had the largest positive effect on fish abundances and species diversity in the upper freshwater zone where most fish orient to structure or cover, prefer vegetated surroundings, and consume organisms supported by vegetation.

The brackish portion of the estuary yielded the fewest species, primarily generalists (e.g., white perch) and other pelagic fishes common in estuarine and marine waters. White perch, white catfish, and spottail shiner dominated the SAV beds in the brackish part of the estuary. In this zone, SAV did not support greater numbers of fish than unvegetated areas, but SAV did support slightly more species. Most of the highly abundant fishes are pelagic-oriented (open surface water) species that feed primarily on plankton. Some pelagic fishes avoid vegetation and structure, preferring to remain in turbid, plankton-rich open waters; others are widely distributed without regard to SAV.

Larval fish often concentrate in still and structured habitats, and we captured a variety of small and larval fish in both SAV and unvegetated shallow waters. However, we did not find a significant effect of SAV on larval fish numbers. Unlike SAV beds in some lakes and estuaries that create still water habitat, many SAV beds in the Hudson River had current velocities higher

than the swimming capacity of larval fish. Thus, larval fish would not be able to remain in most SAV habitats in the Hudson River through a tidal cycle.

C. Summary

Despite the obvious shifts in the kinds of plants and animals that live in SAV beds, there are only minor differences in the use of SAV beds along the course of the Hudson River Estuary. While the taxonomic composition of the organisms may change along the River, their higher abundance in SAV versus unvegetated areas points to the value of SAV as habitat. Neither overall plant biomass nor density of invertebrates varied along the course of the Hudson indicating that SAV beds in different parts of the river are equally important for supporting macroinvertebrates. The impact of SAV beds on dissolved oxygen and turbidity likewise did not change in any simple way with river kilometer. Throughout the freshwater Hudson River, SAV clearly supported a greater number of and a higher diversity of fish. Though this link to SAV was not as strong in the brackish zone, fish diversity was still higher in SAV beds. There also exists a strong link between the rich macroinvertebrate community found in the SAV and fish foraging.

Submersed aquatic vegetation in the Hudson River performs an array of valuable ecological functions throughout the River and these are summarized below in the comparison between SAV and unvegetated areas (Table A). Two important findings of this research are that the performance of several of these functions is contingent on the spatial context (nature of the surrounding area) and different functions have different controlling factors. This spatial contingency and variety in regulatory factors leads to large inter-annual variation in overall performance of SAV in the Hudson.

Table A. Summary table of ecological variables across habitat and river zone with ecological predictors

Ecological Variable	Habitat, SAV vs. Unvegetated	River Zone	Strongest Predictors
Dissolved Oxygen	Higher in SAV	Strongest contrast in freshwater	Bed size, Position along river
Turbidity	Higher in SAV	No pattern	SAV in 300 m neighborhood
Invertebrate abundance	Higher in SAV	Everywhere	Plant biomass
Fish species richness and abundance	More in SAV	Highest in freshwater	Bed size

D. Recommendations for Future Research and Monitoring

1. Inter-annual monitoring

This study has provided clear evidence of the importance of SAV but also significant temporal variation in plant abundance, spatial coverage, and degree of ecological functioning. Some effort to track this variability to separate fluctuations from long-term trends is critical for future management of the resource.

2. Invasive fish species

There is a high potential for invasion of the Hudson by herbivorous fishes (several carp species from the Mississippi basin for example). These exotics could have large, negative impacts on the native SAV and there should be strong efforts to prevent their invasion and plan a response.

3. Potential SAV habitat

One of the major gaps in our knowledge is the potential habitat for occupation by SAV. The bathymetry of the Hudson has been well-described for areas deeper than about 4 m but the

critical depths for SAV across most of the river are shallower than 3 m so we are ignorant about where SAV expansion might occur given changes in water clarity. Some effort to determine the shallow water bathymetry would strengthen predictions about future change in SAV coverage.

E. Management Implications

The findings from this four-year study have clearly established the vital role SAV communities play in maintaining water quality and supporting both fish and macroinvertebrate communities in the Hudson River Estuary. SAV beds are literally the support systems for many native forms of life that could not otherwise maintain viable populations after the arrival of zebra mussels in the early 1990s, due to the significant and ecosystem-wide negative impacts of the mussels. These findings are true for all SAV beds, regardless of their size and location in the estuary, and on both an individual and cumulative basis. These results have important implications for regulators, land managers, and resource managers, among others.

We believe our findings justify full protection for SAV by State and Federal regulatory agencies with the responsibility for regulating SAV under a variety of laws and regulations. Strong regulatory protection is warranted for all SAV beds, and their destruction or reduction in size should be assiduously avoided and only permitted under the most extraordinary and stringently controlled circumstances. Although larger beds provide higher levels of ecological function than smaller beds, all provide critical habitat and water quality enhancements. Loss of or damage to individual beds will result in cumulative losses to the Hudson River Estuary ecosystem.

One of the most evident uncontrolled negative impacts to SAV beds is scarring by boat propellers. This impact should be reduced through a variety of methods including 1) avoiding

the establishment of new launch sites and marinas in or near SAV beds, 2) marking the perimeters of SAV beds near boat launch sites and marinas, and 3) boater education.

Regulators and managers should not assume that a one-time field assessment of an individual SAV bed by permit applicants can be used to justify reductions in SAV bed size or value. We measured high year-to-year variability in the size and density of beds, and one-time field assessments are likely to over- or underestimate an SAV bed's attributes. Based on the findings of this study, it is prudent to assume all SAV beds are of high ecological importance unless future research suggests otherwise. It is likely that future research will identify other important ecosystem roles of the Hudson River Estuary SAV communities, for instance habitat for aquatic bird life.

Mitigation, restoration, and creation of Hudson River Estuary SAV beds are not viable options at present. Our observations of the Hudson River Estuary, coupled with studies of recent scientific literature and interactions with professionals working on SAV restoration in other systems, indicate that it is difficult or impossible to replace freshwater and low salinity SAV beds given present knowledge and technology.

There is a need to generate periodic inventories of the Hudson River Estuary SAV communities in order to track changes over time in SAV coverage, community composition, and ecological function. We recommend this be done about every two to five years given the scale and scope of change observed in SAV over the last decade. This information, including the latest scientific information about the ecological functions and importance of these beds, should be conveyed in a timely way to the wide range of regulators and resource managers who are engaged in protection and management of the SAV resource.

II. INTRODUCTION

A. Scope

Submerged aquatic vegetation (SAV) represents an important component of most aquatic ecosystems. SAV includes rooted plants where the bulk of biomass is beneath the water surface. In almost all assessments of aquatic ecosystem "health" or "status" there is some measure of SAV performance or extent. SAV has been extensively researched in many aquatic systems, and increasing the extent of native SAV is an important conservation goal (e.g., Chesapeake Bay Program 2005, Freshwater SAV Partnership 2005). SAV may be spatially extensive but even where its distribution is limited it may contribute to primary production and provide habitat for invertebrates and fishes. In the Hudson River, there are several ecological and management questions related to SAV, and this prompted a concerted effort by a team of researchers, educators, and managers to monitor its distribution, change in extent, and ecological functioning. Since the early biological inventories it has been clear that SAV occupies major portions of some reaches of the River, and we now know that cover can be as high as 25% of the river bottom (Nieder et al. 2004). Additionally, water clarity has improved moderately since the arrival of the zebra mussel (Strayer et al. 1999) potentially allowing expansion of these light-limited plants (Harley and Findlay 1994). One of the more obvious invasive species in the Hudson, water chestnut (*Trapa natans*), has the potential to displace native SAV which has justified efforts to monitor cover by these plants. Lastly, there is the possibility that a range of human activities from recreational boating to shoreline modification may damage SAV plant beds. Any potential regulatory activity requires maps of present plant distributions and documentation of their ecological value. For all these reasons, work on mapping plant distributions was initiated in

1995 (see Nieder et al. 2004), followed by a research program to document ecological processes associated with SAV in the Hudson River.

This report summarizes the results of a functional assessment of submerged vegetation habitats in the tidal freshwater Hudson River. Based on information about the spatial distribution, extent, and characteristics of SAV in the study reach, an assessment was made of effects of SAV beds on water quality and habitat suitability for invertebrates and fishes. Functions chosen for inclusion were based on previous evidence that SAV beds contributed substantially to those functions, as well as the level of interest by DEC. The report is broadly organized around topics including SAV characteristics, water quality, invertebrates, and fishes, and for each of these we deal explicitly with both spatial and temporal variability. The Results and Discussion are combined for each topic and the Significance and Synthesis section draws connections among the separate topics. Management implications and recommendations for the future are covered in the executive summary.

B. The Hudson River Setting

The tidal freshwater Hudson (Fig. 1) extends from the head of tide at the Federal dam in Troy, NY (250 km above the Battery in NYC) to the brackish lower river about 53 km above the Battery. Tidal range varies from 1 to 1.5 m over the neap-spring cycle with maximum currents greater than 1 m/s. The average depth is 11 m with extensive shallows in some reaches flanking the 10 m deep navigation channel. Water is fairly hard with moderate nutrient concentrations: dissolved inorganic nitrogen averages 40 μM and dissolved inorganic phosphorus 1 μM (Lampman et al. 1999). Turbidity is moderate, with suspended sediment concentrations averaging 11 mg dry mass/L; light penetration in the summertime is such that the 1% light level

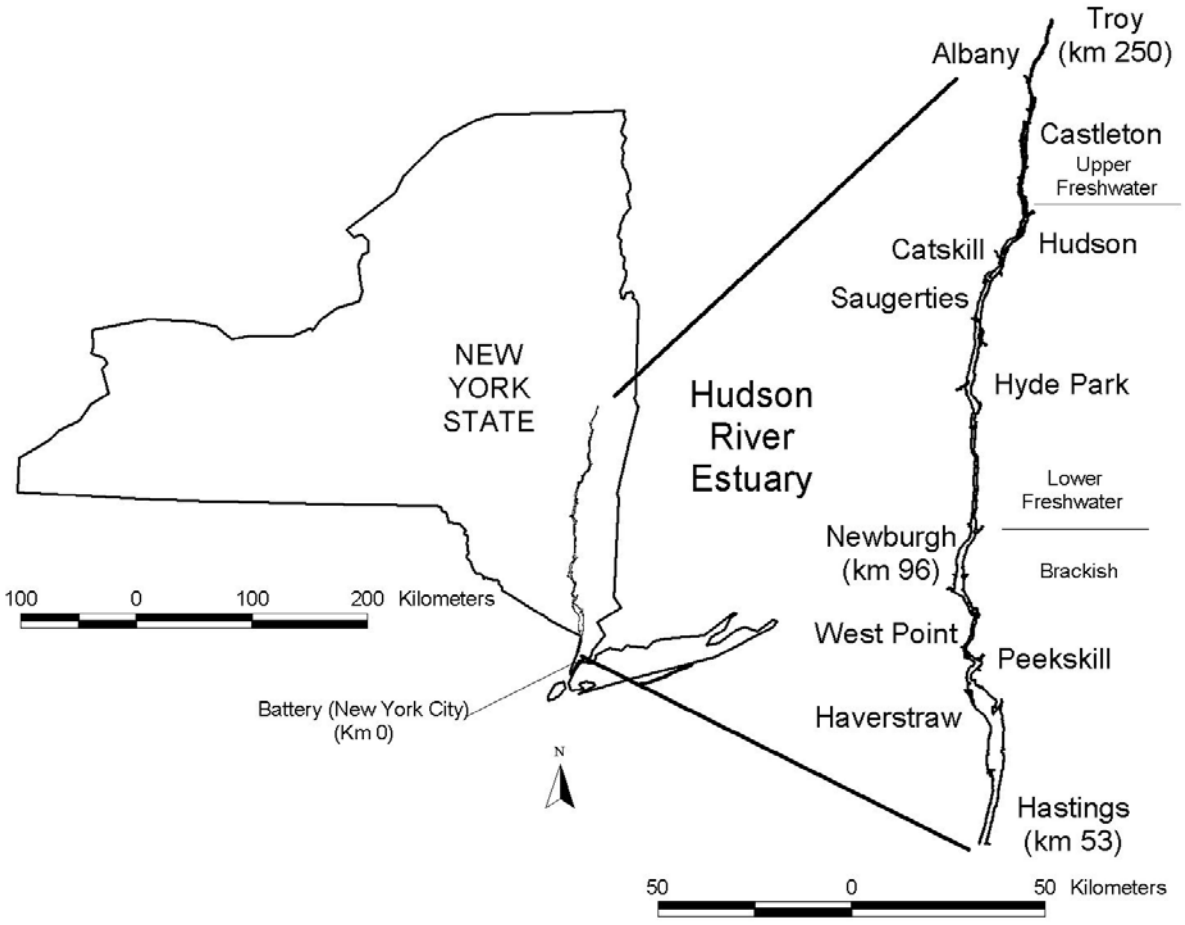

Figure 1. Map of the Hudson River indicating the three zones described in the text. Modified from Nieder et al. 2004.

occurs at about 2.5 m depth. The study region covers three zones as described below.

1. Upper Freshwater Zone: Troy Dam to New Baltimore, River km (Rkm) 250 to 207 (miles 155 to 129).

From Troy downstream to the town of New Baltimore, the Hudson River is confined to a narrow channel that has been greatly modified for ship passage. Much of the river width is a dredged shipping channel and the shorelines are often stabilized and backfilled. This leaves little area of subtidal habitat aside from a narrow nearshore band. SAV is mostly confined to long, thin strips (linear SAV features, described in more detail under Site Selection in the Methods) that parallel the shoreline. The limited area of near shore but undredged habitat is typically 3 to 6 m deep. Water clarity is generally much greater than downriver. Salt water never reaches this far upriver, but tidal amplitude is equal to or greater than downriver.

2. Lower Freshwater Zone: New Baltimore to Newburgh, Rkm 207 to 96 (miles 129 to 60).

This zone is largely fresh water although the most downriver portion can be slightly brackish during period of low river discharge in dry years. The zone includes four of the geomorphic sections of the Hudson River estuary described by Coch and Bokuniewicz (1986): bifurcating channel-shoal, meander segment, narrow river, and wide river. Each of these sections of the freshwater zone differs in channel form. The most upriver section, bifurcating channel-shoal, extends to around Kingston. This part of the Hudson River has many shallow areas and islands in the channel and numerous tributaries with deltaic deposits. Maximum depths are as much as 15 to 17 m, and the channel ranges from 0.3 to 1.0 km wide. Flats, numerous backwaters, stream mouths, and side channels support a wide variety of SAV beds.

From Kingston to Staatsburg, the river meanders with broad flats associated with bends. The channel is typically 0.6 to 1.0 km wide with maximum depths 22 to 31 m. Several

tributaries have created shallow sediment deposits including a large sediment flat downstream of the mouth of Rondout Creek. Several of the largest SAV beds in the Hudson River are in this reach. From Staatsburg to Wappingers Creek the Hudson River is narrow; there are few broad flats and shallows for large SAV beds, and only two study sites were in this section. The river is commonly 0.8 to 1.2 km wide with maximum depths from 29 to 42 m. From Wappingers Creek to slightly below Newburgh, the river is often called Newburgh Bay because of its large width (1.0 to 1.4 km) and shallower depth (maximum 15 to 18 m). Coch and Bokuniewicz (1986) label this section as a wide river. Slightly brackish water reaches into this section during dry years. Turbidity is relatively high, and only one SAV study site was located in the area.

3. Brackish Zone: Newburgh to Hastings, Rkm 96 to 53 (miles 60 to 33).

The Hudson River in this zone is consistently brackish during summer flow conditions with salinity levels varying in response to tides and river discharge. Coch and Bokuniewicz (1986) divided this zone into two different morphological segments: Hudson Highlands and wide estuary. From below Newburgh to Peekskill, the river is narrow (0.5 to 0.8 km), deep (maximum 28 to 48 m), turbulent, and mostly a steep-sided rock channel with minimal shallows. Large rock formations in the channel and broad bends create shallow backwaters supporting SAV. Below Peekskill the river emerges into a broad (1.0 to 1.5 km) and shallow (maximum depth about 13 m) section termed a wide estuary. The section is often called Haverstraw Bay. Large flats extend from shore to the shipping channel, and shoreline features provide protected shallow waters. Despite the shallow water, SAV beds were not common in this reach of the Hudson, perhaps because of the generally high turbidity.

C. Submerged Aquatic Vegetation (SAV) in the Hudson River

There are two predominant species of rooted aquatic plants in the Hudson River, the native submerged *Vallisneria americana* and the exotic floating-leafed water chestnut, *Trapa natans*. Plant coverage averaged over the entire study reach is about 6% of the river bottom area for *V. americana* and 2% for *T. natans* although the distribution of both plants varies greatly among reaches of the tidal freshwater Hudson River (Nieder et al. 2004). Beds of both species vary in size from 30 m^2 (the minimum mapping unit) to a maximum of about 100 ha (1 million m^2). Bed size distributions for *V. americana* are strongly log-normal with far more small beds than large. Due to light limitation plants are generally found in water shallower than 3 m, although beds can be deeper in the most upriver sections.

D. Review of SAV Influence on Water Quality

Submerged aquatic vegetation (SAV) has well-documented effects on water quality and physical conditions in a wide array of lake, river and estuarine ecosystems (e.g. Carpenter and Lodge 1986; Carter et al. 1991). In many cases, SAV standing stocks and photosynthetic rates are sufficient to elevate dissolved oxygen (DO) concentrations for a significant portion of daylight hours (Rybicki et al. 1997) although there are also reports of low DO at night (Carter et al. 1988). The extent to which submerged plants elevate local DO will be a function of several variables, perhaps most importantly the actual biomass and areal extent of plants and their photosynthetic capacity under ambient conditions. Physical conditions affecting gas solubility will affect the degree to which oxygen produced by the plants contributes to local accumulation of DO. Short water residence times in vegetated areas or very rapid gas exchange with the atmosphere will limit fluctuations in concentrations. Some plants may vent oxygen directly to

the atmosphere and so will not contribute to diel DO increases (Caraco et al. 2002).

SAV can also have significant effects on water currents and turbulence such that the capacity of water masses to transport particles or keep particles in suspension is diminished (Fonseca et al. 1982; Harlinand Thorne-Miller 1982; Carpenter and Lodge 1986; Losee and Wetzel 1988). Particle trapping may lead to increased material retention (Rooney and Kalff 2003), increased rates of sedimentation and decreased resuspension of fine-grained sediments (Kenworthy et al. 1982; Kemp et al. 1984; Ward et al. 1984; Posey et al. 1993; Rooney et al. 2003). Plant biomass and architecture influence the degree to which sediment dynamics are affected, with denser beds of plants that occupy a greater proportion of the water column generally having the largest effects (Vermaat et al. 2000). Plants may indirectly lead to increased resuspension if sediment accumulation is sufficiently rapid to raise bed sediments to an elevation where they are subject to greater shear stress (Koch 1999).

Aside from altering sediment accumulation, submerged plants are expected to affect sediment chemistry by depleting porewater nutrients and potentially transferring oxygen to deeper sediment layers. In the Hudson we did not find evidence for draw-down of porewater nutrients over the course of a growing season (Wigand et al. 1997) due to the sediment trapping capacity of the SAV beds studied. There have been quite a few studies of rhizosphere oxidation by submerged plants (Christiansen et al. 1998) and the extent to which this occurs depends on plant species, capacity for photosynthesis and chemical reducing power of the sediment itself. Sediment redox status will affect phosphorus availability, metal solubility, and activity of diverse microbial groups.

We examined the capacity of beds of *Vallisneria americana* to influence local DO and suspended sediment concentrations in the tidal freshwater Hudson River considering local,

neighborhood and reach-scale controls. Local effects are those associated with the characteristics of the actual patch sampled, neighborhood scale extends to a few 100 m radius, and reach-scale considers position along the entire study reach (10's of km). DO in the Hudson is generally undersaturated due to the heterotrophic nature of the ecosystem (Howarth et al. 1996; Findlay et al. 1998; Cole and Caraco 2001) and high metabolic demand by zebra mussels (Caraco et al. 2000). Low DO due to sewage inputs is still an occasional problem in the upper reaches around Albany and in New York harbor although there has been a general and substantial improvement in water quality since the 1970's. Phytoplankton are strongly light-limited due to moderate turbidity and a well-mixed water column (Cole et al. 1992) and SAV is generally limited to water depths less than 3m (Harley and Findlay 1994). Turbidity during summer low flows is governed by resuspension rather than loadings from the catchment (Findlay et al. 1996), so there is the potential for vegetated regions to improve water clarity.

