



Macroinvertebrate communities of hypoxic habitats created by an invasive plant (*Trapa natans*) in the freshwater tidal Hudson River

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With 6 figures and 2 tables

Abstract: Like other floating-leaved plants, dense beds of water-chestnut (*Trapa natans*) may cause the underlying water to become hypoxic or even anoxic. Despite this potential stress, previous studies have reported dense and diverse invertebrate communities in water-chestnut beds. However, none of these previous studies simultaneously measured dissolved oxygen concentrations and invertebrate communities, leaving open the possibility that these study sites were not severely hypoxic. Here, we report the results of a study in which we measured both invertebrates and dissolved oxygen in a large, dense water-chestnut bed in the freshwater tidal Hudson River, New York. We sampled invertebrates at nine sites in the bed using a modified Downing box-sampler and a corer. We took samples both early in the growing season (June), when the water-chestnut canopy was not fully developed and hypoxia was only moderate, and in the middle of the growing season (July), when the canopy was fully developed and hypoxia was frequent and severe. We hypothesized that the effects of hypoxia would be more severe in July than in June, in the interior of the bed than near its edge, and for sediment-dwelling animals than for epiphytic animals. We also hypothesized that predatory invertebrates would be especially abundant in the most hypoxic sites, where fish predation presumably would be reduced. None of these hypotheses was supported. Instead, we found that all locations and microhabitats that we studied supported dense, diverse communities of invertebrates, including insects, oligochaetes, crustaceans, and other taxa. The mechanisms by which these animals tolerate short-term hypoxia need to be elucidated. We suggest that water-chestnut beds in the Hudson are valuable habitats for invertebrate biodiversity and production, and may contribute substantially to fish production.

Key words: Hypoxia, invasive species, alien species, exotic species, macrophyte, macroinvertebrates, estuary.

Introduction

Macrophytes generally are considered to improve habitat quality for aquatic invertebrates by increasing food availability, surfaces for attachment, and shelter from predators. Many studies (e.g., Schramm & Jirka 1989, Kornijów et al. 1990, Strayer & Malcom 2007) have shown that invertebrate communities are denser and more diverse in macrophyte beds than in nearby unvegetated habitats. However, dense beds of float-

ing-leaved macrophytes may produce conditions that are stressful for invertebrates by creating hypoxia or even anoxia beneath their canopies (Caraco & Cole 2002, Caraco et al. 2006). Perhaps the best-known of these plants is water-chestnut (*Trapa natans*), a Eurasian plant that was introduced into North America as an ornamental plant, and which now forms beds as large as hundreds of hectares (Nieder et al. 2004) that may become completely anoxic (Caraco & Cole 2002).

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The invertebrate communities of these hypoxia-inducing plants are not well understood. Although the dense physical structure and high primary production in these plant beds should favor dense and diverse invertebrate communities, the low oxygen concentrations should exclude many invertebrate species, leading to communities that are low in species richness if not density. Dissolved oxygen concentrations <2–4 mg/L are widely considered to be limiting to aquatic invertebrates and other animals (e.g., USEPA 1986, 2000), and often are reached in such dense plant beds (e.g., Goodwin et al. 2008). Invertebrate communities in such hypoxic environments often are dominated by species that are tolerant to low oxygen (e.g., some tubificid oligochaetes and nematodes), or which possess special physiological, morphological, or behavioral adaptations such as hemoglobin (e.g., some cladocerans and chironomid midges), plastrons (some insects), or other use of atmospheric oxygen (e.g., pulmonate snails and some insects).

The few studies that have been done on invertebrates in dense beds of floating-leaved macrophytes have been inconclusive. Some reported relatively low density of invertebrates (Efitre et al. 2001, Feldman 2001), but others found as many (Cattaneo et al. 1998) or more (Masifwa et al. 2001, Strayer et al. 2003) invertebrates in water-chestnut beds than in other nearby habitats. However, none of these previous studies measured oxygen dynamics in the beds that were studied. Because the degree of hypoxia induced by these plants varies widely depending on the thickness of the canopy, intensity of water exchange, and area of the bed (Hummel & Findlay 2006), it is difficult to know the extent to which differences among studies might simply be a result of differences in oxygen stress among the beds.