E. Review of SAV Role in Supporting Animals

Macrophytes are a key feature of aquatic environments because of their role in shaping the physical environment, and creating habitat for invertebrates and fish (Carpenter and Lodge 1986; Engel 1990). SAV beds create complex structured habitats used by many aquatic organisms. The surface area of plants can be 30 to 50 times larger than unvegetated substrate (Engel 1990), and this added space and structure harbors small fish and invertebrates. The high surface area provided by macrophytes provides a unique habitat for epiphytic animals, which is likely to contribute to the high macroinvertebrate productivity in macrophyte beds. The physical complexity provided by macrophyte beds provides an effective refuge against predators, leading to locally dense populations of invertebrates and small fish that are susceptible to predators. The

physical structure that macrophytes provide may also offer an important habitat for animals that favor the reduced currents and soft sediments typical in many macrophyte beds.

Plant surfaces are colonized by diatoms, algae, small insects, oligochaetes, and crustaceans, and these organisms will contribute to the abundance and diversity of organisms in the water column. Macrophyte beds are sites of high primary production by the plants and their attached epiphytes. Together with organic matter trapped by the beds, this results in high local food availability for herbivores, and ultimately for their predators, including fish. Many studies have shown that SAV beds can essentially create a local community and food web entirely unlike what would be present in an open unvegetated state (Engel 1985; Dibble et al. 1996, Strayer et al. 2003).

III. METHODS

A. Site Selection

The general study design was intended to encompass beds of submerged vegetation that spanned a wide range of sizes over the entire study area (Fig. 1 and 2). We defined five classes of beds. The first three were based on the area of the bed: small (55-1097 m^2, or roughly 10-37 percentile in the size distribution of beds in the river), medium (1098-8103 m^2, or 37-63 percentile), and large (8104-59,874 m^2, or 63-90 percentile). We selected beds randomly within each size class for sampling. We rejected randomly chosen beds if they were near sites 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 213-130 (mostly lower freshwater zone). In 2001, we sampled two beds in each size category between Rkm 130-53 (brackish and lower freshwater zones). In 2002, we sampled four linear features between Rkm 250-213 (upper freshwater zone). Linear features 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, five very large beds having areas of 88,592-250,747 m^2 were designated as "keystone" beds: Cheviot (bed # 504, Fig. 2), Cruger South (601), Esopus Meadows (688), Iona (1069), and Peekskill (1079). These were sampled every year from 2000 or 2001 to 2005, although there is not a complete set of data for all site-year combinations.

All bed characteristics such as size or shape were based on the digital coverage derived from 1997 aerial photographs. A newer coverage based on 2002 photographs showed that

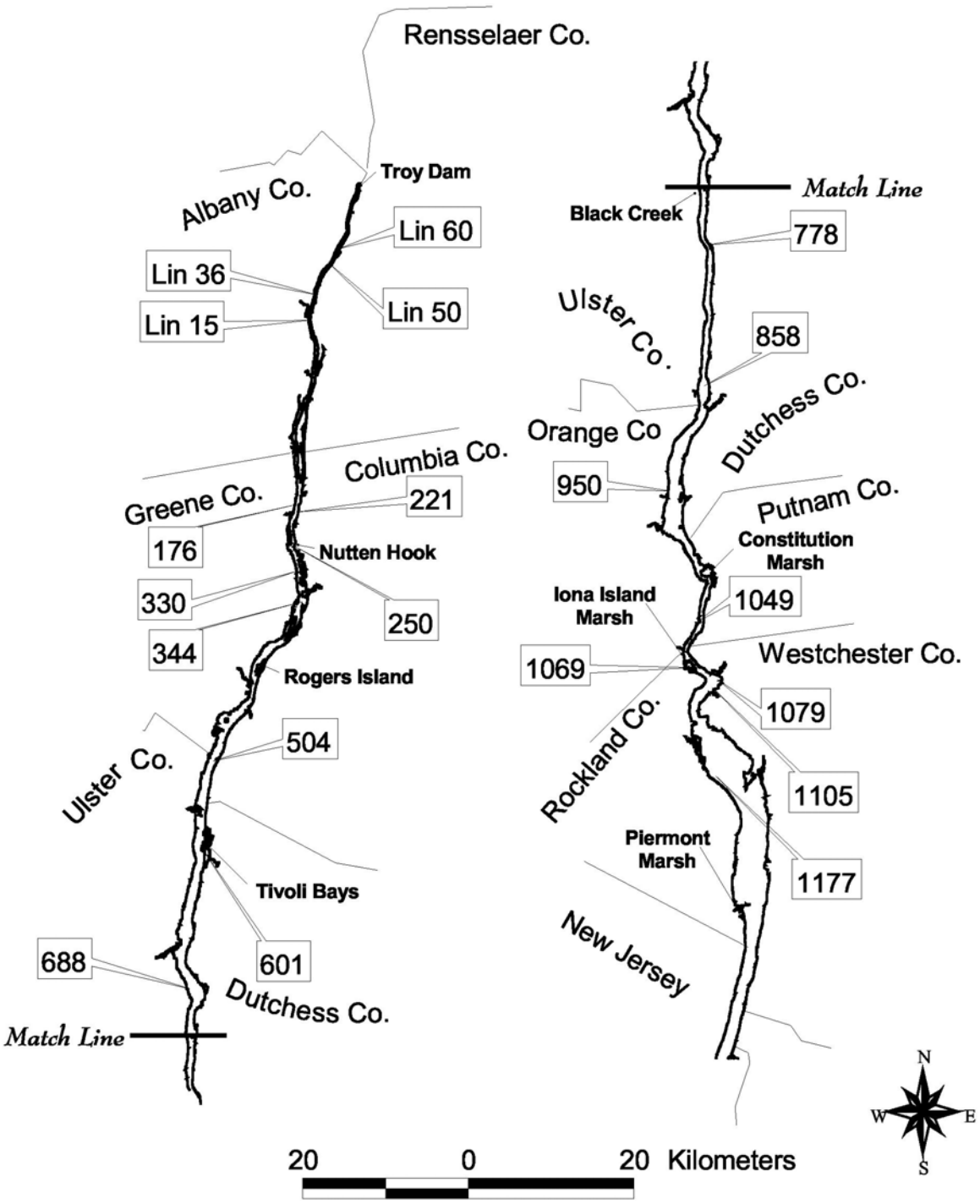

Figure 2. Map of SAV study sites, with bed identification numbers referred to in text.

overall there was a significant correlation (r = 0.94) between surface area of study beds in 1997 and 2002, although there were sites that changed by as much as five-fold. The largest percentage changes were increases in mapped area for some small beds, generally due to amalgamation with adjacent SAV beds. Details on mapping variables are provided in Appendix 1. Bed shape was characterized by two variables, the ratio of maximum length to width at midpoint and a shape index calculated by Patch Analyst software.

B. Plant Demographics: Biomass and Species Composition

Macrophytes were sampled using a standard (23 x 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 size beds and at Indian Point (1105), we took a total of eight PONAR samples scattered throughout the bed. We clipped vegetation in 0.25 m^2 quadrats in the linear features and at Quassaic (950), where the sediments were too hard for the PONAR grab. We also clipped quadrats at Stuyvesant (221) in 2003. We sampled 4-12 quadrats per site, depending on the size of the bed, plant density, and available time. In 2003 at Peekskill (1079), we clipped sixteen 0.79 m^2 circular quadrats. For all samples, we included only above-ground plant parts. 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^{o}C before weighing them.

C. Sediments

We took core samples for sediment analysis at six sites within each bed. In keystone beds, large beds, and medium-size 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, linear features, and at Indian Point (1105), we simply spaced the six samples widely through the bed. Samples were taken in August to coincide with peak plant biomass. 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 hand-held corer (20.2 cm^2 cross-sectional area), put into a cooler, and frozen upon return to the laboratory. Samples were later thawed and dried at 60^oC for at least 24 h. Granulometry (% 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 hours at 500^oC.

D. Dissolved Oxygen, Turbidity, and Water Exchange

We deployed YSI Sondes at the approximate centroids of *V. americana* beds for 3-7 days to obtain high frequency, continuous observations of DO, turbidity, temperature, pH and depth. For each period of sonde deployment in vegetated areas, we deployed a sonde in nearby deep water to track the same variables in the absence of direct plant effects. The oxygen, pH, and turbidity probes on each sonde were calibrated in the lab prior to deployment following YSI protocols. The oxygen probes were checked for drift by comparing pre- and post deployment oxygen values in water-saturated air at ambient temperature.

Sonde data for a site were condensed into two summary statistics for each variable. Median DO and turbidity values were calculated for the duration of each sonde deployment. Also, we calculated the proportion of time DO at a site was above 8 mg/L (approximate saturation value for summertime temperatures) and the proportion of time turbidity was above 40 NTU (arbitrary value representing about 4X the turbidity in the main channel).

Water exchange between plant beds and open water was estimated by releasing a plug of fluorescein dye (about 4 L of a 1:16 dilution of dye concentrate) at the bed centroid, and collecting water samples at known locations as the dye cloud drifted during an ebb tide. Fluorescence in water samples was measured in the laboratory on a Perkin Elmer LS-50 at 515 nm. We conducted dye releases at approximately mid-ebb tide for comparability among releases. Velocities estimated at various times during the ebb tide cycle were corrected to velocity at mid-ebb tide assuming velocity varied sinusoidally over a tidal cycle.

E. Macroinvertebrates

We sampled macroinvertebrates using two different methods. Animals living in the sediments were collected using a hand-held coring tube (20.2 cm^2 cross-sectional area) at the same six sampling points per bed used to collect sediment samples. Three cores about 5 cm long were taken from each sampling site and pooled in the field. No sample of sediment-dwelling macroinvertebrates was taken if the sediments were too coarse to be sampled with the hand-held corer. This occurred only at Quassaic (950) and at eight points in the linear features. Macroinvertebrates living on macrophytes were collected with a Downing box sampler (Downing 1986). Generally, we collected three Downing samples per site, which were pooled in the field.

All samples were sieved through a 0.5mm mesh sieve and preserved in buffered 10% formalin in the field. We sorted samples under 6X-12X magnification, and placed animals 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) of oligochaetes, chironomids, and nematodes were slide-mounted in CMC-10 on microscope slides prior to identification. Most animals 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). Voucher specimens have been deposited in the American Museum of Natural History, New York City.

We used nonmetric multidimensional scaling (NMS), an ordination technique (McCune and Grace 2002), to express variation in macroinvertebrate community structure across sites. NMS uses information on the types of animals 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. Ordination scores can be regressed against environmental factors (e.g., location along the river, plant biomass) to identify which factors are related to variation in the overall composition of the macroinvertebrate community.

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 software using the autopilot mode.

F. Fish

Fish sampling focused on the lower freshwater zone in 2000, on the brackish and lower

freshwater zones in 2001, and on all three zones in 2002 and 2003. We sampled fish from SAV beds (labeled as SAV in figures), linear features (LSAV in figures), or nearby unvegetated sites without significant SAV but with similar habitat features such as distance to shore, water depth, and water movement (unvegetated, UNV in figures). Some but not all sites in each category were sampled in multiple years; see Table 1 for sampling details. Fish larger than 25mm total length were sampled. Some fish sampling methods were modified among sites or years as detailed below. In concert with fish sampling, we used a YSI model 33 S-C-T meter to measure salinity, conductivity and water temperature at each site.

Juvenile and adult fish were sampled by carefully standardized applications of gill nets (passive capture gear) and/or electrofishing (active capture gear). Total length of each fish was measured and they were released, with the exception of those retained for identification or diet analysis. Adult and larval fish used for species identification and counts were fixed in a 10% formaldehyde solution and later preserved in 70% ethanol; those kept for stomach contents were anesthetized with ice and then preserved in 70% ethanol.

Simple diet analyses were conducted on field-preserved adult fish of the most commonly encountered species. Identification of stomach contents was completed in the laboratory under 40X magnification following the simple frequency of occurrence diet analysis of Bowen (1996). White perch, *Morone americana*, were used with the following exceptions where white perch catch was low. At the Rogers Point site (778) in 2001 golden shiners, *Notemigonus crysoleucas*, were used. In 2002 and 2003 in the upper freshwater river most analyses were done with other non-detritivorous species, primarily sunfish and perch (families Centrarchidae and Percidae).

Standard electrofishing consisted of a 15 minute session using an aluminum boat (4.87m in 2000 and 2001, 6.5m in 2002), outfitted with a Smith-Root pulsator. Settings of 345 Volts

Table 1. Days of fish fieldwork by year with sampling zone, habitat type, and other site identifying information.

Site Name (Bed ID#)	River km	River Zone	Habitat type	Fish sampling				Fish diets				Larval fish			Invertebrate Experiment
				2000	2001	2002	2003	2000	2001	2002	2003	2000	2001	2002	
Lin 60	239	Upper Freshwater	LSAV			3	3			1	1			2	1
Lin 50	237		LSAV			3	3			1	1			2	1
Lin 36	234		LSAV			3				1				2	
Lin 15	230		LSAV			3	3			1	1			2	1
60 UNV	239		SAV				3				1				
P50 (16)	237		SAV				3				1				
P15 (34)	230		SAV				3				1				
Lin 95	248		UNV			3								2	
Lin 1	228		UNV			3									
Mill Creek (169)	202	Lower Freshwater	SAV	3	1			1				1	1		
Stuyvesant (221)	200		SAV	4	1		4				1	1	1		1
NuttHk (250)	197		SAV	3	1			1					1		
Stockp (344)	191		SAV	3	1			1				1	1		
Cruger South (601)	156		SAV	4	2	4	4	1		2	1	1		2	1
Esopus Meadows (688)	139		SAV	3	2	4	5	1		1	1			2	1
Rogers Point (778)	127		SAV		3				1				2		
Stuyvesant UNV (221)	200		UNV	6	3								1		
NuttHk UNV	198		UNV	3	1								1		
Stockp UNV	191		UNV	6	2								1		
Vanderburg UNV	138		UNV		3	3			1	1			2	1	
ConHook (1049)	80	Brackish	SAV		6				1				2		
Iona (1069)	74		SAV		4	3	3		1	1	1		2	2	
Peekskill (1079)	71		SAV		3	3			1	1	1		2	2	1
Indian Point (1105)	70		SAV		3				1				2		
Haverstraw (1177)	59		SAV		3		3		1		1		2		1
Peekskill UNV	71		UNV		3	3			1				2	2	
Croton UNV	54		UNV		3				1				2		

direct current and 120 pulses per second remained constant across all sites, however, pulse width was adjusted from 3.0 to 5.5 ms to maximize the output amperage on a site-by-site basis. Keystone sites (Cruger South (601), Esopus Meadows (688), Iona (1069), and Peekskill (1079)) received a 15 minute electrofishing session in each of two subareas to provide good coverage of the vegetated habitat. Electrofishing cannot be used in highly conductive water (i.e., water with measurable salinity) and this gear was not used in the brackish zone.

Standard gill net samples were 30 minute sets of four 8.0 x 1.8 m nets that differed in stretch mesh sizes: 10, 5, 3.75 and 2.5 cm. Twice as many sets were deployed in the large keystone beds. The gill nets were anchored to the river bottom but extended up to or near the water surface. Gill nets were set during slack tide and all gears were deployed to avoid interference among sampling gears. Gill nets could not be used within linear features because of their small size so all linear features were sampled only with electrofishing.

Larval fish were collected at four SAV sites using a set of eight to ten custom-built quatrefoil light traps, modeled after a design developed by Secor et al. (1992). The larval fish traps were deployed at sunset with chemical light sticks for fish attraction and retrieved close to sunrise. A buoyant top collar kept the traps positioned just under the water surface. In 2002, half (four or five) of the larval fish light traps set at a site were anchored about 0.3 m above the substrate, and the other half were subsurface sets. Captured fish larvae were preserved in the field in a 10 % formaldehyde solution and later preserved in 70% ethanol. They were identified to family or lower at 40X magnification. Larval fish light trap sampling was not repeated in 2003.

New in 2003 was an experiment to test for the effect of fish predation on macroinvertebrates in SAV habitats. Modified Hester-Dendy multi-plate, artificial substrate

macroinvertebrate samplers (Hester and Dendy 1962, Acorn Naturalists 2002) were placed in eight vegetated sites throughout the Hudson River (see Table 1; an additional sampler was lost at Iona (1069)). This deployment included two sets of three multi-plate samplers per site, one set enclosed in a milk crate covered by 4 mm mesh and the other left open. Modifications from standard nine or fourteen plate sampler designs involved construction details: five 7 cm diameter circular Masonite® plates spaced with 3 cm lengths of 1.6 cm polyvinyl chloride pipe connected by a 21.5 cm eyebolt. We affixed each set of multi-plate samplers to a 13.5 kg patio tile, spaced 20 cm apart, effectively sampling 0.15 m^2. Figure 3 shows our modified sampler designed to allow forage access by fish while still providing cover for macroinvertebrates.

Screened and open Hester-Dendy samplers were deployed within the same vegetation habitats spaced 2 m apart. Samplers were deployed between August 6 and 9, 2003, and remained in place for a month or slightly longer. The Hester-Dendy samplers were recovered by a skin diver who removed enclosures, placed a mesh bag over each sampler underwater, and slowly lifted the entire unit to the sugoorface. Each sampler was then disassembled and macroinvertebrates were rinsed and gently brushed into a pan with a toothbrush. Samples were preserved in 70% ethanol and stored for identification and enumeration in the laboratory. All macroinvertebrates were identified to the lowest practical taxon (in most cases family).

Figure 3. Open (top) and screened (bottom) Hester-Dendy artificial substrate sampler units for the macroinvertebrate colonization experiment.

IV. RESULTS AND DISCUSSION

A. General Bed Characteristics

As described above, SAV bed area varied broadly from 100 to 360,000 m^2. Measures of bed shape were also variable with length/width ratios ranging from 1.2 to 400 and the shape index ranging from 1.0 (approximately circular) to 5 (elongated). Bed area and river kilometer were only weakly correlated ($r^2 = 0.09$, $p = 0.27$, excluding linear features).

B. Plant Demographics: Biomass and Species Composition

Macrophyte biomass was highly variable across beds, ranging from 2.5 g dry mass/m^2 at Peekskill (1079) to 479 g/m^2 at Quassaic (950). This variation was not significantly related to position along the river or bed area (Fig. 4). Macrophyte biomass tended to be higher in bed interiors than along their edges, but this difference was not consistent across beds and was not significant ($p = 0.14$, paired t-test). Biomass also varied considerably across beds that were sampled in more than one year (Appendix 1). For instance, macrophyte biomass at Esopus Meadows ranged from 6 to 268 g dry mass/m^2 over the four years of our study. For the keystone sites resampled over four years, plant biomass varied by almost 10-fold.

Vallisneria americana strongly dominated submersed macrophyte beds in the Hudson, constituting > 90% of plant biomass overall. Other species made up the majority of biomass at a few of the sites with soft sediments in the lower half of the study area: *Potamogeton crispus* at Peekskill (1079) and Indian Point (1105), *Myriophyllum spicatum* at Iona (1069), and *Najas flexilis* at Rogers Point (778).

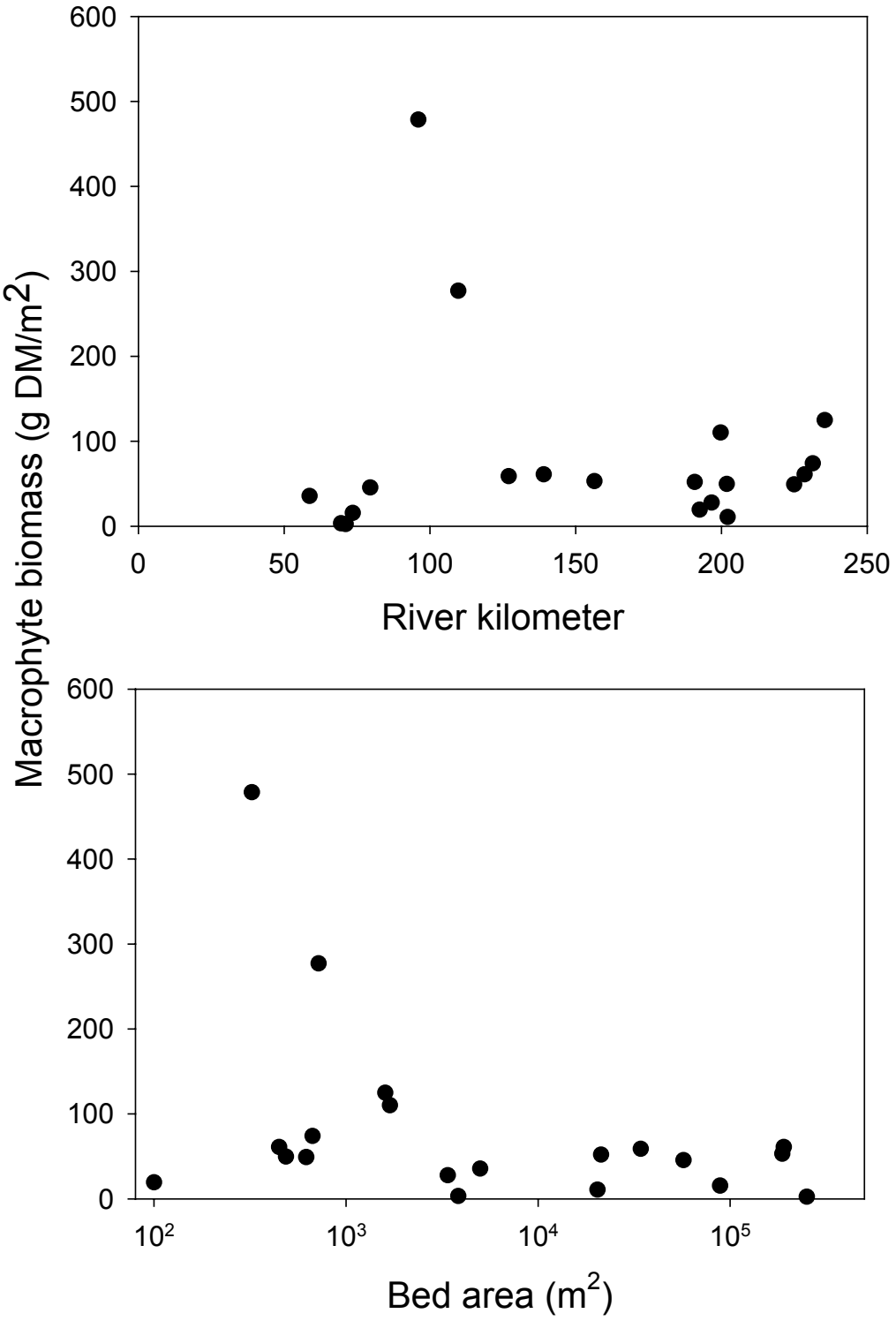

Figure 4. Macrophyte biomass (g dry mass per m^2) as a function of position along the river (r^2 = 0.01, p = 0.63) and bed area (r^2 = 0.15, p = 0.09). Each point is the mean for a site (see methods). Note that the x-axis in the lower panel is scaled logarithmically.

C. Sediments

Sediments at the study sites were predominately sand and silt, but highly variable across beds (Appendix 1). Both the texture (% sand) and organic content (% loss on ignition) of the sediments in the beds changed along the course of the river, from sandy, organic-poor sediments upriver to muddy, organic-rich sediments downriver (Fig. 5). Sediments in the linear features upriver were sometimes too coarse to core, containing cobbles, boulders, and riprap.

SAV bed area was strongly associated with sediment characteristics (Fig. 6) – sediments in large beds were finer and richer in organic matter than sediments in small beds. Neither sediment organic content nor texture was significantly correlated with the biomass of plants in the bed ($r^2 < 0.1$, $p > 0.2$ in both cases). There was no difference ($p > 0.25$) between edge and interior samples in texture or organic content.

Two beds had peculiar sediments. The sediments at Haverstraw (1177) were coarser and poorer in organic matter than those of other downriver beds, presumably reflecting the exposed, windswept position of this bed. The sediments at Quassaic (950) were entirely hard, and appeared to consist of some sort of human-made pavement, with macrophytes growing out of the cracks.

D. Dissolved Oxygen, Turbidity, and Water Exchange

Deployment of sondes to record dissolved oxygen (DO), turbidity, and depth revealed highly variable water quality conditions over a several day period for most of the sites. Typical features of the time series are large diel swings in DO (Fig. 7A) with daytime values as much as 50% supersaturated (about 12 mg/L). Using the median values during deployment to characterize conditions in all SAV beds vs. open water sites shows that median DO did not differ

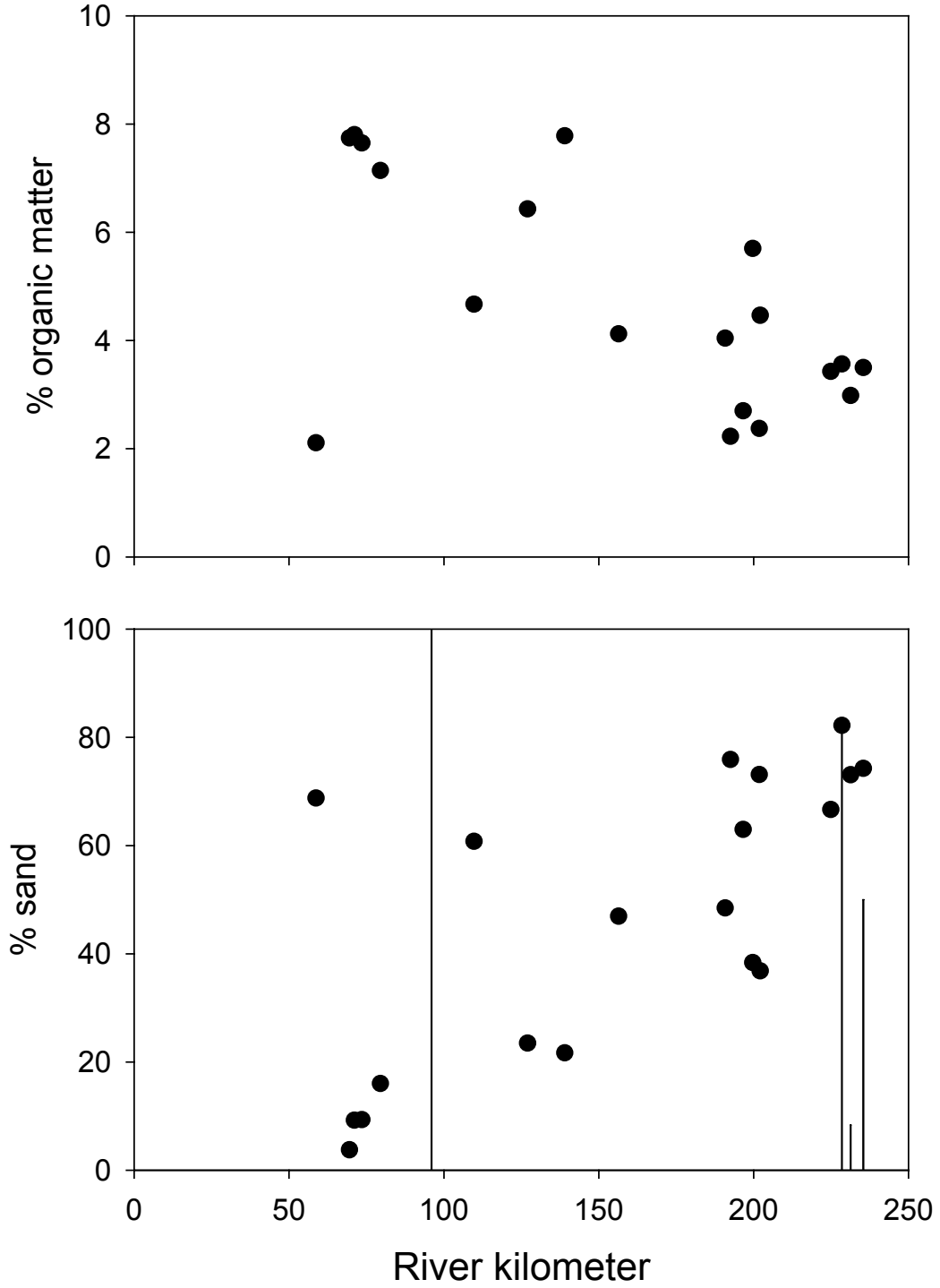

Figure 5. Sediment organic content and texture as a function of position along the river. The bars in the lower panel show the percentage of sediments at a site that were too coarse to core (i.e., were cobbles or coarser). For the upper panel, $r^2 = 0.39$, $p = 0.004$; for the lower panel, $r^2 = 0.48$, $p = 0.001$. The obvious outlier near Rkm 59 is Haverstraw.

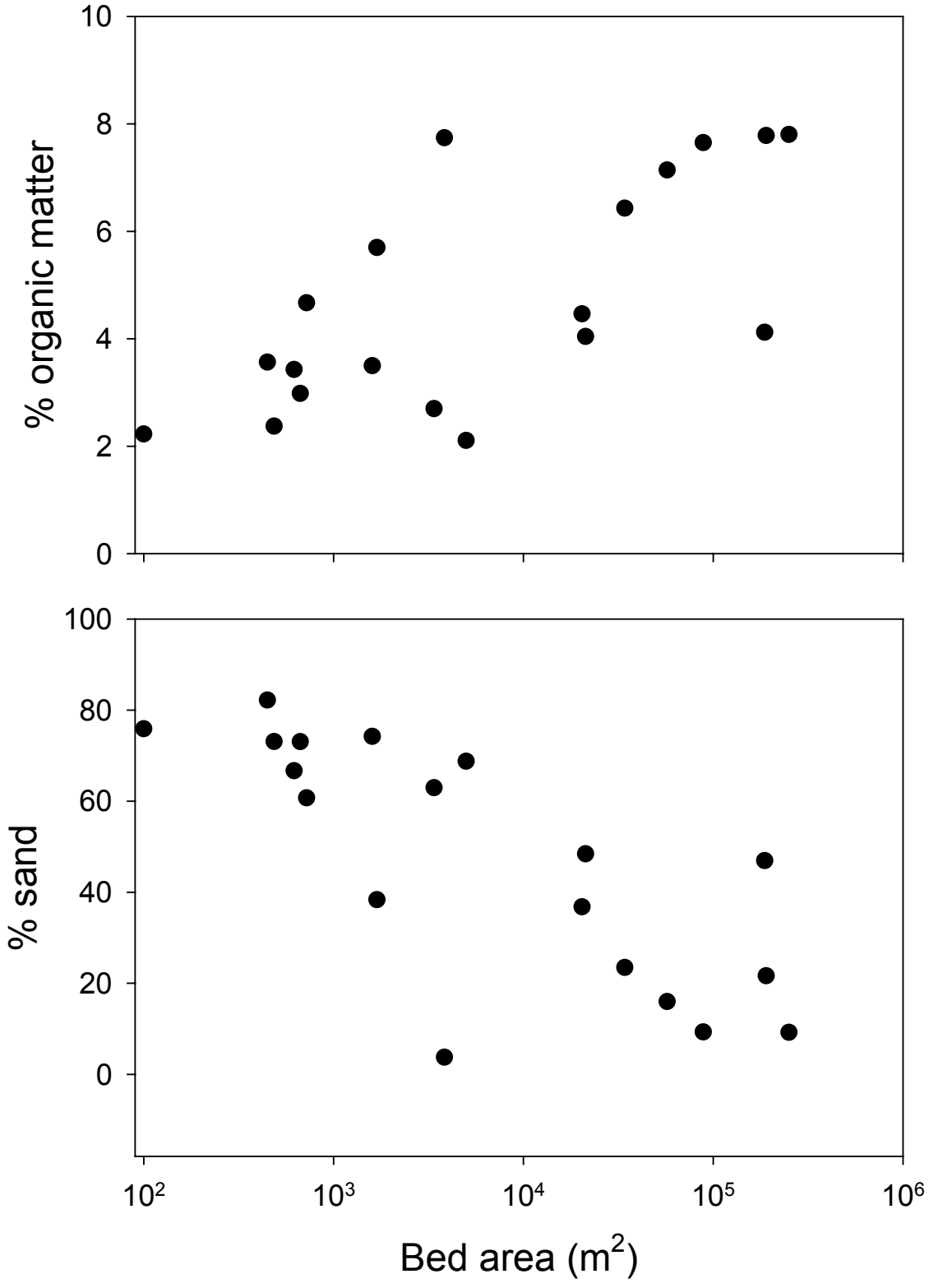

Figure 6. Sediment organic content (% loss on ignition) and texture (% sand) as a function of the size of the macrophyte bed (scaled logarithmically). For the upper panel, $r^2 = 0.47$, $p = 0.01$; for the lower panel, $r^2 = 0.59$, $p = 0.001$.

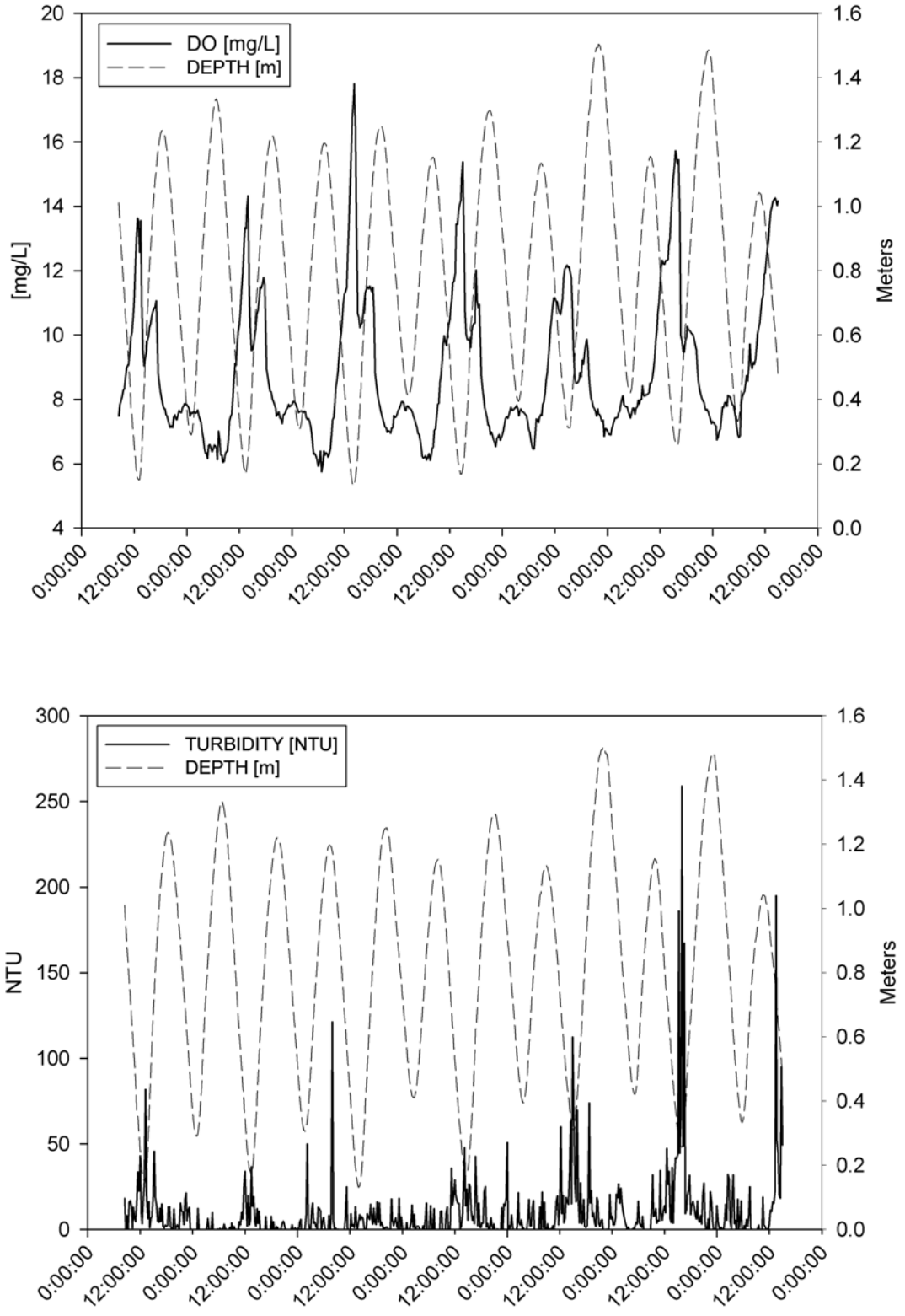

Figure 7. Sample result of diel cycles of water depth and (A, top panel) dissolved oxygen in mg/L and (B, bottom panel) turbidity in NTU.

(7.5 and 7.0 mg/L, respectively, p = 0.13), but the highest median observed in SAV (10.8 mg/L) was substantially greater than the highest median observed in open water (7.9 mg/L). The proportion of time with DO > 8 mg/L was significantly higher (p = 0.03) in SAV beds (mean ± SD, 29.5 ± 25.3, n = 34) relative to open water sites (11.0 ± 17.8, n = 11) although there was substantial variability among sites. The median and temporal statistics for DO were positively correlated (r = 0.75).

Turbidity showed extreme diel variability (Fig. 7B) with peak values of several hundred NTU. The median turbidity did not differ between SAV and open water (15.7 and 15.1 NTU, respectively, p = 0.84) and the highest medians observed were practically identical (35.4 SAV and 35.8 open water). The proportion of time with turbidity > 40 NTU did not differ between SAV (10.1 ± 15.1) and unvegetated sites (7.9 ± 7.9) and again there was substantial variability among sites. The median and temporal statistics for turbidity were positively correlated (r = 0.74).

Water velocities estimated from dye releases during ebb tides averaged 0.12 m/s and were unrelated to bed area (r = -0.07, p > 0.05) or other patch characteristics. Velocity was significantly related to tidal range on the day of measurement (p = 0.02, r = 0.64). The largest bed area in our sample set was 360,000 m^2 with an equivalent spherical radius of 340 m, and so at the mean velocity a water mass would move from the centroid to the edge of the bed in about 45 minutes.

We expected that size of SAV beds would help explain variability among sites for both DO and turbidity because water masses reaching our measurement point at the bed centroids would have been affected by vegetation for longer periods in larger plant beds. Bed size was significantly correlated with the proportion of time a site had DO greater than 8 mg/L, although

the explanatory power of the relationship was low ($r = 0.41$, $p = 0.004$, Fig. 8). Beds larger than about 50,000 m^2 (5 ha) can spend as much as twelve hours out of twenty-four hour period super-saturated with oxygen. For turbidity, the relationship between the proportion of time a site was > 40 NTU and bed area was not significant ($p = 0.06$, $r = -0.27$, Fig. 9).

The total biomass of plants in the analysis (sampled biomass density times total bed area) was not significantly correlated with DO or turbidity ($r = -0.15$, $p = 0.42$ and $r = 0.3$, $p = 0.09$, respectively). Of the SAV patch characteristics, only the bed width showed any association with the water quality variables, being weakly negatively correlated with the proportion of time a bed had turbidity > 40 NTU ($p = 0.07$, $r = -0.32$; data not shown). Attempts to relate turbidity to bed sediments revealed no significant relationships; the highest r^2 was <0.05 for correlations between the proportion of time turbidity was > 40 NTU and either % clay or organic content ($p = 0.33$ for each).