Here, we describe the invertebrate communities of a large water-chestnut bed in which we simultaneously measured oxygen dynamics. We sampled invertebrate communities both before the plant canopy had fully developed, when oxygen stress should have been low, and after the canopy was well developed and hypoxia had set in. We also sampled several locations in the bed, both near its edge and deep in the interior of the bed, as well as different microhabitats within the bed: the sediments, the floating leaves, and the submerged leaves. Our hypotheses were (1) species richness, species diversity, and total density should follow the pattern of oxygenation in all three microhabitats and therefore be lower in the interior of the bed than at its edge; (2) the strength of this spatial patterning would be more clearly marked at the peak of plant biomass

in July than in June before the canopy was fully developed; (3) the most susceptible animal communities to oxygen deficiency would be the zoobenthos, and the least the epiphytic fauna leaving on the floating leaves, which has access to the atmosphere; and (4) because the interior, less oxygenated areas of the bed might serve as refuge for invertebrates against fish predation, these areas should have a higher percentage of invertebrate predators than edge habitats.

Material and methods

The study site was a large (120 ha), dense, and nearly monospecific bed of water-chestnut in Imbocht Bay, along the west bank of the Hudson River at river kilometer 172 (42° 10' N, 73° 54' W) (Caraco & Cole 2002). The water at this site is entirely fresh, although the average tidal range is 1.2 m. The depth in the study area at low tide ranged from 0.3 to 1.5 m, and the bottom sediments consisted of soft sand and mud. At nearby *Trapa* beds, sediments were ~44 % sand, 43 % silt, and 14 % clay (Strayer et al. 2003).

We sampled along the south edge of this bed, where a small channel allowed access to the interior of the bed (Fig. 1). We sampled along three transects marked by buoys: *outer* – near the river channel, at a distance of ca. 230 m from the edge of the *Trapa* bed; *middle* – in the central part of the bed; and *inner* – close to the river bank. These transects were separated by a distance of ca. 200 m, and were ~15 m long. We took samples from a boat that was pulled along an anchored line at three sampling sites along each transect, at ~7 m intervals.

We collected invertebrate samples during low tide on 21 June 2005 (mid-morning), the beginning of the development of *Trapa* bed, and on 27 July (mid-afternoon), when the stand was fully developed. Epiphytic animals were collected with a modified Downing sampler (Downing 1986) of 30 × 21 × 10 cm. We modified the sampler by making 20 × 12 cm slots in both sides, and covering them with 280-µm mesh Nitex screen to prevent back-pressure while closing the sampler. Samples were taken separately from the rosettes of floating leaves and from the underwater stems with their feather-like leaves. Benthic samples were collected beneath the water-chestnut by means of an acrylic tube, 6 cm in diameter, closed by a rubber stopper. Material collected was then sieved through a 280-µm mesh screen.

Both plant and sediment samples were transferred to plastic bags and kept in a cooler. In the lab, samples were refrigerated for no more than five days and processed by rinsing plants under flowing tap water onto a 280-µm mesh screen, while sliding our fingers over the plant surfaces. Then we checked the plants for animals after placing the material on white trays filled with water. The same trays were used for picking benthic invertebrates from the sediment samples. We preserved collected animals with 70 % ethanol.

The wet weight of each plant sample was determined to calculate invertebrate density per g WW (wet weight) of plant. Knowing the actual biomass of the vegetation in the field (Goodwin et al. 2008), we also calculated densities of epiphytic invertebrates per area of river bottom by multiplying the density of invertebrates per gram of plant by the measured plant biomass.

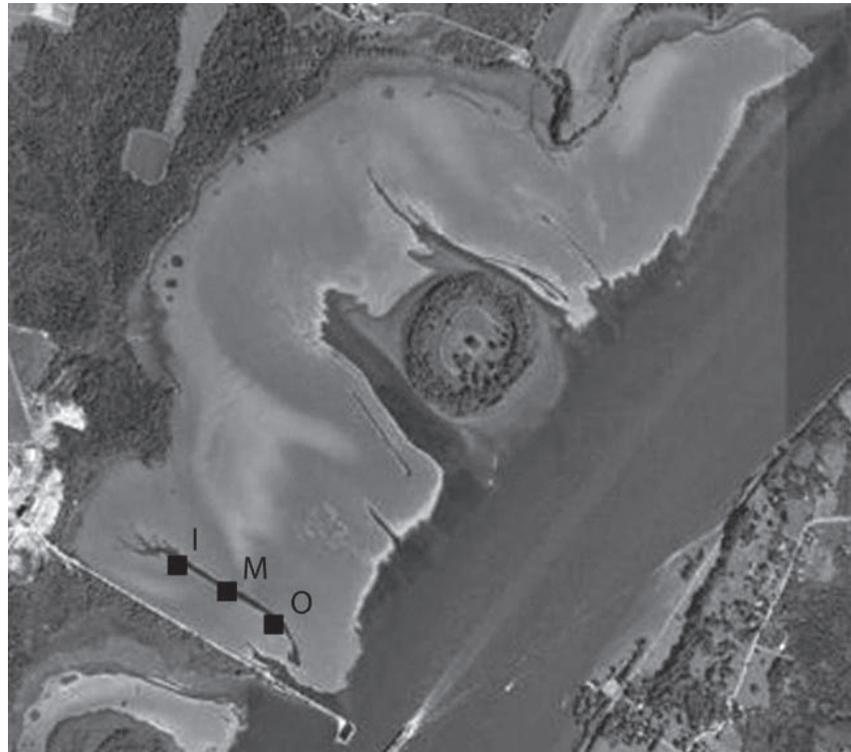


Fig. 1. Aerial photograph of study area, showing the location of the three transects, which are ~200 m apart. The large area of pale green is the water-chestnut bed, and the main channel of the Hudson River is along the lower right of the photograph. Sampling transects were oriented perpendicular to the small channel through the water-chestnut bed.

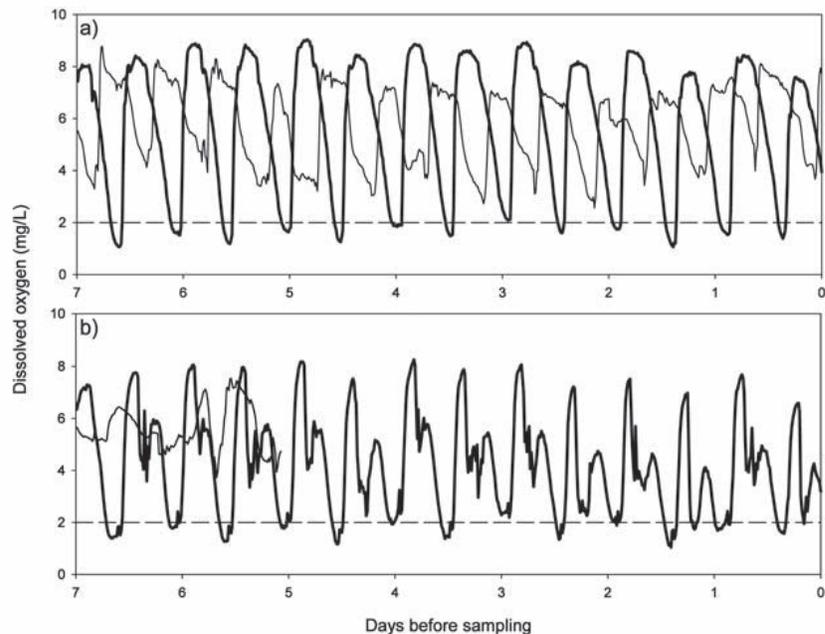


Fig. 2. Dissolved oxygen dynamics at the outer transect (a) and inner transect (b) in the week immediately before sampling in June (thin line) and July (thick line). The dashed line shows an oxygen concentration of 2 mg/L, indicating severe hypoxia. Data are missing from the inner transect for several days in June.