There were not simple associations between position in the river (Rkm) and effects of SAV beds on either DO or turbidity ($r = -0.13$, $p = 0.4$ for $O_2 > 8$ mg/L; $r = -0.1$, $p = 0.51$ for NTU > 40). Next we considered summer-mean main channel DO data collected as part of our routine monitoring (as in Findlay et al. 1996). Summertime main channel DO differs significantly at points in the Hudson with highest values of about 8 mg/L near Kingston (Rkm 146) and minima of about 6 mg/L between Poughkeepsie and Peekskill (Rkm 117 to 71) (Fig. 10). DO in our open water sites (those with no SAV) is significantly positively correlated with main channel DO ($n = 5$, slope = 0.99, $p = 0.05$; data not shown). Therefore, water entering SAV beds at different locations along the river will differ in initial DO concentrations, affecting whether an SAV bed of a given size will be able to generate local DO > 8 mg/L. Residuals from the regression of percent time DO > 8 mg/L versus SAV bed area (Fig. 8) were associated with

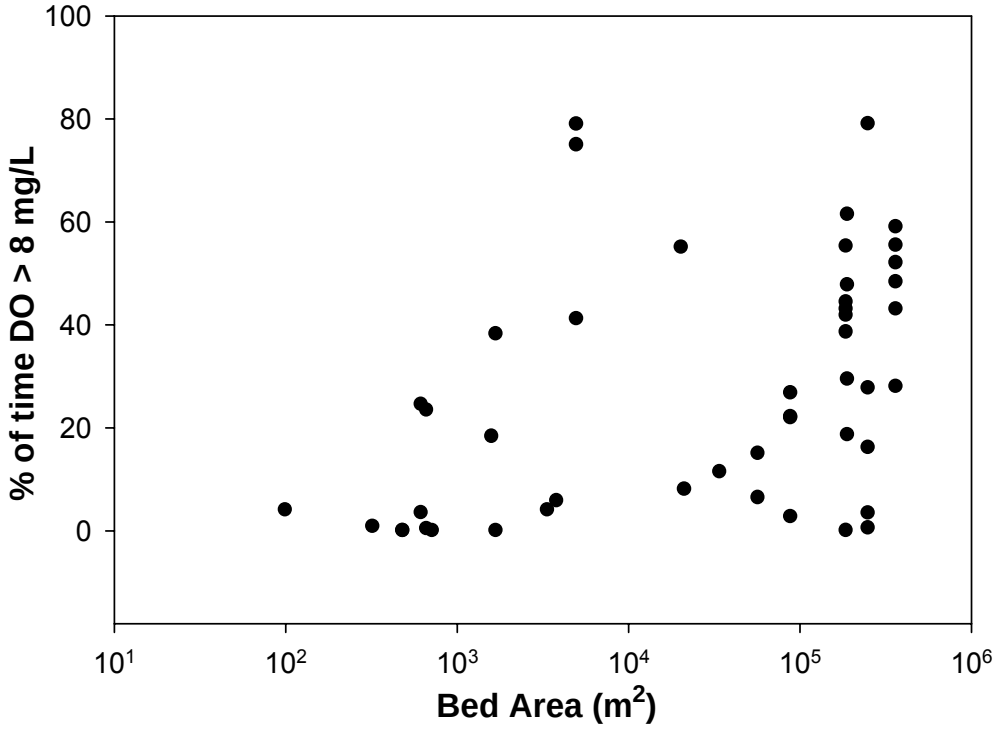

Figure 8. Percentage of time a site has dissolved oxygen > 8 mg/L as a function of SAV bed area (graphed on a logarithmic scale). p = 0.004, r = 0.41, n = 47

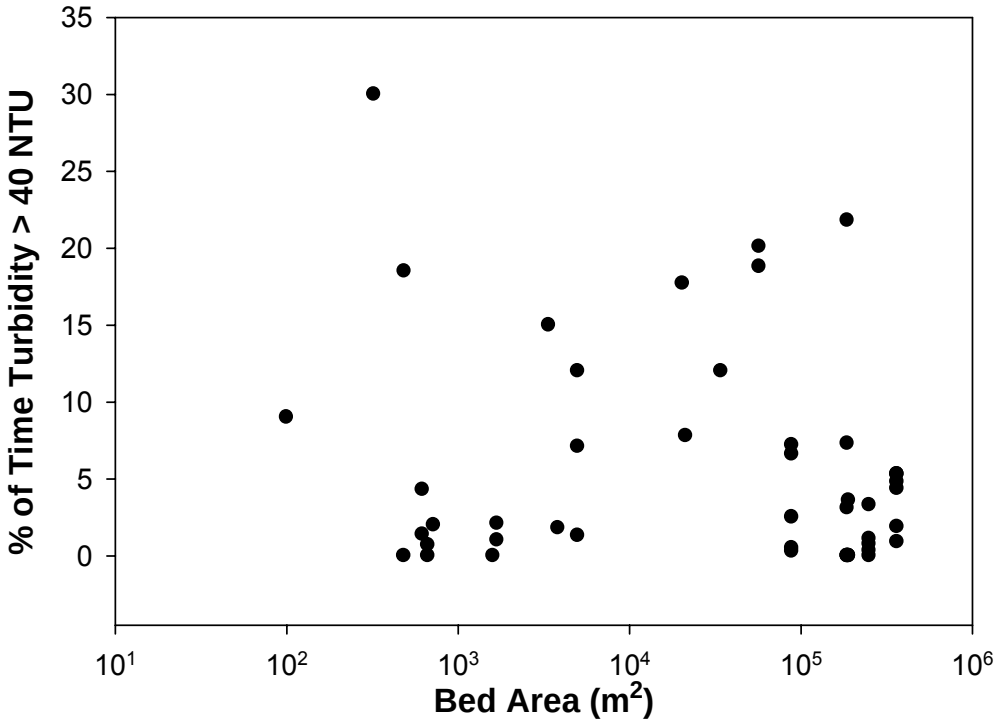

Figure 9. Percentage of time a site has turbidity > 40 NTU as a function of SAV bed area (graphed on a logarithmic scale). p = 0.06, r = -0.27, n = 48

main channel DO, with regions of the river having higher main channel DO showing positive residuals (i.e., observed values were greater than predicted by the regression) and negative residuals in reaches with lower main channel DO (Fig. 10). The residuals and main channel DO are significantly positively correlated. Thus, the proportion of time a bed spends super-saturated with oxygen is partially a function of bed size but is also related to main channel DO which varies spatially.

To look for finer spatial patterns, next we considered "neighborhood effects" on water chemistry by regressing DO or turbidity against varying neighborhood sizes (area of vegetation within circles around the sonde location of 50, 150 or 300 m radius). This analysis showed no improvement in the DO relationship; the nominal case using actual polygon areas had the highest correlation coefficient (Table 2). The explanatory relationship between percent of time a site had turbidity > 40 NTU versus vegetation area did improve as larger neighborhood sizes were considered. The relationship for simple bed area was not significant but the p value decreased and the magnitude of the correlation coefficient increased when vegetation within 50 to 300 m of the sampling point was used as the independent variable (Table 2).

There was a significant negative relationship between the proportion of time turbidity was above 40 NTU and the distance from bed centroid to deep water (> 5 m) ($r^2 = 0.12$, $p = 0.02$). This pattern may be related to the effect of neighboring vegetation described above: since there cannot be vegetation deeper than 5 m, SAV beds near the 5 m depth contour do not have the potential to be surrounded by other vegetated areas.

For the keystone bed sites we measured DO and turbidity over six years to examine interannual variation. There was a general increase in the proportion of time these large beds spend super-saturated, increasing from about 20 to about 50% of a 24 hr period (Fig. 11).

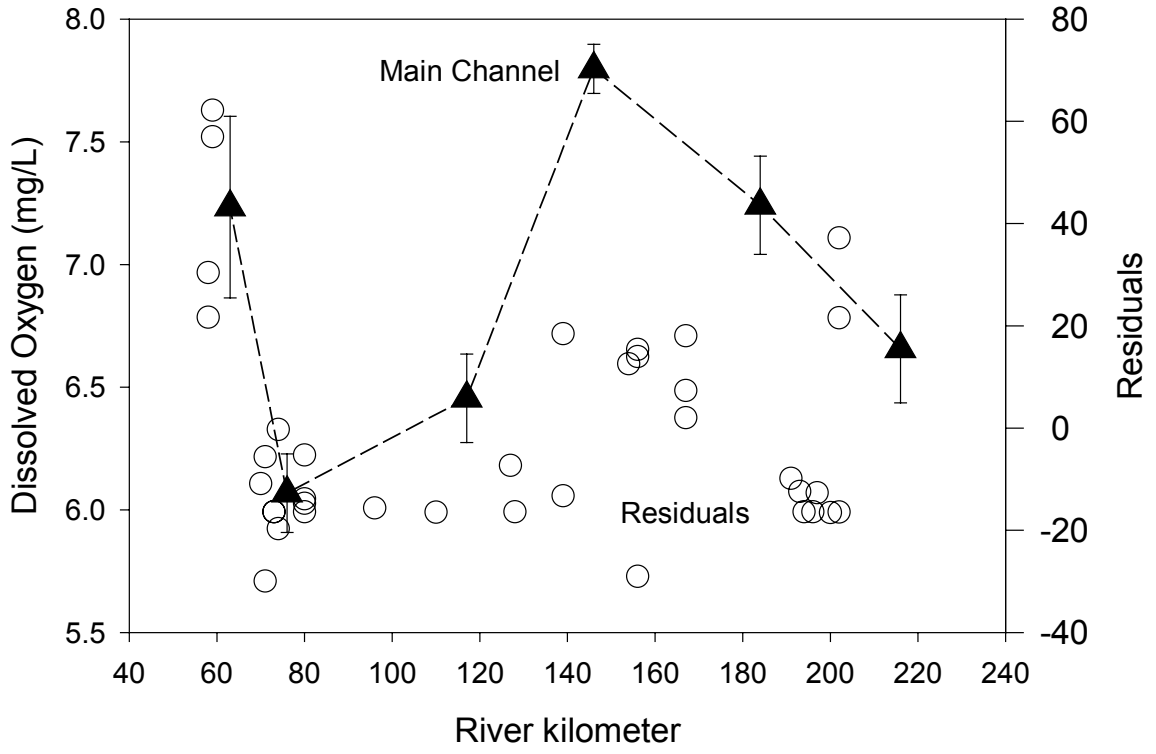

Figure 10. Left axis and triangles: mean dissolved oxygen at six main channel stations along the Hudson, derived from multiple years' sampling. Right axis and circles: residuals from the regression of % Time O_2 > 8 mg/L vs. SAV bed area, also plotted by location.

Table 2. Statistical models of high oxygen and high turbidity as a function of vegetation area.

Predictor	% Time O_2 > 8 mg/L		% Time Turbidity > 40 NTU	
	r	p	r	p
Actual bed area	0.43	0.003	- 0.24	0.11
Vegetation area within 50m radius	0.37	0.012	- 0.22	0.15
Vegetation area within 150m radius	0.32	0.035	- 0.27	0.07
Vegetation area within 300m radius	0.32	0.033	- 0.31	0.04

While there were also differences among years for effects on turbidity (Fig. 12) there was no directional change.

The difference among years in proportion of time keystone sites were supersaturated in DO was related to main channel water clarity. There was a significant relationship between the percent of time DO was greater than 8 mg/L and summertime water clarity measured by Secchi depth at stations in the main channel of the river (Fig. 13, $p = 0.05$, $r^2 = 0.65$).

For both water quality variables we found evidence for spatial variation. Dissolved oxygen was affected by main channel DO dynamics and SAV bed area. For turbidity the effect was more local with stronger effects of vegetated areas as one included progressively larger "neighborhoods". Both our neighborhood analysis and effect of proximity to deep water indicate that turbidity patterns at a given site are at least partially controlled by characteristics of the neighborhood. Patch characteristics (plant biomass, sediment composition, and bed size) were remarkably unsuccessful in predicting the turbidity within a bed.

From both a science and management perspective these findings suggest that performance or "value" can not be adequately determined just from patch characteristics but external variables must be considered. Therefore models attempting to predict whole-system contribution of SAV patches will need considerable information on the spatial context rather than just patch descriptors. Management and protection efforts will similarly require knowledge of the area surrounding a focal patch in order to judge the performance of that patch.

E. Macroinvertebrates

Macroinvertebrates were abundant and diverse in plant beds, and sometimes surpassed 100,000 individuals/m^2. The mean density of macroinvertebrates over all beds and years was

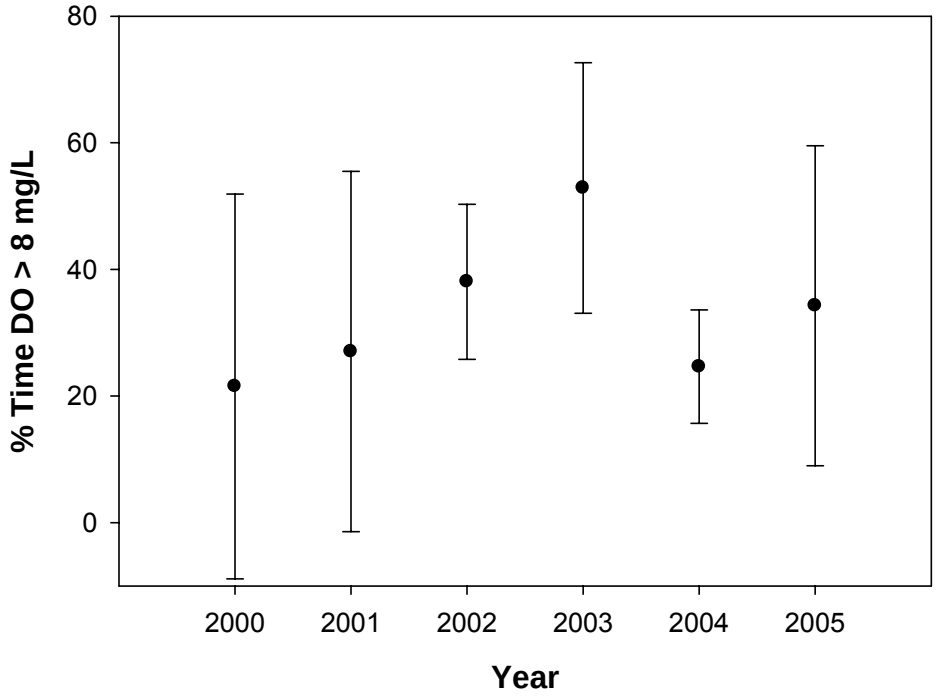

Figure 11. Percent of time each keystone site had DO > 8 mg/L over the six years of sampling (mean across sites + standard deviation).

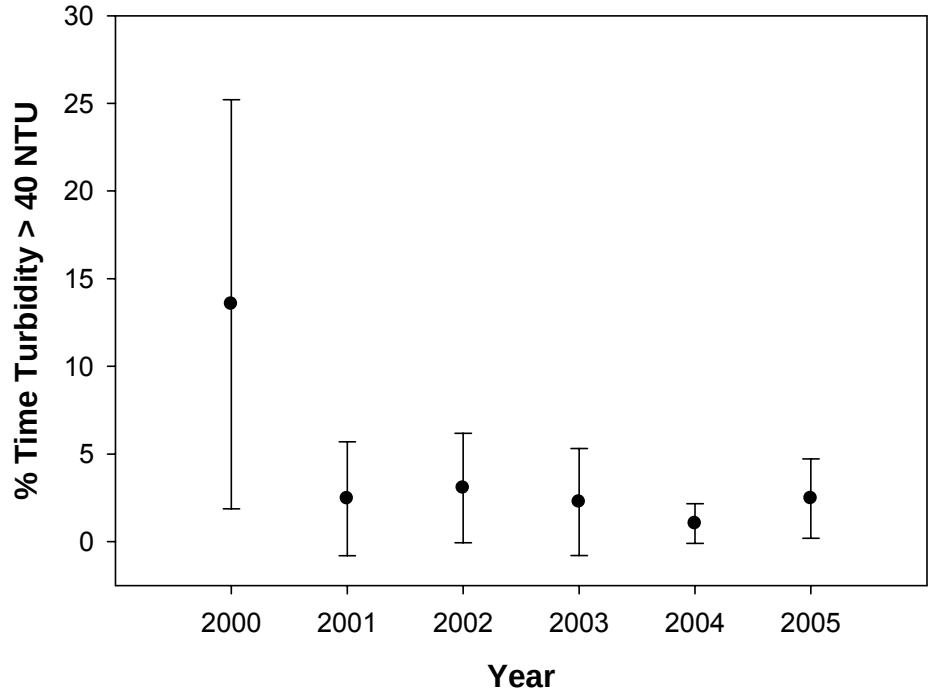

Figure 12. Percent of time each keystone site had turbidity greater than 40 NTU over the six years of sampling (mean across sites + standard deviation).

20,500/m^2, considerably higher than the mean density in unvegetated sediments (5805/m^2, Strayer and Smith 2001, after the zebra mussel invasion). We estimate that 18% of the macroinvertebrates in the Hudson live in *Vallisneria* SAV beds, with an additional 4% in *Trapa* beds. If SAV beds were to be removed from the Hudson, and macroinvertebrate populations fell to those typical of unvegetated sediments, 13% of the macroinvertebrates in the river would be lost.

Macroinvertebrate density was strongly related to plant biomass in the beds (Fig. 14). 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 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.

We identified more than 100 taxa of macroinvertebrates from plant beds (Appendix 2), even though we did not identify some animals (e.g., nematodes) to the genus or species level. 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 animals were taken less frequently.

Community composition depended chiefly on whether the samples were benthic or epiphytic. The fauna is clearly differentiated into benthic and epiphytic (plant-dwelling) forms; very few taxa are abundant both on the plants and in the sediments. Hydroids, most gastropods, cladocerans, mites, odonates, most naidid oligochaetes, the nudibranch *Tenellia fuscata*, the flatworm *Dugesia*, and many chironomids live on the plants themselves, whereas tubificid oligochaetes, polychaetes, isopods, bivalves other than zebra mussels, nematodes, ostracods,

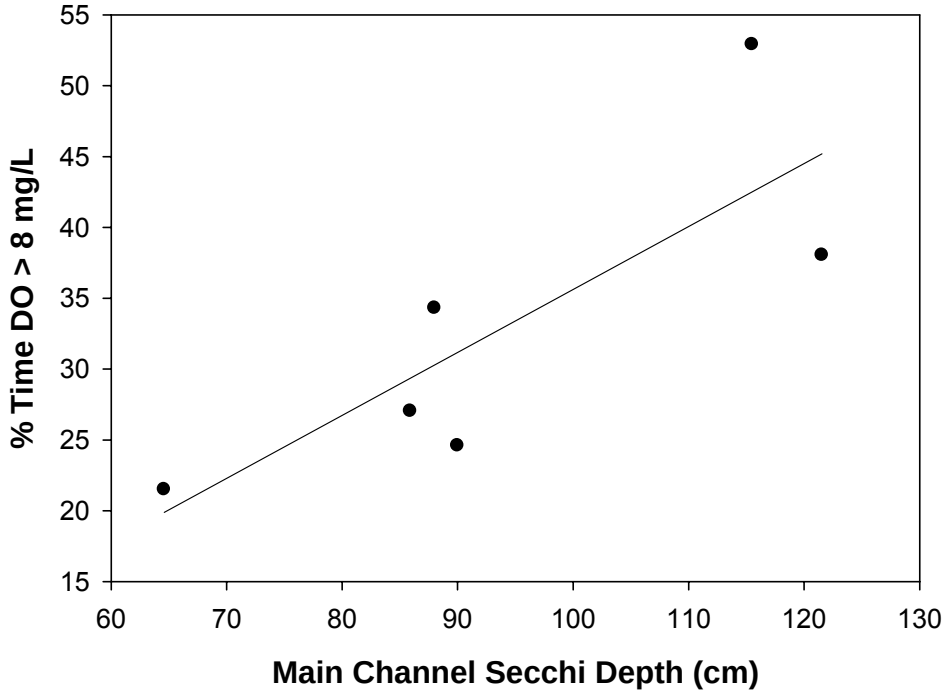

Figure 13. Proportion of time keystone sites had DO > 8 mg/L versus water clarity (Secchi depth) in the main channel ($p = 0.05$ $r^2 = 0.65$).