At each sampling date, we measured the water temperature and oxygen by means of YSI meter at the water surface and near the bottom. In addition, dissolved oxygen concentrations were automatically recorded every 15 min by YSI Endeco sondes (UPG 6000) at the outer and inner transects, from the end of May until the end of July (for details see Goodwin et al. 2008).

Invertebrates from both the water-chestnut and from the sediment samples were identified to the lowest taxonomic rank possible (Wiederholm 1983, Peckarsky et al. 1990, Kathman &

Brinkhurst 1998, Epler 2001). We classified the taxa as predators using Armitage et al. (1995) and Bass & Potts (2001).

Statistical analyses

Differences in invertebrate population densities among months, transects, and positions were tested with a repeated-measures ANOVA. Population densities were transformed by $\log_{10}(x+1)$ before statistical analysis. We used non-metric multidimension-

Table 1. Densities (number per m² of river) of invertebrates associated with floating leaves of *Trapa*, underwater stems and leaves of *Trapa*, and bottom sediments in June and July, 2005. Insects are larvae, unless stated otherwise.

Taxon	June			July		
	Leaves	Stems	Sediments	Leaves	Stems	Sediments
OLIGOCHAETA						
<i>Nais</i> sp.	4	6	0	305	145	0
<i>Stylaria lacustris</i>	0	0	0	68	814	0
<i>Aulodrilus americanus</i>	0	0	0	0	0	6
<i>Aulodrilus paucichaeta</i>	0	0	6	0	0	0
<i>Limnodrilus hoffmeisteri</i>	0	0	11	0	0	43
<i>Limnodrilus udekemianus</i>	0	0	6	0	0	6
Tubificidae with hair setae	0	0	6	0	0	13
Tubificidae without hair setae	0	0	4	0	0	170
HIRUDINEA	0	0	0	0	16	0
CRUSTACEA						
<i>Gammarus tigrinus</i>	3	1	38	318	266	261
<i>Caecidotea</i> sp.	0	0	0	0	0	13
HYDRACHNIDA						
<i>Limnesia undulata</i>	2	7	6	13	177	69
<i>Piona</i> sp.	0	0	0	0	0	35
EPHEMEROPTERA						
<i>Caenis punctata</i>	0	1	0	756	3203	50
ZYGOPTEA						
<i>Enallagma</i> sp.	0	0	0	26	0	0
HETEROPTERA						
Gerridae	0	0	0	43	0	0
<i>Mesovelis</i> sp.	0	0	0	32	0	0
CHIRONOMIDAE						
<i>Ablabesmyia mallochi</i>	0	0	4	0	0	19
<i>Ablabesmyia peleensis</i>	6	2	0	89	51	0
<i>Chironomus decorus</i> group	0	0	312	0	0	720
<i>Cladoplema</i> sp.	0	0	0	0	0	150
<i>Clinotanytus</i> sp.	0	0	0	0	0	75
<i>Cricotopus</i> sp.	436	272	0	22	49	0
<i>Cryptochironomus</i> sp.	0	0	108	0	0	68
<i>Dicrotendipes</i> sp.	4	41	4	50	402	76
<i>Endochironomus subtendens</i>	0.3	29	11	44	171	31
<i>Endochironomus nigricans</i>	0	0	0	0	0	80
<i>Glyptotendipes</i> sp.	0	0	0	13	39	0
<i>Labrundinia neopilosella</i>	0	0	0	6	88	0
<i>Nanocladius</i> sp.	0	0	0	0	8	0
<i>Parachironomus chaetoalus</i>	0	2	4	0	150	6
<i>Paratanytarsus</i> sp.	0	0	0	0	9	0
<i>Phaenopsectra punctipes</i>	0	0	0	24	8	0
<i>Polypedilum illinoisense</i> group	6	10	30	894	213	0
<i>Polypedilum halterale</i> group	0	0	46	0	0	105
<i>Polypedilum scalaenum</i> group	0	0	4	0	0	0
<i>Polypedilum</i> sp.	0	0	0	0	0	6
<i>Procladius</i> sp.	0	0	67	0	0	319
<i>Rheotanytarsus</i> sp.	0	21	0	0	24	0
<i>Tanytarsus</i> sp.	0	0	25	0	0	18
<i>Tribelos jucundum</i>	0	0	19	0	0	19
<i>Zavreliella marmorata</i>	0	0	4	0	0	12
CHIRONOMIDAE (pupae)	7	2	21	13	17	18
CERATOPOGONIDAE (larvae + pupae)	14	1	11	20	57	6
COLEOPTERA						
<i>Pyrrhalta nymphaeae</i> (larvae, pupae, + adults)	24	1	0	1000	103	56
TRICHOPTERA						
<i>Oecetis cinerascens</i>	0	0	0	0	35	0
<i>Oecetis</i> sp.	0	2	13	0	141	0
<i>Orthotrichia</i> sp.	0	0	0	0	256	0
<i>Oxyethira</i> sp.	0	0	0	0	17	0
Polycentropodidae	0	0	0	0	9	13
MOLLUSCA						
<i>Amnicola limosa</i>	0	1	0	0	96	19
<i>Dreissena polymorpha</i>	0	0	0	0	21	0
<i>Gyraulus parvus</i>	0	0	0	9	41	0
<i>Physella</i> sp.	0	0	0	0	41	0
Total density (no./m ²)	506	399	760	3745	6667	2482
Number of taxa	10	15	20	20	28	26

al scaling (NMS) to ordinate the invertebrate samples, using PC-ORD in autopilot mode after eliminating species found in < 3 samples (McCune & Grace 2002). We used Multi-Response Permutation Procedures (MRPP, McCune & Grace 2002) to test for differences among groups in the ordinations.

Results

The mean biomass of water-chestnut in Outer, Middle and Inner transects, respectively, was 22, 53, and 57 g DW/m² in June, and 348, 482, and 423 g DW/m² in July. The temperature varied little among the sampling sites, from 25.8 to 29.2 °C in June, when the surface water was more exposed to solar radiation, and from 26.0 to 26.3 °C in July, when a dense carpet of vegetation covered the water. Dissolved oxygen concentrations varied strongly with the tidal cycle (Fig. 2), and fluctuated more widely in July, when the water-chestnut canopy was fully developed, than in June. In

June, oxygen concentrations never fell below 2.5 mg/L in the week prior to invertebrate sampling, but fell below 2 mg/L during most ebb tides in July, and reached values as low as 1.0 mg/L.

We found 50 macroinvertebrate taxa in our samples (Table 1). Species richness was higher in the sediments (30 taxa) than on the stems (28 taxa) or floating leaves (20 taxa). Contrary to our expectations, we found higher number of taxa in July (48 taxa) than in June (28 taxa), and there were only small differences in richness among transects (Fig. 3).

Density of macroinvertebrates also was much higher in July (12,850/m²) than June (1671/m²). Animal density in all three microhabitats varied significantly between months (Table 2). Density on floating leaves and in sediments did not vary significantly with location in the *Trapa* bed or show a location*time interaction. ANOVA of animal density on stems showed some effects of sampling transect ($p = 0.11$) and

Table 2. Repeated-measures analysis of variance of densities of all macroinvertebrate and just predatory macroinvertebrates within various habitats in the *Trapa* bed. Values in the table are F -values (***) indicates $p < 0.001$, ** indicates $p < 0.01$, * indicates $p < 0.05$). All data were $\log_{10}(X+1)$ -transformed before analysis.