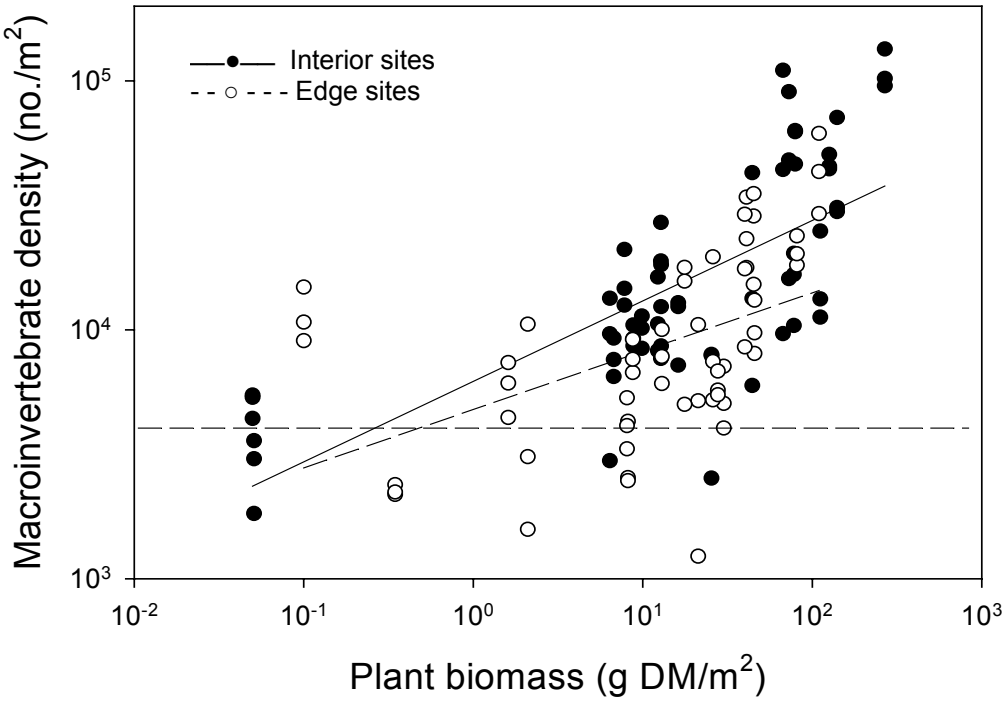

Figure 14. Density of macroinvertebrates (benthic + epiphytic) as a function of plant biomass and position within the bed. Both the correlation with plant biomass ($p < 0.0001$) and the difference between interior and edge sites ($p < 0.0001$) are significant (ANCOVA). The horizontal dashed line represents the mean density in unvegetated sediments (Strayer and Smith 2001).

the amphipod *Leptocheirus*, the flatworm *Hydrolimax*, 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 common on both sediments and plants. Consequently, we will treat the epiphytic and benthic faunas separately for the remainder of this section of the report.

The average density of epiphytic (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 density (in g/m^2, $p < 0.0001$, $r^2 = 0.85$). It was not correlated 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 even after plant biomass was taken into account.

The epiphytic fauna was dominated by the suspension-feeding chironomid *Rheotanytarsus*, several taxa of browsing chironomids (especially *Cricotopus bicinctus*, *Dicrotendipes* spp., and *Polypedilum* spp.), the cnidarians *Cordylophora lacustris* and *Hydra* spp., naidid oligochaetes (especially *Nais variabilis* and *Stylaria lacustris*), and the suspension-feeding cladoceran *Sida crystallina*.

The average density of benthic (sediment-dwelling) invertebrates was 8060/m^2, or 39% of the macroinvertebrates in the plant beds. This number is higher than the average density of benthic macroinvertebrates in unvegetated sediments in the Hudson after the zebra mussel invasion (5805/m^2, Strayer and Smith 2001). The density of benthic macroinvertebrates tended to be higher where plant biomass was greatest, upriver, and (surprisingly) where sediments were poor in organic matter, but none of these relationships was strong (r^2 always < 0.19, p always > 0.017). There was a weak indication that the size of the plant bed also affected benthic

community composition. Only position along the river was included in a multiple regression model (based on corrected Akaike Information Criterion (AIC_c)) to explain benthic macroinvertebrate density. Density of benthic macroinvertebrates tended to be about 11% higher in the interior of plant beds than along their edges, much weaker than the difference seen for epiphytic macroinvertebrates.

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

Ordinations successfully summarized spatial variation in macroinvertebrate community structure (Fig 15). Nonmetric Multidimensional Scaling (NMS) ordinations based on the 70 most widespread macroinvertebrates had a stress value of 13.4, indicating a satisfactory ordination (McCune and Grace 2002). The NMS ordination of benthic samples was adequate, giving a three-dimensional solution with a stress value of 16.0. Community composition was strongly related to position along the river, especially below Rkm 100.

Position along the river strongly influenced several measures of macroinvertebrate community composition (Fig 15). In particular, community composition was relatively constant above Rkm 100, then changed sharply through the transition into brackish water between Rkm 96 (Quassaic) and Rkm 59 (Haverstraw). 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 animals as the hydroid *Cordylophora*, the amphipods *Corophium* and *Leptocheirus*, barnacles, the bivalve *Rangia*, and polychaetes. Communities of linear features in the upper estuary (Rkm 225-235) also were distinctive, with large numbers of gastropods and the amphipod *Gammarus*.

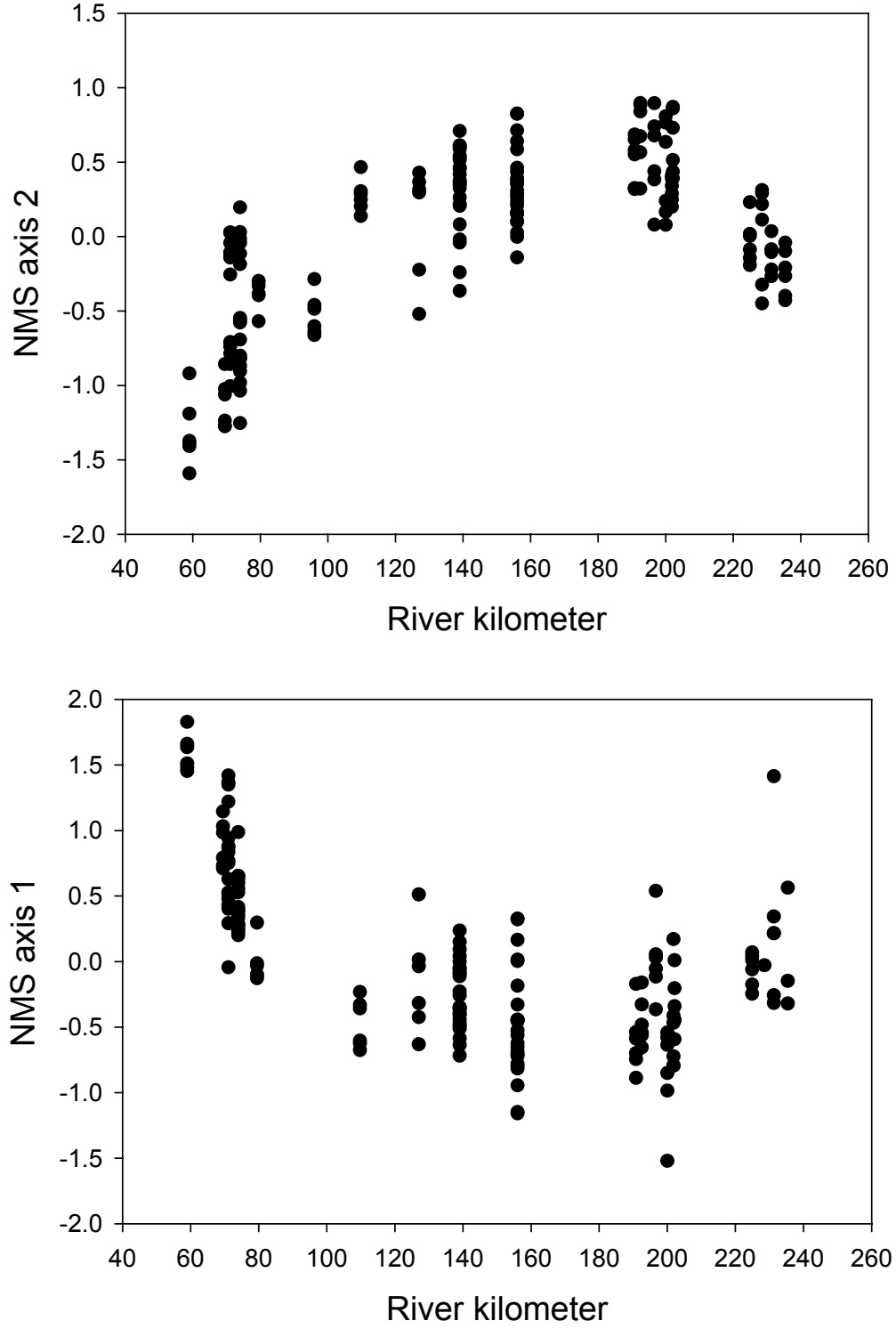

Figure 15. Changes in community structure of macroinvertebrates (expressed as ordination scores) as a function of position along the river. Upper panel is based on epiphytic species and lower panel is based on benthic samples ($p < 0.0001$ for both panels).

Over the three or four years during which particular keystone beds were sampled, the average ranges in areal densities were 2.6-fold for benthic macroinvertebrates, 117-fold for epiphytic macroinvertebrates, and 5.5-fold for total macroinvertebrates. Epiphytic densities were especially variable because of the substantial interannual variation in plant biomass (Appendix 1). When epiphytic macroinvertebrate densities were expressed per gram of plant, they varied only 5.1-fold, on average.

SAV beds are an important habitat for macroinvertebrates in the Hudson River. Densities of macroinvertebrates are much higher in plant beds than in unvegetated habitats, suggesting that they may be the richest feeding grounds in the Hudson for fish. Further, many species of macroinvertebrates that are common in plant beds are rare or absent from unvegetated sites. Thus, SAV beds play important roles in maintaining high population densities and high biodiversity of macroinvertebrates in the Hudson.

The macroinvertebrate community of plant beds in the Hudson includes a long list of species from seven phyla. Chironomid midges, oligochaete worms, hydroids, gastropods, and amphipods are especially abundant and widespread. Functionally, the macroinvertebrate community includes species that feed on attached algae and biofilms (most amphipods, gastropods, many chironomids), species that eat sediments (tubificid oligochaetes, some polychaetes and chironomids), suspension-feeders (bivalves, barnacles, the amphipod *Corophium*, the cladoceran *Sida*, the chironomids *Rheotanytarsus* and *Tanytarsus*), predators (cnidarians, many chironomids, odonates, flatworms, some polychaetes), and species that eat the plants themselves (plant-parasitic nematodes). It is worth noting how many of the animals living in plant beds depend directly on food that is brought into the beds by tidal currents. Of course, the suspension-feeders, which are among the most abundant animals in plant beds (summed

density > 5000/m^2) strip edible particles from the water as it moves through plant beds. In addition, the cnidarians, which were extraordinarily numerous in many plant beds (riverwide mean density = 1700/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.

Several factors affect the abundance and species composition of the macroinvertebrate community. Community composition (but not density) of the macroinvertebrate community varies along the length of the river. Changes in community composition are especially marked for SAV beds between Rkm 59 and Rkm 96, presumably in response to spatial variation in salinity in this part of the Hudson. The linear features in the upper estuary also support a distinctive fauna.

Unsurprisingly, plant biomass has a very strong effect on the density of the epiphytic (plant-dwelling) fauna, as well as a weak influence on the density of the benthic fauna. Consequently, dense plant beds provide the most valuable habitat for macroinvertebrates in the Hudson. However, there is only weak evidence that plant density affects the kinds of macroinvertebrates living in a plant bed – dense beds seem simply to support more of the same kinds of animals that live in sparse beds.

There were interesting and important differences in macroinvertebrate communities between bed interiors and bed edges. Density of epiphytic macroinvertebrates was very much (3.6 times) higher in bed interiors than in bed edges, and benthic macroinvertebrates weakly echoed this pattern. The degree to which macroinvertebrate species preferred bed interiors or edges seemed to depend on the functional attributes of the species. Thus, suspension-feeders,

which presumably benefit from rapid movement of fresh river water, were more likely than other epiphytic species to be found near bed edges. Likewise, large, active animals (the amphipod *Gammarus* and odonates), were especially likely to be found in bed interiors, where they might be relatively protected from fish predation. The ordinations also picked up hints of these differences in community composition between bed interiors and bed edges.

Bed size did not have a strong influence on either the number or kinds of macroinvertebrates. Likewise, we saw little evidence that sediment quality (% sand or organic content) affects the numbers or kinds of macroinvertebrates living in a plant bed.

Macroinvertebrate communities varied substantially from year to year. If we assume that the years we studied are typical in terms of year-to-year variation, and that year-to-year variation in macroinvertebrate density is lognormally distributed (neither assumption can be tested at present), we can project that the 95% confidence limits on interannual variation in macroinvertebrate density would cover a range of 7-fold for benthic animals, 3300-fold for epiphytic animals (on a per-m^2 basis), 16-fold for epiphytic animals (on a per-g basis), and 21-fold for total macroinvertebrates. Whatever the exact numbers, it is clear that macroinvertebrate populations in plant beds vary substantially from year to year.

We assessed interannual variation in community composition by running NMS ordinations of benthic and epiphytic samples separately for all beds and years. If interannual variation is small, then all of the points from a keystone bed that was sampled in multiple years should lie near to one another in ordination space. If interannual variation is large, then the multiple points from a keystone bed should be widely scattered throughout ordination space. The ordinations for benthic and epiphytic samples each yielded two-dimensional solutions, and had stress values of 15.7 and 13.3, respectively, indicating satisfactory results.

The composition of both benthic and epiphytic macroinvertebrate communities varied substantially from year to year in the keystone sites. It appears that benthic macroinvertebrates may vary less from year to year than epiphytic macroinvertebrates. It also appears that brackish-water communities may vary more from year to year than freshwater communities; this may be a result of year to year changes in salinity at the brackish sites. For example, the points from Iona (1069) and Peekskill (1079) are more widely spaced than those from Cruger South (601) and Esopus Meadows (688), at least for benthic macroinvertebrate samples.

All of this suggests that interannual variation in plant biomass, macroinvertebrate density, and macroinvertebrate community composition is substantial, roughly the same magnitude as spatial variation in these characteristics among beds throughout the study area. A better assessment of the size, causes, and consequences of this interannual variation would help in understanding the function of plant beds in the Hudson River ecosystem.

F. Fish

Over the four year (2000-2003) study period, 300 standardized fish samples using either electrofishing or gill nets were made in vegetated and unvegetated sites throughout the tidal Hudson River. All of the 102 electrofishing attempts and 183 of 189 gill net attempts recorded fish. A total of 7,489 fish were captured with most (5,378) coming from the electrofishing samples. The median electrofishing catch rate among all sites and samples was 44 fish per sample with a interquartile range from 23 to 73 fish per sample. For species richness, the median electrofishing catch rate was 8 species per sample with a interquartile range from 5 to 10 species per sample. Gill net samples had a median catch rate of 7 fish per sample with a interquartile range from 3 to 15 fish per sample. For species richness, the median gill net sample catch rate

was 2 species per sample with a interquartile range from 1 to 3 species per sample.

Electrofishing samples were made at 19 sites that had a wide range of catch rates and species richness values (Table 3). The median catch rate ranged from 4 fish/sample (unvegetated Vanderburg) to 152 fish/sample (site 34). The unvegetated Vanderburg site also had the lowest median species richness, 2 species, and Site 34 also had the highest median species richness, 16 species. Gill net sampling was done at 18 sites that yielded a wide range of catch rates and species richness values (Table 3). The unvegetated Croton site produced the highest median catch rate (27 fish/sample) while site 1105 and the unvegetated Peekskill site both had the lowest median catch rates (3 fish/sample). Median species richness did not vary greatly by site; total range was 1 to 4 species/sample. Sites 221 and 344 in the upper freshwater zone and site 778 in the lower freshwater zone had the highest median species richness values, while one upper freshwater site (250) and four sites at the downstream brackish end of the study reach (unvegetated Peekskill, 1105, 1177, and unvegetated Croton) had the lowest median species richness per sample (1 species).

Fish catch rate, species diversity, and community composition differed among the three river zones (Table 4). Direct statistical comparisons cannot be made because of differences in sampling gear that could be used in different locations, and different sampling effort. In the upper freshwater zone we conducted 18 standardized electrofishing samples in 2002 and another 18 in 2003. This zone yielded 1672 fish (46.4 per sample) and had the largest number of species (33) of the three zones. Most species were freshwater residents (Table 5, Appendix 3). American eel and spottail shiner composed nearly half of all fish recorded.

The lower freshwater zone was the most sampled: 150 standardized electrofishing and gill net samples from 2001 through 2003. Total fish catch was 4676 individuals in 28 species

Table 3. Median (m) and interquartile range values for catch rate (# fish / sample) and species richness (species / sample) for all electrofishing and gill net samples (n) by study site. FW = freshwater. UNV = unvegetated. LSAV = linear SAV feature.

					Electrofishing samples						Gill net samples					
					Catch rate			Richness			Catch rate			Richness		
Site Name (Bed ID #)	**Rkm**	**Zone**	**Vegetation**	**N**	m	25%ile	75%ile	m	25%ile	75%ile	m	25%ile	75%ile	m	25%ile	75%ile
Lin 95	248	Upper Freshwater	UNV	3	6	6	8	4	3	4						
Lin 60	239		LSAV	6	31	13	40	9	7	10						
P 60	239		SAV	3	61	24	77	11	8	16						
Lin 50	237		LSAV	6	48	39	53	9	8	10						
P50 (16)	237		SAV	3	65	27	101	10	9	13						
Lin 36	234		LSAV	3	33	21	41	8	7	10						
Lin 15	230		LSAV	6	50	36	75	11	10	12						
P15 (34)	230		SAV	3	15	72	169	16	14	18						
Lin 1	228		UNV	3	23	11	28	4	2	6						
Mill Creek (169)	202	Lower Freshwater	SAV	8	37	17	121	5	5	7	14	8	26	4	3	5
Stuyvesant (221)	200		SAV	8	9	3	17	3	2	4	6	1	9	2	0	2
Stuyvesant UNV	200		UNV	1	62	35	70	10	7	11	7	4	10	3	2	3
NuttHk (250)	197		SAV	8	46	37	52	7	4	7	8	3	13	1	1	3
NuttHk UNV	198		UNV	8	27	14	40	6	5	7	5	3	5	3	2	4
Stockp (344)	191		SAV	8	56	30	81	9	8	10	23	12	49	4	3	4
Stock UNV	191		UNV	8	32	20	43	4	2	7	4	2	17	3	1	4
Cruger South (601)	156		SAV	3	78	56	102	7	7	10	16	5	28	3	2	3
Esopus Meadows (688)	139		SAV	3	52	36	90	8	6	9	8	2	15	2	1	3
Vanderburg UNV	138		UNV	1	4	0	7	2	0	3	5	1	7	2	1	2
Rogers Point (778)	127		SAV	6							4	3	14	4	2	4
ConHook (1049)	80	Brackish	SAV	6							5	2	7	2	1	2
Iona (1069)	74		SAV	3							8	4	11	2	1	3
Peekskill (1079)	71		SAV	3							13	8	19	3	2	4
Peekskill-unv	71		UNV	1							3	1	9	1	1	2
Indian Point (1105)	70		SAV	6							3	1	3	1	1	1
Haverstraw (1177)	59		SAV	1							4	3	6	1	1	2
Croton UNV	54		UNV	6							27	12	50	1	1	2

Table 4. Fish catch and species richness by river zone. e = electrofishing, g = gill net.

Zone	# Samples	Total Fish	Mean Fish per sample	Species Richness
Upper Freshwater	36 (e)	1672	46.4	33
Lower Freshwater	150 (total)	4676	31.2	28
	66 (e)	3706	56.2	
	84 (g)	970	11.6	
Brackish	114 (g)	1141	10.0	17

Table 5. Fish species by river zone and abundance. Species accounting for half or more of the total collection in a zone are shown in bold type.