Habitat	Month	Transect	Position within transect	Month * Transect	Month * Position	Transect * Position
All macroinvertebrates						
Sediment	30.6 **	0.1	2.5	0.4	0.6	0.6
Stems	642.4 ***	40.0	13.6	48.6 **	3.0	4.3
Floating leaves	54.1 **	1.1	0.5	0.2	0.4	1.4
Predators						
Sediment	7.0	1.8	0.2	2.5	1.0	1.2
Stems	46.1 **	0.4	0.3	1.3	0.2	0.7
Leaves	19.1 *	0.9	1.3	3.0	2.1	0.7

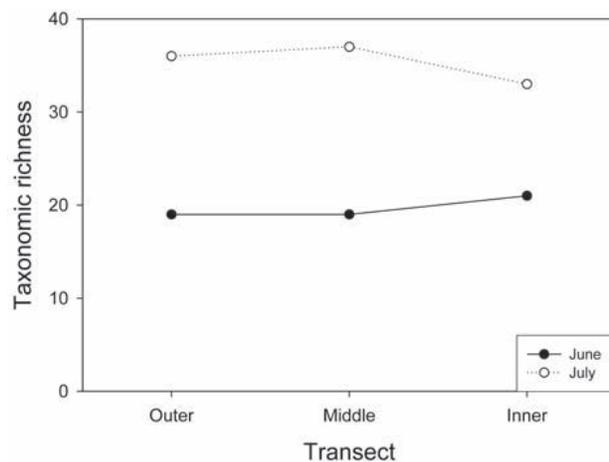


Fig. 3. Taxonomic richness (number of taxa) in the three transects in June and July.

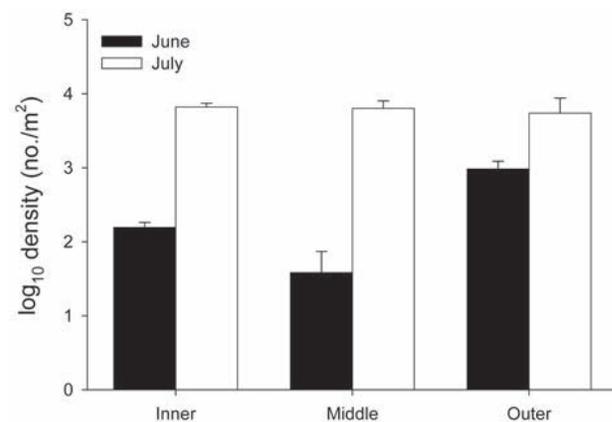


Fig. 4. Density (+1SE) of macroinvertebrates on *Trapa* stems, the only microhabitat in which transect or transect*month was a significant factor in the ANOVA. See Table 2 for details.

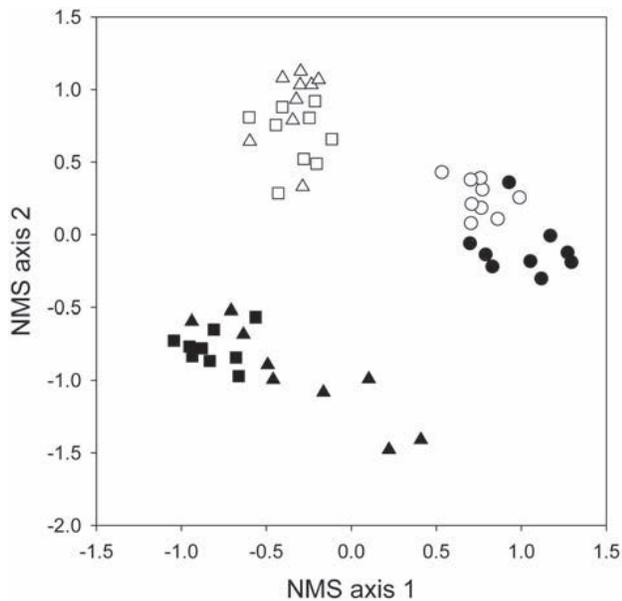


Fig. 5. Nonmetric multidimensional scaling (NMS) ordination of benthic plus epiphytic samples. Benthic samples are shown as circles, stem samples as triangles, and leaf samples as squares. Black symbols show June samples and white symbols show July samples. The recommended two-dimensional solution has a stress value of 14.2, indicating a satisfactory ordination (McCune & Grace 2002).

transect * month ($p = 0.002$), but these effects (Fig. 4) differed from our hypotheses about how sampling location would affect animal density (i.e., lower densities in inner transects than outer, and spatial patterns stronger in July than in June).