Abundance	Upper Freshwater	Lower Freshwater	Brackish
Highly abundant	**spottail shiner** **American eel** common carp largemouth bass striped bass bluegill alewife white perch redbreast sunfish pumpkinseed	**white perch** **spottail shiner** banded killifish yellow perch blueback herring brown bullhead pumpkinseed American shad Atlantic menhaden alewife	**white perch** white catfish spottail shiner Atlantic menhaden bluefish gizzard shad
Commonly recorded in substantial numbers	white catfish tesselated darter banded killifish redfin pickerel Northern pike blueback herring golden shiner black crappie brown bullhead rock bass American shad white sucker smallmouth bass	goldfish tesselated darter white sucker gizzard shad bluegill redbreast sunfish common carp golden shiner largemouth bass striped bass American eel	alewife mummichog spot striped bass white sucker common carp yellow perch
Rarely captured	blacknose dace channel catfish common shiner hogchoker logperch river redhorse chain pickerel gizzard shad goldfish	walleye hickory shad redfin pickerel rock bass channel catfish white catfish smallmouth bass	crevalle jack golden shiner pumpkinseed weakfish

(Table 4) and exactly half (150) of all standardized sampling occurred in this zone. The overall catch rate (30.6 fish per sample, combined gear) was about two-thirds of the catch rate in the upper freshwater zone and species richness was high. The electrofishing catch rate was higher in the lower than in the upper freshwater zone. Estuarine and marine migrant fishes were a substantial portion of the species recorded, especially the shads or alewife species (Table 5, Appendix 3). Spottail shiner and white perch accounted for about half of all fish captured in the freshwater zone.

Although many samples (114) were taken in the brackish water zone from 2001 to 2003, the total catch was smallest (1141 fish, 10.0 fish per sample, Table 4). Only gill nets were used in this zone and this gear captures fish at a lower rate that electrofishing when deployed simultaneously in the Hudson River. Species richness was low (17 species) with many estuarine and marine fishes (Table 5, Appendix 3). White perch accounted for more than 70% of the total catch.

Fish use of SAV beds were studied independently in each river zone. In the upper freshwater zone, a total of 36 standard electrofishing samples were conducted in linear features (LSAV, n = 21), SAV beds (SAV, n = 9), and unvegetated habitat (UNV, n = 6) during 2002 and 2003. SAV beds had much higher catch rates than the other two habitats (ANOVA, $p = 0.001$, Fig. 16), and the catch rate in linear features was not significantly different than in unvegetated habitat (Scheffé Post Hoc Test, $p = 0.186$). In terms of species richness of fish, all habitats differed (ANOVA, $p < 0.001$, Scheffé Post Hoc Tests, $p \leq 0.006$, Fig. 16) with SAV beds supporting the most species and unvegetated habitats the fewest. American eel, spottail shiner, and pumpkinseed were the dominant fishes of these habitats, with longer lists of abundant species in vegetated habitats (Table 5, Appendix 3).

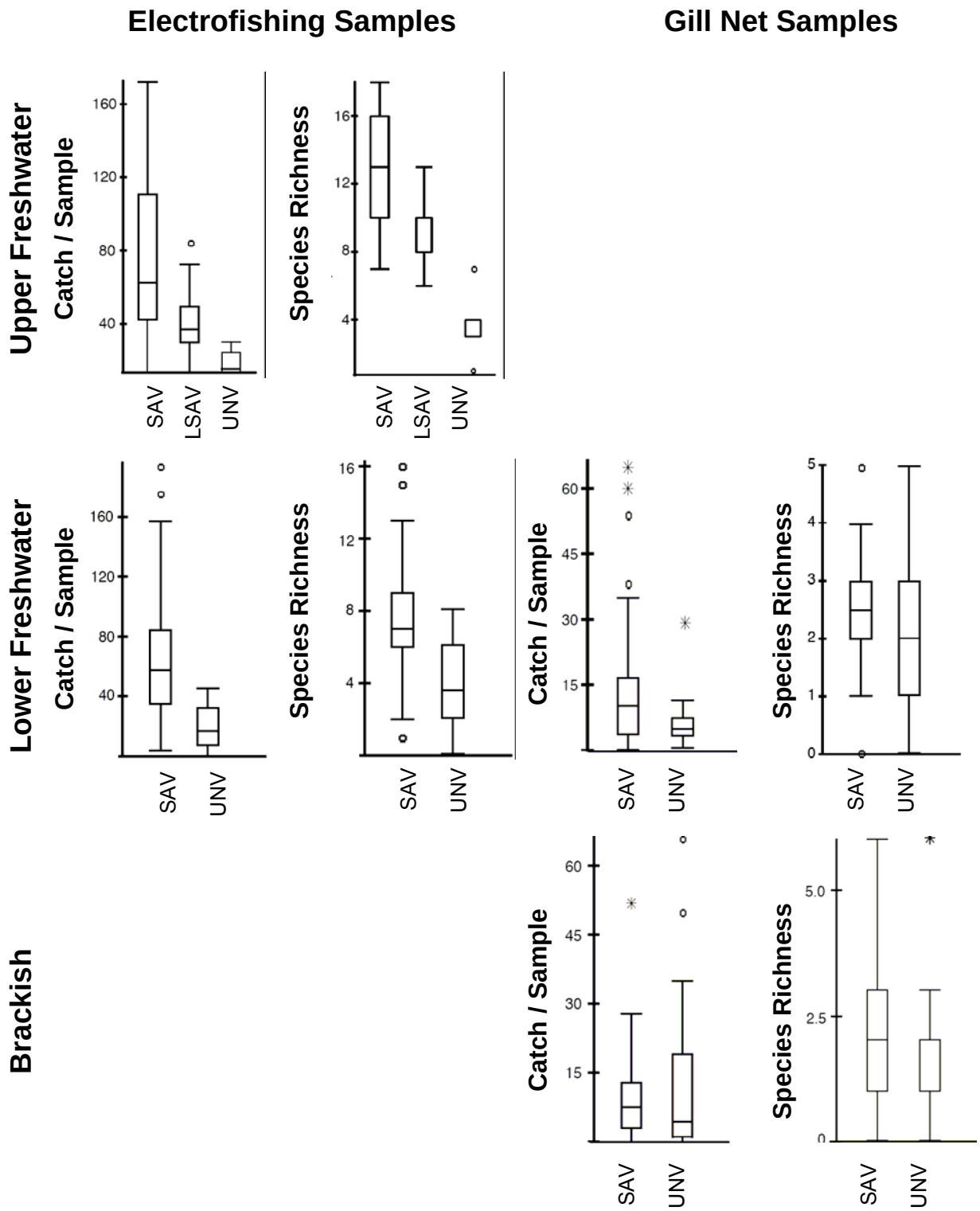

Figure 16. Fish catch rate and species richness by zone, sampling method, and habitat type. The boxplots show the middle 50% of the data in the box; the line across the box is the median; the whiskers above and below the box show the range of data, except for outliers; and outliers are shown with a small circle or asterisk.

The lower freshwater zone was sampled more times and in more years than the other zones, and both gears were used regularly during the study period. A total of 66 electrofishing samples were made in SAV (n = 52) and UNV (n = 14). Catch rates and species richness were much higher in SAV (ANOVA, $p < 0.001$ for both, Fig. 16). A total of 84 standard gill net samples were made in SAV (n = 62) and UNV (n = 22). As with electrofishing, catch rates were much higher in SAV (ANOVA, $p = 0.011$, Fig. 16). However, species richness of gill net samples in SAV beds and unvegetated habitats were similar, about 2 species per sample. (ANOVA, $p = 0.178$, Fig. 16).

In the brackish water zone, 114 gill net samples were taken in either SAV beds or unvegetated habitat. Catch rate was not different among habitats (ANOVA, $p = 0.103$, Fig. 16). However, species richness was higher in SAV habitats (ANOVA, $p = 0.011$, Fig. 16), but the difference was only about one additional species. The overall diversity of fish in brackish zone gill net samples was low (median of 1 to 3 species depending on vegetation, Fig. 16, Appendix 2) so an increase of one species on average is biologically relevant given the overall low diversity in the brackish zone. Some of the additional species in SAV habitats such as bluefish, spot, mummichog, and spottail shiner indicate the beds provide critical habitat because these fish were either not recorded in unvegetated habitats or were found at very low numbers.

Fish abundance per sample, standardized by sampling gear, is positively correlated with SAV bed area ($p = 0.01$, $r = 0.453$, Fig. 17). Larger beds support higher fish densities throughout the Hudson suggesting that an aggregation of small patches is not as valuable for fish habitat as a single patch of equivalent size.

Fish were collected from some sites in multiple years. In the upper freshwater zone, 12 linear feature sites were sampled in 2002 and 9 in 2003. These samples provide the only direct

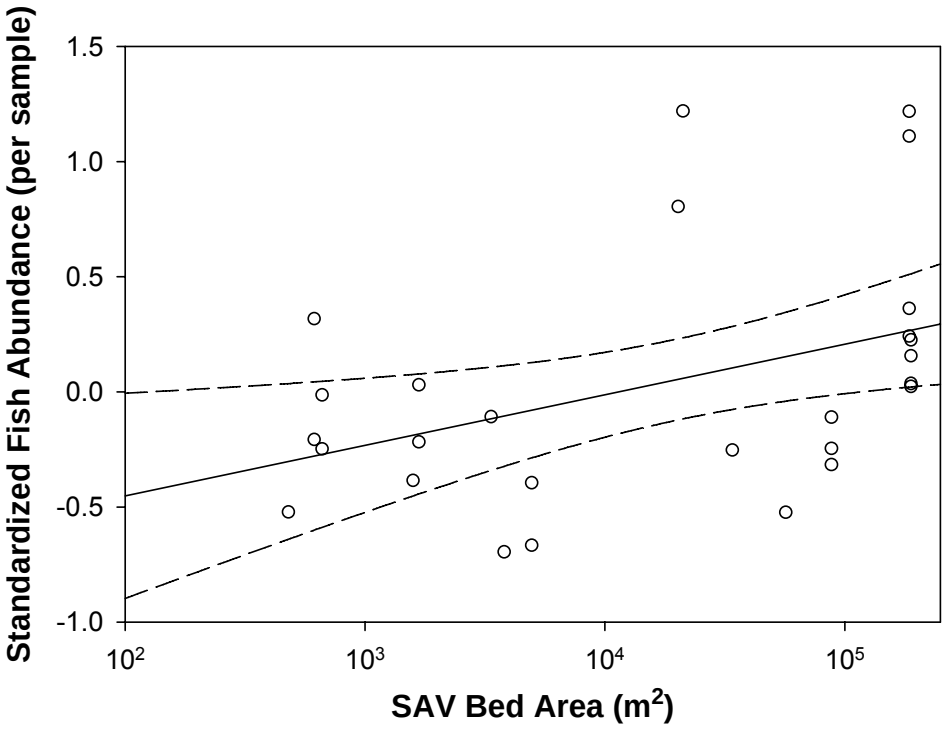

Figure 17. Standardized fish abundance as a function of SAV bed area. Fish abundance is standardized (subtracting the grand mean then dividing by the grand mean) to account for differences in gear used in different parts of the River.

test for differences among years in this zone. No interannual differences in catch rate were found (ANOVA, p = 0.424, Fig. 18). Similar results were found for species richness among years (ANOVA, p = 0.124, Fig. 18).

The lower freshwater zone had repeated sampling across four years (2000-2003) using both electrofishing and gill netting at two keystone sites: Cruger South (601) and Esopus Meadows (688). Overall, no evidence was found for year to year differences in catch rates or species richness. With electrofishing, interannual variation was not significant for catch rates (n = 32, ANOVA, p = 0.800, Fig. 18) or species richness (ANOVA, p = 0.088). Gill net results also did not vary among the four years in catch rates (n=37, ANOVA, p = 0.386, Fig. 18) or species richness (ANOVA, p = 0.279).

Two keystone sites in the brackish zone, Iona (1069) and Peekskill (1079), were sampled

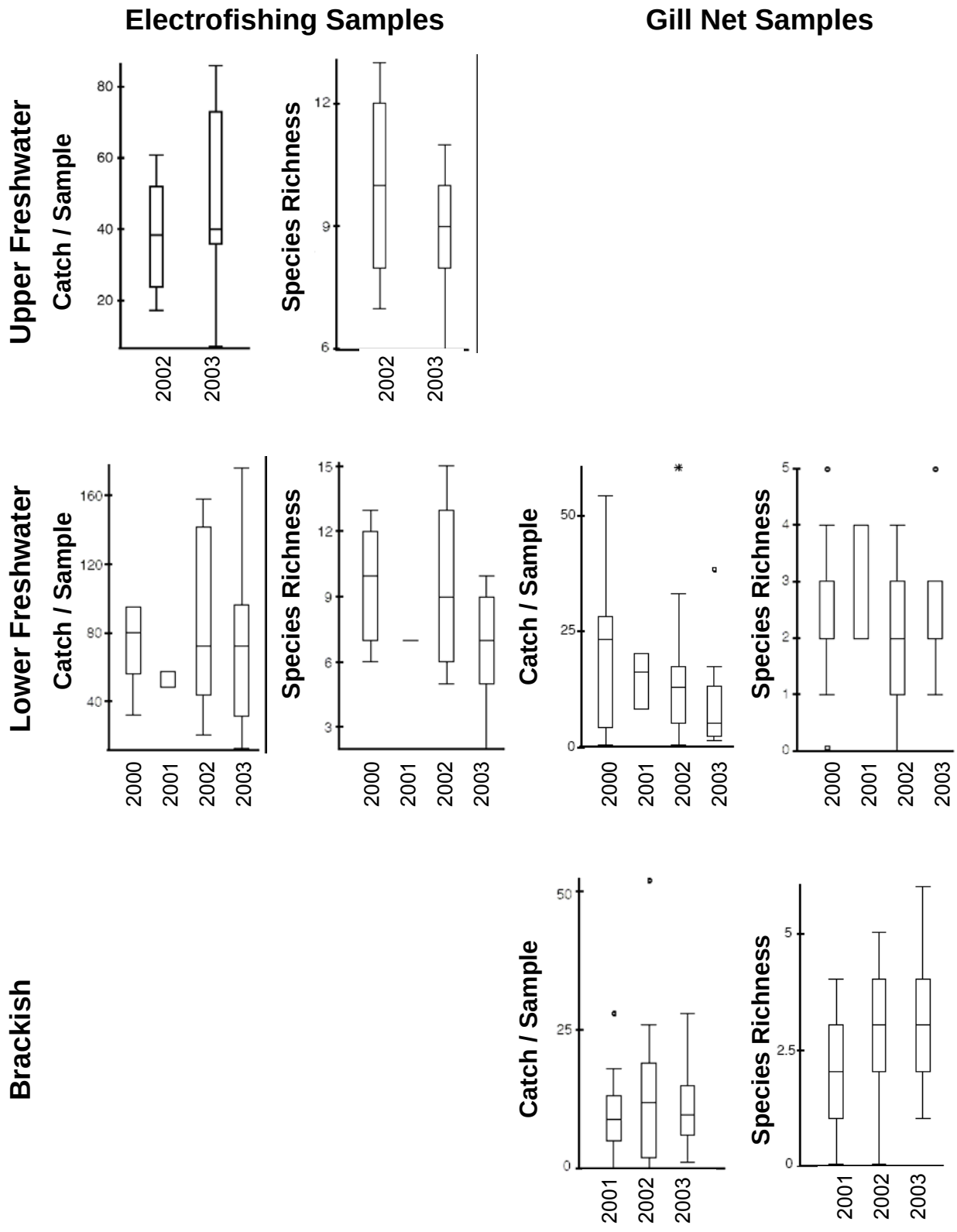

Figure 18. Fish catch rate and species richness by zone, sampling method, and year. Boxplots as described for Fig. 16.

with 24 standard gill net samples per year in 2001, 2002, and 2003. No evidence was found for interannual differences in catch rates (ANOVA, $p = 0.441$, Fig. 18). Species richness was slightly lower in 2001, but the interannual variation was marginally significant statistically (ANOVA, $p = 0.057$, Fig. 18).

Stomach contents were analyzed to indicate which items and organisms were frequently consumed by fish inhabiting different zones and habitats. Food items from 584 fish collected from 2000-2003 were counted and identified to 43 taxa. Some taxa were found in a large percentage of fish in all habitats, yet a shift in food composition can be seen between freshwater and brackish zones. The variety of food items was large, spanning plant material, aquatic insects, arthropods, annelids, decapods, mollusks, and many others. The most frequently observed food items by zone and habitat are summarized in Table 6 with basic data on sample size and taxonomic richness. Taxa recovered from guts at high frequency (≥10% of fish per habitat) included some of the same organisms across all zones and habitats: Chironomidae (aquatic midges) and Amphipoda (aquatic scuds). Other taxa occurring at high abundance in multiple habitats were: Isopoda (aquatic sow bugs), Diptera (true flies), Osteichthyes (bony fish), Ancylidae (limpet snails), and Cladocera (water fleas). Differences in dominant food items could be due to the fish species using different habitats with different potential food items. However, these were the fish commonly captured across multiple habitats, suggesting the diet shifts probably reflect broad-scale differences in food available.

The field predator exclosure experiment conducted in 2003 with Hester-Dendy artificial substrate samplers provided information on macroinvertebrate colonization and survival in SAV habitats with and without fish predation. Paired deployments at eight sites of Hester-Dendy samplers with and without screening yielded data for a simple one-tailed paired t-test. We

expected the screened sampler sets to have more macroinvertebrate organisms in them than the open samplers subject to fish predators.

Pooled by river zone, screened samplers had higher numbers of organisms than open samplers, and zones differed in organism numbers per sampler ($p = 0.013$, 2-way ANOVA, Fig. 19). Differences between open and screened samplers were dramatic in the upper freshwater zone, and modest in the brackish zone (Fig. 19). There did not appear to be a difference in screened and open samplers in the lower freshwater zone. Finally, the dominant organisms collected from the artificial substrate samplers (Chironomidae in all cases, also the dominant organisms living on plants) were often the most common group of organisms found in fish stomachs (Table 6).

Our study of fish use of SAV in the Hudson River Estuary was a component of a larger multidisciplinary investigation. Consequently, we did not have a simple randomized replicated design. Nevertheless, a consistent pattern of results across years and gears provides broad evidence of SAV's importance in supporting an abundant and diverse fish fauna in the Hudson River. Our general hypothesis was that SAV provided important habitat that varied by environmental setting (zone) and local community context. Our results indicate that SAV influenced local fish faunas but that the specific location in the river and composition of the surrounding fish community was important in the strength of the association between fishes and SAV.

Fish sampling in SAV and unvegetated habitats was repeated annually for three or four years depending on zone with some sites resampled each year. We found no evidence of significant interannual variation in fish catch rates, species richness, or taxonomic composition despite interannual variation in the plant and macroinvertebrate communities described above.

Table 6. Fish stomach contents by zone and habitat. The most frequently encountered taxa are listed in decreasing order. Taxa listed were found in at least 10% of the analyzed fish, or in more than two fish in the unvegetated lower freshwater habitat. UNV = unvegetated.

Zone and Habitat		Sample years	Sites	# of fish	Fish species analyzed	Total prey taxa	Dominant taxa in stomach
Upper Freshwater	SAV	2003	3	61	7 common fishes	19	Ancylidae, Chironomidae, Amphipoda, Trichoptera, Diptera, Physidae, Coleoptera, Planorbidae, Osteichthyes
	LSAV	2002-3	7	118	8 common fishes	26	Chironomidae, Amphipoda, Ancylidae, Osteichthyes, Odonata, Diptera
Lower Freshwater	SAV	2000-3	13	240	Mostly white perch	34	Chironomidae, Amphipoda, Cladocera, Ostracoda
	UNV	2001-2	2	9	Mostly white perch	10	Chironomidae, Nematoda, Amphipoda, Nematomorpha
Brackish	SAV	2001-3	9	126	Mostly white perch	18	Amphipoda, Chironomidae, Isopoda, Macrophytes, Polychaeta, Grapsidae, Cladocera
	UNV	2001	2	30	Mostly white perch	10	Amphipoda, Isopoda, Chironomidae

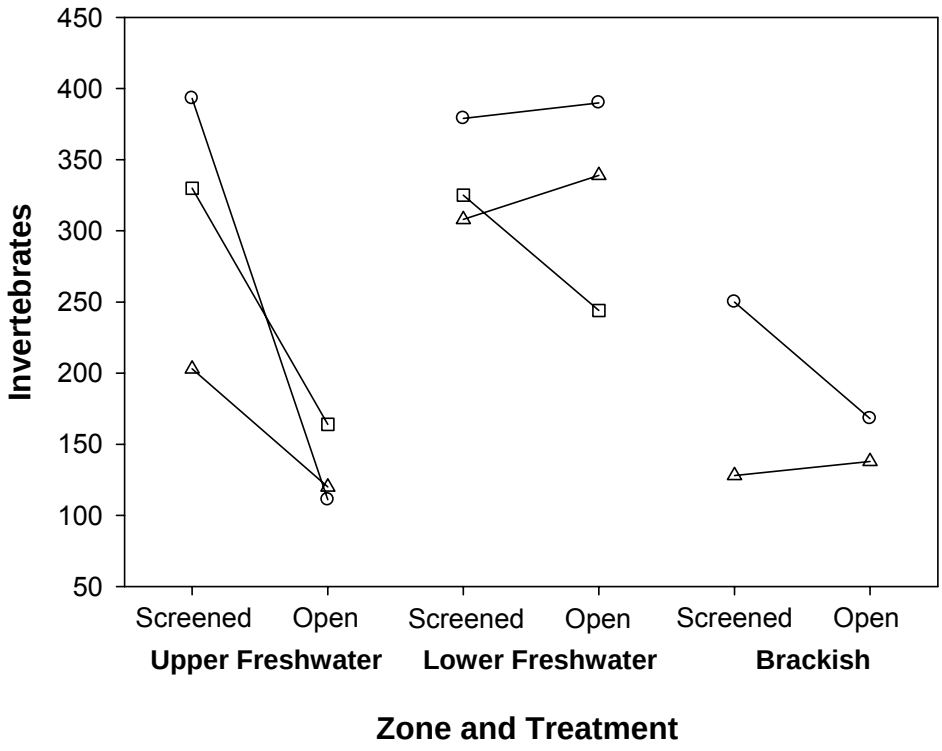

Figure 19. Number of organisms collected from predator exclusion experiment by sampling zone. Line segments connect the pair of results from each site.

Fish sampling and data analyses were partitioned by major zone of the Hudson River Estuary: upper freshwater, lower freshwater, and brackish. These zones differed in fish communities as expected for a river-estuary gradient. The upper freshwater zone had the longest list of fish species; it was dominated by spottail shiners and American eel with other species largely being resident freshwater fishes. The lower freshwater zone fish were dominated by spottail shiners and white perch. Anadromous species were among the most common fishes in the lower freshwater zone. The less common members of the community included a mix of inland resident fishes and species with migratory (anadromous, catadromous) life cycles. The brackish zone yielded the fewest species and lowest catches which could be partly attributed to differences in sampling gear (gill net only). However, the brackish zone fish fauna was clearly less diverse. White perch overwhelmingly dominated the catch, and the list of all fish species was short. The less common species included some fish typically found in freshwater, estuarine, and marine habitats.

Much of our fish community sampling was designed to detect differences in shallow water habitats with and without SAV, and in the upper freshwater zone we compared SAV beds and narrower linear SAV features. SAV beds supported more fish and a greater variety of species than unvegetated habitats in the upper and lower freshwater zones. Elevated abundance of fish in vegetated freshwater habitats has been reported repeatedly in past fish and plant interaction studies (Dibble et al. 1996; Randall et al. 1996). Fish abundance and species numbers were similar in linear features and unvegetated shoreline. Distinguishing linear SAV features from shoreline waters may be difficult because many young and small fish seek both marginal and vegetated habitats (Killgore et al. 1999). Most species utilizing SAV in the upper and lower freshwater zones were fish that are known to orient to structure or cover, prefer vegetated

surroundings, and consume of organisms supported by vegetation (Poe et al. 1986; Killgore et al. 1989). Examples of these fish are Centrarchidae (sunfishes, freshwater bass), Cyprinidae (minnows), and Percidae (darters, yellow perch, walleye).

In the brackish zone, SAV habitats did not appear to support more fish than unvegetated areas, but did support slightly more species. The lack of an SAV effect on fish density like that seen in the two freshwater zones may reflect the fish community of the brackish estuary. In this zone, most of the abundant fishes are pelagic (open surface water) species that feed primarily on plankton. Some pelagic fishes avoid vegetation and structure, (e.g., menhaden and herring; Killgore et al. 1993) or are widely distributed without regard to SAV (anchovies, clupeids, silversides; Killgore et al. 1989). For these fish, SAV is not a preferred habitat (Bailey 1978; Bettoli et al. 1991) so we would not expect SAV to show differences from unvegetated habitats. The few additional species found in brackish water SAV include littoral, structure oriented fishes.

Many larval fish have been documented concentrating in vegetated habitats (Floyd et al. 1984; Paller 1987). We captured a variety of small and larval fish in both SAV and unvegetated shallow waters (data not shown). However, we were not able to detect a significant effect of SAV on larval fish numbers. Unlike SAV beds in lakes or slow-moving rivers that create still water habitat, many SAV beds in the Hudson River had current velocities (average 12 cm/s) higher than the swimming capacity of larval fish (8.4 cm/s, Scheidegger and Bain 1995). Thus, larval fish would not be able to remain in SAV habitats in the Hudson River through a tidal cycle. The highest larval fish catches irrespective of habitat were in the brackish zone, and a large majority of fish larvae were anchovies that spawn through much of the warm portion of the year.

No clear differences were found in common food items of fish captured in SAV versus unvegetated habitats for any sampling zone. Many common food items (identified to the Family level) were the same across all zones, sites, and habitats. Chironomids and amphipods were the most commonly consumed organisms. Our artificial substrate colonization experiment provided good evidence that fish in SAV beds are grazing on epiphytic invertebrates at rates that can reduce the number of organisms. We can infer then that fish are using invertebrates supported by SAV as previously concluded by Keast (1985) and Hoover et al. (1989). Elevated macroinvertebrate food supply for fish has been reported for SAV in many settings (Gerking 1957; Lodge 1985; Hanson 1990; Beckett et al. 1992; Nakamura and Sano 2005). This effect was most clearly seen in the upper freshwater zone of the river where SAV enhances fish abundance and species richness. Also, many of the species of fish using SAV habitats in the upper freshwater zone are particularly effective macroinvertebrate consumers, as shown by the dramatic difference between macroinvertebrate densities on screened versus open surfaces. Finally, the most common organisms on the artificial substrate samplers, as on actual plants, were chironomids, the dominant food item in the fish we analyzed.

V. SIGNIFICANCE AND SYNTHESIS

A. SAV Significance for the Hudson River

1. Primary Production

We estimated the standing biomass of SAV for comparison with other major groupings of aquatic plants in the Hudson River ecosystem (water chestnut (*Trapa natans*), emergent and broadleaf marsh vegetation and phytoplankton; Table 7). For all these groups we used information on standing crops from our direct field measurements with estimates of spatial extent derived from multiple sources. Interestingly, SAV has the second lowest biomass per unit area and second lowest total biomass in the whole Hudson River yet it apparently makes disproportionate contributions as both habitat and food resource. As described above, 18% of the macroinvertebrates in the Hudson are associated with SAV despite the relatively small areal extent of this habitat and its standing stock. Moreover, shallow water invertebrates have increased since the zebra mussel invasion (Strayer and Smith 2001) and have quite possibly increased their reliance on SAV as a food resource. Evidence from isotopic tracers also shows a potential connection from SAV to some fishes (Caraco et al. 1998).

The comparison of standing stocks will underestimate the actual contribution of SAV and other high turnover components to annual production. It is likely that the underestimation for *Vallisneria* is at least two-fold while for phytoplankton annual turnover would be much greater. Total net production by aquatic plants will still be small relative to allochthonous loading from the upper watershed (Cole and Caraco 2006) yet these plant communities make a significant contribution to food webs of the Hudson.

2. Dissolved Oxygen

Dissolved oxygen in the Hudson River is generally undersaturated although concentrations in the main channel are no longer below critical values for most fishes. The zebra mussel invasion caused a decline in DO and the net effect would have been greater if not for some compensation by SAV O_2 production under the somewhat improved water clarity (Caraco et al. 2002). The SAV beds clearly have the potential to raise local oxygen, and by using our relationship between bed size and the proportion of time a bed has super-saturated DO, we can extrapolate the extent of this effect to the whole river. Figure 20 shows the time spent supersaturated for all sites ranked by size. From this figure we estimate that a bed > 400,000 m^2 in area will spend more than half of a 24 hr period with DO above 8 mg/L. The cumulative area of SAV beds of this size or greater is 720 ha or about 40% of the total SAV area. Therefore, 40% of the vegetated area represents locations of high DO in the main channel which may be significant for some animals, and can influence many redox-sensitive biogeochemical processes.

3. Invertebrates

Macrophyte beds in the Hudson support dense and diverse macroinvertebrate communities. Densities in macrophyte beds were more than three times as high as densities on unvegetated sediments (Strayer and Smith 2001). Thus, SAV beds support 18% of all of the macroinvertebrates in the study region, even though they cover just 6% of its surface area. Perhaps more importantly, macrophyte beds are "hotspots" for populations of prey items for fish. The rich parts of macrophyte beds, where macroinvertebrate densities may reach as high as 100,000 animals/m^2, may be the richest foraging grounds in the Hudson. Dozens of species of invertebrates are specialized for life among macrophytes, and are rare or absent elsewhere.

Thus, macrophyte beds play an essential role in supporting the biodiversity of invertebrates in the Hudson.

Table 7. Summary of approximate standing stock of primary producers in the Hudson River

Producers	Area (100 ha)	Mass/Area (g dry mass/m^2)	Biomass in whole river (mT dry mass)
SAV	17.7	66.4	1173
Trapa natans	8.0	300	2416
Marsh Graminoid	11.8	1800	21185
Marsh Broadleaf	5.9	150	891
Phytoplankton	200	11	2200

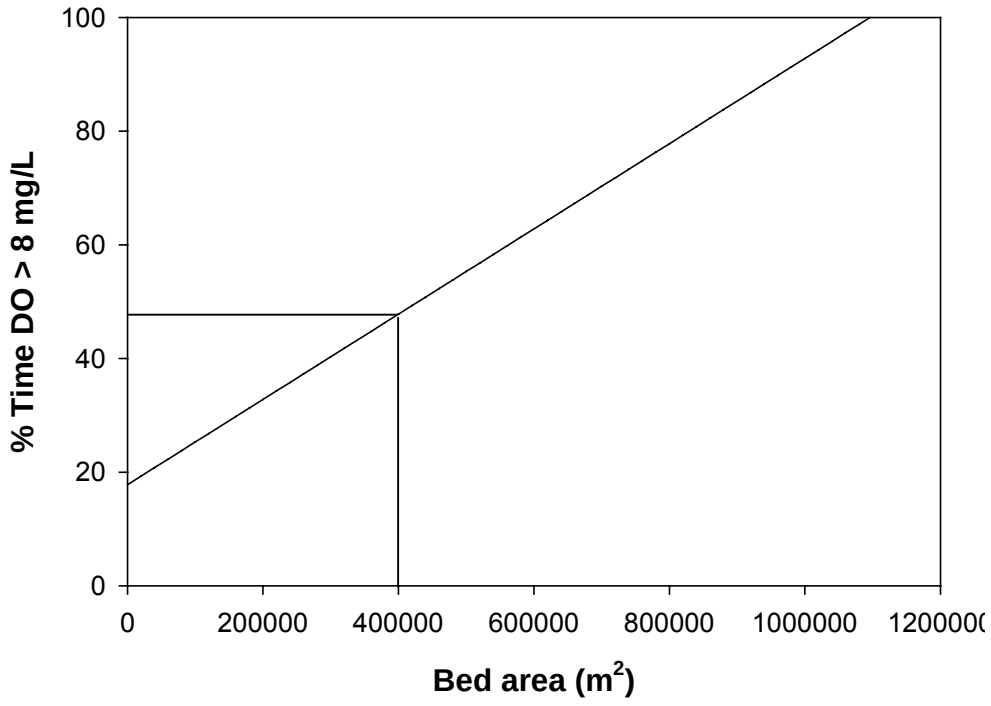

Figure 20. The proportion of time beds across the entire size range have supersaturated DO concentrations. Values are derived from a linear regression of sampled sites (Fig. 8). SAV Beds above about 0.4 km^2 spend 50% of a 24 hr period with DO > 8 mg/L.

4. Fish

Our findings were consistent with past research on fish interactions with aquatic vegetation, and they provide specific evidence for the ecosystem value of SAV in the Hudson River Estuary. We can conclude that on the scale of the whole Hudson River Estuary SAV supports more fish, a greater diversity of species, and a highly available food supply relative to open and unvegetated habitats. We were able to document that the dominant food items consumed by fish in SAV were associated with aquatic plants, and that these organisms were significantly reduced on artificial substrates vulnerable to fish predation. Details of the relationship between fish and SAV across the river-estuary gradient reveal how SAV support for fish is affected by both the environmental setting (river zone) and nature of the fish community in the particular zone.

B. Similarities in Controlling Factors Among Variables

Different SAV beds in the Hudson have different functional characteristics, as shown by the large amount of scatter in many graphs and the wide range in values for functions such as water quality and animal abundance. We have identified four factors that contribute to explaining this variation: (1) position along the river (river kilometer); (2) neighborhood (the local setting in which the bed occurs); (3) bed area; and (4) the density of plant growth in the bed.

The ecological characteristics of the Hudson change greatly along the 175 km between the northernmost and the southernmost beds. Changes in salinity are most important. Above about Rkm 100, the water rarely contains any trace of sea salt, but the water becomes increasingly salty from Rkm 100 to the southern end of the study area. Most aquatic plants and

animals are sensitive to salinity, so the composition of the plants and animals in the SAV beds progressively changes seaward of Rkm 100. The plant beds themselves shift from nearly pure *Vallisneria* to a mixture of *Vallisneria*, *Potamogeton crispus*, and *Myriophyllum spicatum*. Macroinvertebrate communities change markedly in composition (Fig. 15) from typically freshwater animals such as chironomid midges and oligochaete worms to such characteristically brackish-water animals as the hydroid *Cordylophora*, the amphipods *Corophium* and *Leptocheirus*, barnacles, the alien bivalve *Rangia*, and polychaete worms. Fish communities in the freshwater part of the estuary contain spottail shiner, white perch, shads, herrings and sunfish species, while those in brackish-water beds are strongly dominated by white perch. There are also analogous but smaller shifts in macroinvertebrate and fish species composition between the beds in the upper versus lower freshwater zones.

Despite these obvious shifts in the kinds of plants and animals that live in SAV beds, there are only minor differences in the habitat value for invertebrates and fishes of SAV beds along the course of the Hudson. While the taxonomic composition of the organisms may change along the River, their higher abundance in SAV versus unvegetated areas points to the value of SAV as habitat. Neither overall plant biomass nor density of invertebrates varied along the course of the Hudson (Fig. 4A and Fig. 15). The impact of SAV beds on dissolved oxygen and turbidity likewise did not change in any simple way with river kilometer (Fig. 10). There are some hints that SAV may be less valuable as fish habitat in the brackish Hudson than further upriver (Fig. 16), perhaps because the Hudson's fish community contains few species that both specialize in vegetated habitats and tolerate brackish water. In summary, SAV beds play much the same important ecological role everywhere in the Hudson.

The characteristics of the neighborhood in which the SAV bed is located had an

important influence on the effects of SAV on dissolved oxygen and turbidity. The dissolved oxygen in SAV beds was clearly correlated with the dissolved oxygen in the main-channel water that flushed through the beds (Fig. 10). The ability of SAV beds to reduce turbidity appears to depend on not just the SAV bed itself, but the amount of vegetation within a 300 meter radius of the sampling point (Table 2). We did not look for neighborhood effects on plant biomass, invertebrates, or fish, and it is doubtful if we could detect neighborhood effects in the relatively "noisy" biological data. Nevertheless, it seems likely that such neighborhood effects might affect the number or kinds of animals that use SAV beds. When we designed this study, we suspected that the size of the SAV bed would be a good predictor of its function. Consequently, we deliberately sampled beds over a wide range of sizes to estimate the effect of bed size. We were surprised to find that bed size affected few functions of SAV beds in the Hudson. Plant biomass (per m^2) was unrelated to bed size, although a few small beds had exceptionally high biomass (Fig. 4). Larger beds were more likely to have supersaturated dissolved oxygen than small beds (Fig. 8), and slightly less likely to have very turbid water (Fig. 9). Neither the number nor the kind of invertebrates living in SAV beds depended strongly on the size of the bed. The sediments in large beds were finer and richer in organic matter than those in small beds, but we do not know if the beds caused the difference or responded to pre-existing differences in sediments. Thus, a few but certainly not all of the functions of SAV beds depended on bed size, and the correlations between bed size and function were generally weak.

The thickness of plants in the bed (i.e., plant biomass per m^2) strongly influenced the number of invertebrates living in the bed (Fig. 14), but not the kinds of invertebrates. Plant biomass did not affect turbidity or dissolved oxygen, nor was it related to the catch rates of fish in different beds.

Even in a five-year data set, we could see that many aspects of bed function varied from year to year. The range in plant biomass over the three to four years of study at the four keystone beds was 49-fold (Appendix 1), or 20-fold without the highly variable Peekskill keystone bed. The amount of time that water in SAV beds was supersaturated varied by 2.5-fold across years, and was strongly related to water clarity in the main channel (Fig. 10). Macroinvertebrate communities also varied substantially from year to year. Over the three or four years during which the keystone beds were sampled, the ranges in average areal densities were 2.6-fold for benthic macroinvertebrates, 117-fold for epiphytic macroinvertebrates, and 5.5-fold for total macroinvertebrates. Epiphytic densities were especially variable because of the substantial interannual variation in plant biomass. The composition of both benthic and epiphytic macroinvertebrate communities varied substantially from year to year, especially in the brackish parts of the river. In contrast, fish communities varied little from year to year (Fig. 18).

Thus, year-to-year variation in SAV function was large, about the same size as bed-to-bed variation in a single year. At least some of this variation was caused by year-to-year variation in hydrology and turbidity. In view of the importance of SAV beds in overall function of the Hudson River, and the very large year-to-year variation in function that we saw, we think that it would be worthwhile to better document and understand the year-to-year variation in SAV function in the Hudson and other rivers and estuaries.

C. Relationships Among Functions

Simple correlation analyses among the six commonly measured functions (% time DO > 8 mg/L, % time turbidity > 40 NTU, density of benthic invertebrates, density of epiphytic invertebrates, fish abundance, and fish species richness) showed only one significant correlation,

between abundance and diversity of fishes ($p = 0.008$, $r = 0.48$). The relationship with the next lowest p value was a negative association between high DO and high turbidity ($p = 0.17$, $r = -0.2$).

A principal components analysis (PCA) was used to show in two-dimensional space the relationships among functions in the sampled beds (Fig. 21). The loadings for functions revealed some interpretable patterns, for instance the proportion of time a bed had DO > 8 mg/L loaded positively on PCA Axis 2, while local turbidity loaded negatively on this axis. Therefore, on the PCA figure, sites with higher oxygen will be substantially displaced from sites exhibiting high turbidity. Such patterns are reasonable given the strong light limitation of species of SAV in the Hudson (Harley and Findlay 1994). Similarly, standardized fish abundance and richness load positively on PCA Axis 1 while abundance of both benthic and epiphytic invertebrates load negatively, i.e., sites tending towards high values for the fish-related functions had fewer invertebrates in the sediments or on the plants themselves. As described previously there are several lines of evidence (predator exclosures, lower abundance of invertebrates at bed edges) implying that fish predation is a significant source of mortality for invertebrates in these habitats. The different loadings for these functions probably reflect these processes. The vertical axis may be associated with plant abundance, either mass per unit area or absolute bed size. Epiphytic invertebrate density was strongly associated with plant biomass while high DO was correlated with bed size. This analysis suggests we do in fact have an understanding of factors controlling individual functions but these regulators differ among functions. The overall effect is that the various functions we followed vary semi-independently, and conditions in time or space that lead to high values for a particular function may lead to declines in others. In aggregate, SAV beds perform important functions but these do not coincide in time or space.