Community structure of benthic and epiphytic macroinvertebrates was related chiefly to microhabitat (floating leaves vs. stems vs. sediments) and month (Figs 5, 6). The ordination of all samples showed a clear separation of three groups ($p < 0.001$, MRPP) – all benthic samples (within which there was a subdivision between the June and July samples), all epiphytic samples (i.e., stem plus leaf samples) in June, and all epiphytic samples in July. The stem and leaf samples were somewhat distinct from one another in June, but not at all in July. When samples from each habitat (sediment, stem, and leaf) were ordinated separately, they showed a clear separation between June and July samples ($p < 0.01$ in all three cases, MRPP). The ordination of leaf samples produced just one axis, which was made up entirely of the difference between June samples (with an ordination score of +1) and July samples (with an ordination score of -1). The June stem samples showed some distinction among the three transects, but such a distinction was reduced in July,

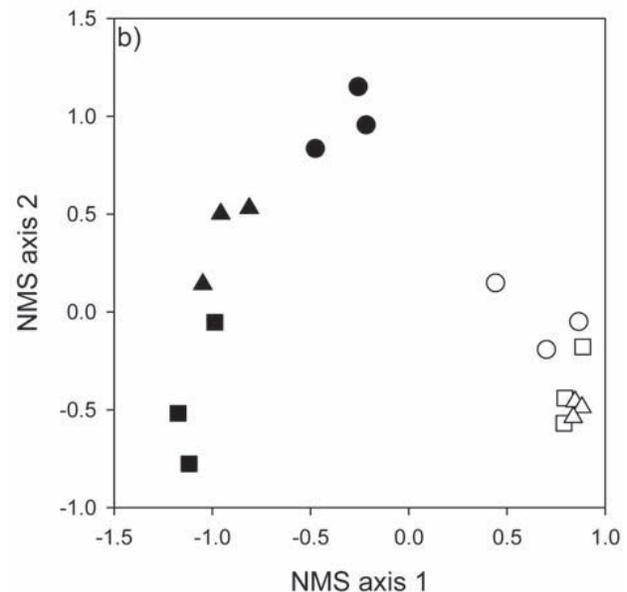
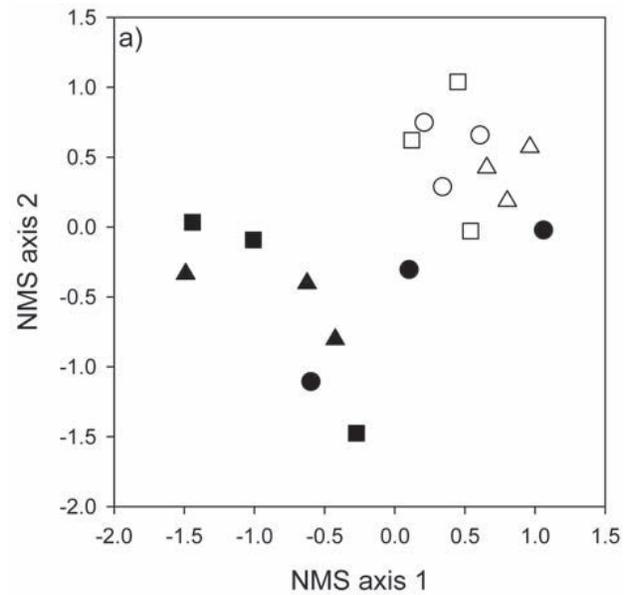