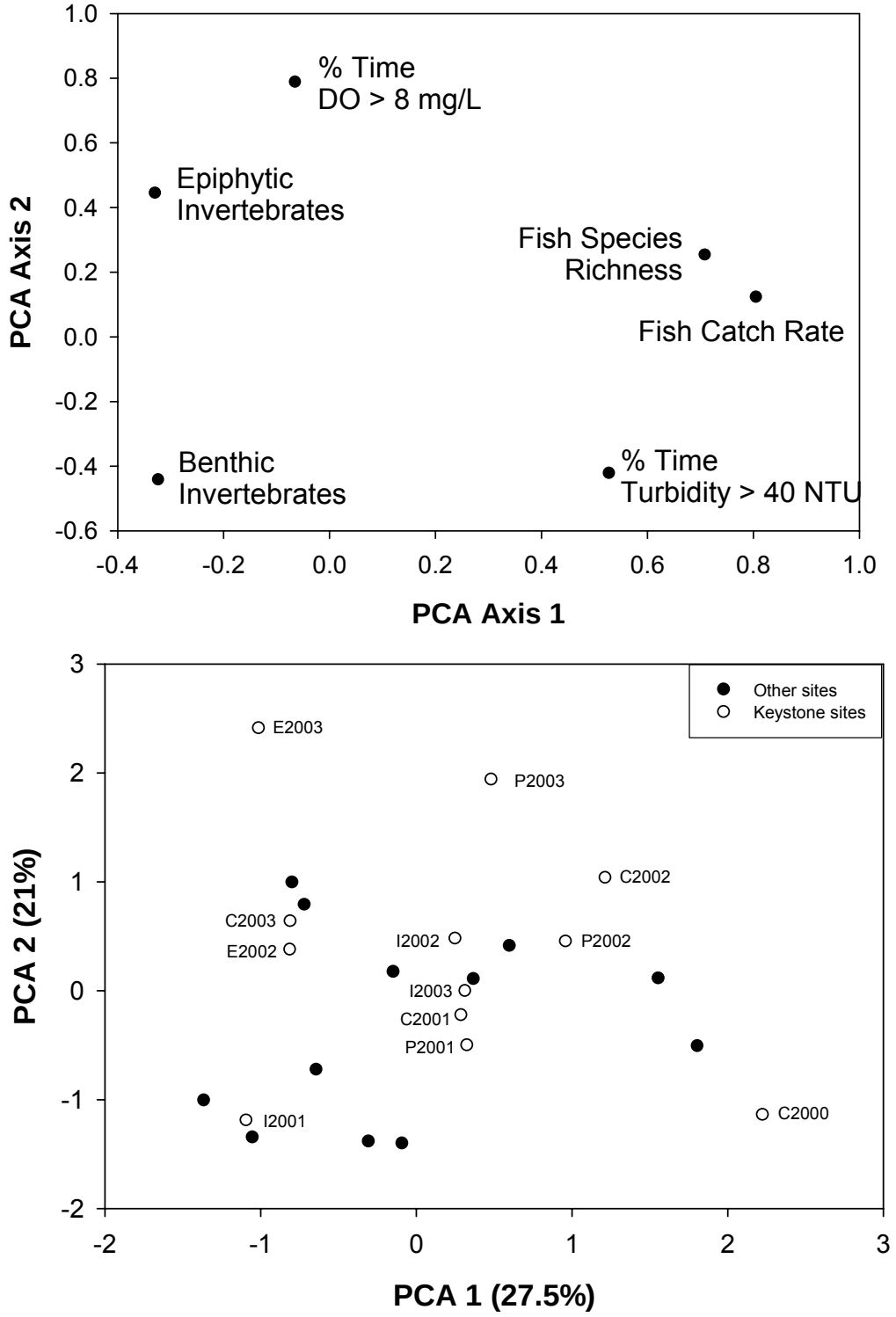

Figure 21. Plot of PCA analysis of the six measured functions for SAV study sites. Closed circles are sites visited just once; keystone sites were visited repeatedly. C = Cruger South (601), E = Esopus Meadows (688), I = Iona (1069), P = Peekskill (1079). Values in parentheses are proportion of total variance accounted for by each Principal Component.

The locations of sampled beds on the first two PC Axes also demonstrate the large temporal variability among beds resampled in multiple years. The keystone beds with full data sets for functional measures across three or more years show wide dispersion of sites in different years. For instance, the Cruger South site spans three units on the first PC axis across the four years of sampling, demonstrating little year-to-year coherence in how these functions are performing at this site. The Peekskill site similarly spans two units on the second axis across the three years of data collection.

The lack of simple correlations among functions and large interannual variability highlight the importance of different controlling factors for the various functions and absence of one or two "master variables" capable of providing significant predictive power for these functions. As different controlling factors, quite likely operating at different spatial scales exert an influence on this range of functions, the particular functions performing at high levels will fluctuate across space and time. From a management/protection point of view, this means that the performance of a site may change substantially in subsequent years. Also, the task of identifying site characteristics that consistently yield high performance across multiple functions becomes much more difficult. The study as a whole shows the importance of SAV as habitat for organisms and an influence on water chemistry, yet this high variability means one can not determine with a single assessment whether a particular site is (or is not) particularly "valuable".

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VIII. APPENDICES

Appendix 1. SAV bed characteristics and ecological functions

Bed Identification						Bed size and shape							
Bed ID # [a]	Bed Name (* = keystone site)	Rkm [b]	Vegetation	Sampling Year	Bed centroid [c]	Area (m^2)	Peri-meter (m)	Shape Index [d]	Perimeter / Area	Fractional Dimension	Length (m)	Width (m)	Length / Width
Lin 60		235	linear	2002	604948.24, 4725757.91	1600					800	2	400
Lin 50		231	linear	2002	603924.07, 4724252.87	668					334	2	167
Lin 50		231	linear	2003	603924.07, 4724252.87	668					334	2	167
Lin 36		229	linear	2002	602639.53, 4721612.07	484					242	2	121
Lin 15		225	linear	2002	601455.96, 4717628.28	620					310	2	155
Lin 15		225	linear	2003	601455.96, 4717628.28	620					310	2	155
169	Mill Creek	202	bed	2000	600438.43, 4695567.78	20376	945	1.868	0.046	1.381	400	44	9
176	Opp. Mill Ck	202	bed	2000	599849.62, 4695148.99	486	109	1.396	0.225	1.517	28	11	3
221	Stuyvesant	200	bed	2000	600066.88, 4693766.7	1692	286	1.960	0.169	1.522	132	14	10
221	Stuyvesant	200	bed	2003	600066.88, 4693766.7	1692	286	1.960	0.169	1.522	132	14	9
250	NuttHk	197	bed	2000	599777.2 , 4690555	3383	333	1.616	0.098	1.430	130	34	4
330	Opp. Stockp	193	bed	2000	600164.49, 4684887.28	100	37	1.029	0.364	1.561	12	10	1
344	Stockp	191	bed	2000	600633.65, 4683506.48	21295	652	1.261	0.031	1.300	243	93	3
504	Cheviot *	167	bed	2000	589613.09, 4663318.48	364273	7691	3.595	0.021	1.397	2075	247	8
504	Cheviot *	167	bed	2001	589613.09, 4663318.48	364273	7691	3.595	0.021	1.397	2075	247	8
504	Cheviot *	167	bed	2002	589613.09, 4663318.48	364273	7691	3.595	0.021	1.397	2075	247	8
504	Cheviot *	167	bed	2003	589613.09, 4663318.48	364273	7691	3.595	0.021	1.397	2075	247	8
504	Cheviot *	167	bed	2004	589613.09, 4663318.48	364273	7691	3.595	0.021	1.397	2075	247	8
504	Cheviot *	167	bed	2005	589613.09, 4663318.48	364273	7691	3.595	0.021	1.397	2075	247	8
601	Cruger South *	156	bed	2000	588747.19, 4653047.32	186917	3476	2.268	0.019	1.343	1327	12	108
601	Cruger South *	156	bed	2001	588747.19, 4653047.32	186917	3476	2.268	0.019	1.343	1327	12	108
601	Cruger South *	156	bed	2002	588747.19, 4653047.32	186917	3476	2.268	0.019	1.343	1327	12	108
601	Cruger South *	156	bed	2003	588747.19, 4653047.32	186917	3476	2.268	0.019	1.343	1327	12	111
601	Cruger South *	156	bed	2004	588747.19, 4653047.32	186917	3476	2.268	0.019	1.343	1327	12	108
601	Cruger South *	156	bed	2005	588747.19, 4653047.32	186917	3476	2.268	0.019	1.343	1327	12	108

a) bed numbers from GIS polygon analysis
b) kilometers north of Battery Park
c) GPS UTM coordinates (East, North)
d) Patch Analyst software, 1.0=circle

Bed Identification						Bed size and shape							
Bed ID # [a]	**Bed Name (* = keystone site)**	**Rkm [b]**	**Vegetation**	**Sampling Year**	**Bed centroid [c]**	**Area (m^2)**	**Peri-meter (m)**	**Shape Index [d]**	**Perimeter / Area**	**Fractional Dimension**	**Length (m)**	**Width (m)**	**Length / Width**
688	Esopus Meadows *	139	bed	2000	587613.65, 4636094.55	190306	6772	4.379	0.036	1.451	1951	46	43
688	Esopus Meadows *	139	bed	2001	587613.65, 4636094.55	190306	6772	4.379	0.036	1.451	1951	46	43
688	Esopus Meadows *	139	bed	2002	587613.65, 4636094.55	190306	6772	4.379	0.036	1.451	1951	46	43
688	Esopus Meadows *	139	bed	2003	587613.65, 4636094.55	190306	6772	4.379	0.036	1.451	1951	46	42
688	Esopus Meadows *	139	bed	2004	587613.65, 4636094.55	190306	6772	4.379	0.036	1.451	1951	46	43
688	Esopus Meadows *	139	bed	2005	587613.65, 4636094.55	190306	6772	4.379	0.036	1.451	1951	46	43
778	Rogers Point	127	bed	2001	587828 , 4624135	34236	3622	5.522	0.106	1.570	1464	18	80
858	WaFalls	110	bed	2001	587874.99, 4606477.59	720	129	1.360	0.180	1.478	56	15	4
950	Quassaic	96	bed	2001	582956.68, 4593778.76	323	73	1.149	0.227	1.486	30	14	2
1049	ConHook	80	bed	2001	586669.5 , 4578195	57207	1869	2.205	0.033	1.375	621	99	6
1049	ConHook	80	bed	2001	586669.5 , 4578195	57207	1869	2.205	0.033	1.375	621	99	6
1069	Iona *	74	bed	2001	586250 , 4572416	88592	1848	1.752	0.021	1.321	459	155	3
1069	Iona *	74	bed	2002	586250 , 4572416	88592	1848	1.752	0.021	1.321	459	155	3
1069	Iona *	74	bed	2002	586250 , 4572416	88592	1848	1.752	0.021	1.321	459	155	3
1069	Iona *	74	bed	2003	586250 , 4572416	88592	1848	1.752	0.021	1.321	459	155	3
1069	Iona *	74	bed	2004	586250 , 4572416	88592	1848	1.752	0.021	1.321	459	155	3
1069	Iona *	74	bed	2005	586250 , 4572416	88592	1848	1.752	0.021	1.321	459	155	3
1079	Peekskill *	71	bed	2001	588834 , 4571342	250747	2314	1.303	0.009	1.246	934	324	3
1079	Peekskill *	71	bed	2002	588834 , 4571342	250747	2314	1.303	0.009	1.246	934	324	3
1079	Peekskill *	71	bed	2003	588834 , 4571342	250747	2314	1.303	0.009	1.246	934	324	3
1079	Peekskill *	71	bed	2004	588834 , 4571342	250747	2314	1.303	0.009	1.246	934	324	3
1079	Peekskill *	71	bed	2005	588834 , 4571342	250747	2314	1.303	0.009	1.246	934	324	3
1105	Indian Point	70	bed	2001	588308 , 4569922	3837	309	1.408	0.081	1.390	101	45	2
1177	Haverstraw	59	bed	2001	588122.9, 4559494	4993	584	2.330	0.117	1.496	171	19	9
1177	Haverstraw	59	bed	2001	588122.9, 4559494	4993	584	2.330	0.117	1.496	171	19	9
1177	Haverstraw	59	bed	2003	588122.9, 4559494	4993	584	2.330	0.117	1.496	171	19	9

a) bed numbers from GIS polygon analysis
b) kilometers north of Battery Park
c) GPS UTM coordinates (East, North)
d) Patch Analyst software, 1.0=circle

		Sediment characteristics					Water chemistry			Plants	
Bed ID #	**Sampling Year**	**% silt**	**% sand**	**% clay**	**% loss on ignition**	**% coreable sediments**	**Main Channel Secchi Depth (cm)**	**% Time DO > 8mg/L**	**% Time Turbidity > 40 NTU**	**Areal biomass (g/m^2)**	**Total biomass (g)**
Lin 60	2002	17	74	9	3	50	140	18.30	0.00	125	199824
Lin 50	2002	12	82	6	3	100	140	23.40	0.00	65	43153
Lin 50	2003	24	64	12	3	83	140	0.35	0.69	83	55751
Lin 36	2002	13	82	5	4	17	140	0.00	0.00	61	29490
Lin 15	2002	19	73	9	3	100	140	24.50	4.30	46	28284
Lin 15	2003	26	61	14	3	100	140	3.47	1.39	53	32711
169	2000	50	37	13	4	100	100	55.00	17.70	11	219816
176	2000	21	73	5	2	100	100	0.00	18.50	50	24134
221	2000	49	34	17	5	100	60	0.00	2.10	84	141351
221	2003	38	43	19	6	100	100	38.18	1.01	137	230958
250	2000	27	63	10	3	100	60	4.00	15.00	28	93946
330	2000	19	76	5	2	100	60	4.00	9.00	20	1954
344	2000	43	48	8	4	100	60	8.00	7.80	52	1106360
504	2000						60	43.00	5.30		
504	2001						100	59.00	0.90		
504	2002						160	48.30	4.80		
504	2003						100	55.40	4.37		
504	2004						60	27.96	1.88		
504	2005						100	52.00	5.30		
601	2000	45	42	13	4	100	70	0.02	21.80	66	12411663
601	2001	40	46	14	4	100	120	43.00	7.30	15	2854783
601	2002	37	51	11	4	100	135	44.40	0.00	36	6764339
601	2003	36	49	15	4	100	120	41.80	0.00	95	17687956
601	2004						90	38.55	0.00		
601	2005						100	55.20	3.10		

		Sediment characteristics					Water chemistry			Plants	
Bed ID #	**Sampling Year**	**% silt**	**% sand**	**% clay**	**% loss on ignition**	**% coreable sediments**	**Main Channel Secchi Depth (cm)**	**% Time DO > 8mg/L**	**% Time Turbidity > 40 NTU**	**Areal biomass (g/m^2)**	**Total biomass (g)**
688	2000	54	26	21	9	100	70			4	810323
688	2001	57	22	21	7	100	120			9	1620646
688	2002	58	18	24	7	100	135	47.70	0.00	77	14610553
688	2003	52	21	26	8	100	120	61.41	0.00	154	29326155
688	2004						90	18.59	0.00		
688	2005						100	29.40	3.60		
778	2001	54	23	22	6	100	120	11.40	12.00	59	2018246
858	2001	26	61	13	5	100	120	0.00	2.00	277	199534
950	2001					0	120	0.80	30.00	479	154585
1049	2001	63	16	21	7	100	120	15.00	18.80	46	2605207
1049	2001						120	6.40	20.10		
1069	2001	68	5	26	9	100	120	2.70	0.50	4	347546
1069	2002	60	15	25	6	100	130	22.10	7.20	35	3320871
1069	2002						130				
1069	2003	63	7	30	8	100	70	26.73	6.60	8	735314
1069	2004						60	21.91	2.52		
1069	2005						95		0.30		
1079	2001	67	5	27	9	100	120	3.40	1.10	0	6269
1079	2002	56	13	31	7	100	130	27.70	3.30	0	6269
1079	2003	62	9	29	8	100	70	78.98	0.34	7	1859289
1079	2004						60	16.12	0.76		
1079	2005						95	0.50	0.00		
1105	2001	64	4	32	8	100	120	5.80	1.80	3	12574
1177	2001	26	68	7	2	100	140	74.90	7.10	29	144752
1177	2001						140	78.90	12.00		
1177	2003	23	70	7	2	100	70	41.12	1.32	42	210205

		Macroinvertebrates		Fish					
Bed ID #	**Sampling Year**	**Benthic (# / m^2)**	**Epiphytic (# / m^2)**	**Electrofishing CPUE**	**Electrofishing species**	**Gill net CPUE**	**Gill net species**	**Standardized abundance (units)**	**Standardized species richness**
Lin 60	2002	7993	53474	37	10			-0.3890	1
Lin 50	2002	9422	11816	42	10			-0.2518	1
Lin 50	2003			52	9			-0.0176	0
Lin 36	2002	8701	6447	31	8			-0.5263	0
Lin 15	2002	6234	11305	44	12			-0.2114	1
Lin 15	2003			66	10			0.3135	1
169	2000	8821	1646	89	6	19	4	0.8004	0
176	2000	19716	15356						
221	2000	18137	17778	45	8	8	2	-0.2218	0
221	2003			77	12	4	1	0.0271	0
250	2000	4735	1034	51	6	8	1	-0.1119	-1
330	2000	10022	1271						
344	2000	10187	3104	62	10	36	4	1.2155	1
504	2000								
504	2001								
504	2002								
504	2003								
504	2004								
504	2005								
601	2000	5767	5295	85	10	26	3	1.1064	0
601	2001	13665	1683	58	7	16	4	0.2376	0
601	2002	6492	6871	112	10	24	3	1.2142	0
601	2003	17288	33734	74	6	13	3	0.3585	0
601	2004								
601	2005								

		Macroinvertebrates		Fish					
Bed ID #	**Sampling Year**	**Benthic (# / m^2)**	**Epiphytic (# / m^2)**	**Electrofishing CPUE**	**Electrofishing species**	**Gill net CPUE**	**Gill net species**	**Standardized abundance (units)**	**Standardized species richness**
688	2000	6263	605	61	10	13	2	0.2217	0
688	2001	5920	351	48	7	14	3	0.1524	0
688	2002	8836	17184	66	8	8	1	0.0196	0
688	2003	3561	61038	70	7	7	2	0.0324	0
688	2004								
688	2005								
778	2001	5338	33648			8	3	-0.2565	1
858	2001	10538	24159						
950	2001	0	22666						
1049	2001	8187	7179			5	2	-0.5276	0
1049	2001								
1069	2001	11225	2594			7	2	-0.3207	-1
1069	2002	4303	26031			9	3	-0.1137	1
1069	2002								
1069	2003	4968	1573			8	3	-0.2493	0
1069	2004								
1069	2005								
1079	2001	6791	12			13	3	0.1646	0
1079	2002	2634	25			16	3	0.4857	0
1079	2003	2918	3103			14	3	0.2573	0
1079	2004								
1079	2005								
1105	2001	6312	648			3	1	-0.6989	-1
1177	2001	6857	4146			6	2	-0.3992	0
1177	2001								
1177	2003					3	1	-0.6703	-1

Appendix 2. 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

	Mean density (no. / m^2)	% Epiphytic
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 sp.	89	67
Gammarus sp.	549	32
Hyallela sp.	4	100
Leptocheirus sp.	250	0
Isopoda (sow bugs)		
Chiridotea almyra	1	0
Cyathura polita	58	0
Decapoda (crabs)		
Rhithropanopeus harrissi	6	79
Cumacea		
Almyracuma proximoculi	10	0

	Mean density (no. / m^2)	% Epiphytic
Copepoda	38	25
Ostracoda	73	4
Cladocera (water fleas)		
Chydorus sp.	190	99
Eurycercus sp.	8	100
Sida crystallina	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

	Mean density (no. / m^2)	% Epiphytic
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.	43	0
Polypedilum sp.	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**

Appendix 3. Dominant fish species by zone, habitat, and sampling method. Species are listed in decreasing order of abundance up to a cumulative total of at least 75% of all fish captured.

Zone	Vegetation	Sampling method	Dominant Species
Upper Freshwater	SAV	Electrofishing	Spottail shiner, pumpkinseed, alewife, American eel, redbreast sunfish, white perch
	LSAV	Electrofishing	American eel, spottail shiner, pumpkinseed, yellow perch, redbreast sunfish, bluegill
	UNV	Electrofishing	American eel, redbreast sunfish, white perch
Lower Freshwater	SAV	Electrofishing	Spottail shiner, white perch, alewife, American shad, Atlantic menhaden, pumpkinseed
		Gill nets	White perch, American eel, spottail shiner
	UNV	Electrofishing	White perch
		Gill nets	White perch, gizzard shad
Brackish	SAV	Gill nets	White perch, bluefish
	UNV	Gill nets	White perch