Fig. 6. Nonmetric multidimensional scaling (NMS) ordination of sediment samples (a) and stem samples (b). Circles show results from outer transect, squares = middle transect, and triangles = inner transect. June samples are shown by black symbols and July samples are shown by white symbols. Stress values were 11.4 for the sediments and 7.3 for the stem samples, both indicating satisfactory to good ordinations (McCune & Grace 2002). The ordination of leaf samples produced a one-dimensional solution (see text).

and was never evident in the sediment samples. In general, ordinations did not show any clear relationships between sampling location and community structure. Instead, community composition appeared to depend chiefly on month and microhabitat. There were hints that transect position might matter (in the stem sam-

ples), but its influence was clearly secondary to those of microhabitat and season.

Discussion

The water-chestnut bed supported a rich community of benthic and epiphytic macroinvertebrates, despite the common occurrence of hypoxia. Neither the density, richness, taxonomic composition, nor the functional-group composition (i.e., predator densities) of the invertebrate community would suggest that the water-chestnut bed was stressful to invertebrates. The dominant species were not those with known physiological or behavioral mechanisms to tolerate low oxygen. Instead, the water-chestnut bed supported a fauna dominated by chironomids, other insects, oligochaetes, and crustaceans, which is similar to those found in well oxygenated parts of the Hudson and other large rivers (Strayer & Smith 2001).

Our specific hypotheses were not supported. We did not find that species richness or density was lower in the interior of the bed than at its edge, and there was no indication that spatial patterning in these variables was stronger in July than in June. When we looked at invertebrate communities in different microhabitats, we did not find that the sediment-dwelling animals were any more affected by season or sampling position than animals that lived on water-chestnut stems or floating leaves. Finally, although we did not have any direct information on use of the *Trapa* bed by fish, we did not find that interior areas of the bed contained more invertebrate predators than edge areas.

Our results are difficult to explain because simultaneous measurements of dissolved oxygen concentrations showed that the site that we studied was subject to frequent hypoxia, especially in July, when we found animal communities to be densest and most diverse. Thus, we cannot explain away our results by suggesting that our study site was one of those small or well flushed *Trapa* beds in which oxygen is not seriously depleted (Hummel & Findlay 2006).

Instead, we suggest that the animals living in the *Trapa* bed must possess one or more behavioral and physiological mechanisms that allow them to tolerate at least short-term hypoxia. There are a number of possible mechanisms, including use of respiratory pigments such as hemoglobin (as occurs in some cladocerans and chironomid midges; Int Panis et al. 1996, Strayer et al. 2003); use of atmospheric oxygen via lungs or plastrons (as occurs in many pulmonate snails and some insects; e.g., McMahon 1983, Wil-

liams & Feltmate 1992); movement to the relatively well oxygenated near-surface layer of the water column to use “aquatic surface respiration” (as has been shown to occur in various fishes and motile invertebrates; Tinson & Laybourn-Parry 1985, Kornijów & Moss 2002, Stierhoff et al. 2003); or accumulation of a short-term oxygen debt during the hypoxic periods that is redeemed when oxygen concentrations rise during the flood tide a few hours later (e.g., production of organic acids that are later metabolized, as occurs in many kinds of invertebrates – McMahon 1983, Hamburger et al. 2000). The extent to which the various species in *Trapa* beds use these or other mechanisms is not known at present. As we have discussed previously (Strayer et al. 2003), the dominant taxa in water-chestnut beds do not easily fall into any of these classes of invertebrates – most of the chironomids that we collected do not possess hemoglobin, the oligochaetes are dominated by the “naidids” rather than anoxia-tolerant “tubificids” such as *Tubifex*, and many of the species that we collected are not able to access atmospheric oxygen or even the presumably well-oxygenated surface layer.

Hypoxia or anoxia at our study site sometimes is more severe than in 2005 (Goodwin et al. 2008), and water-chestnut beds that are not flushed by tides or currents may have more extended periods of anoxia than we observed. Dense and diverse macroinvertebrate communities might not be able to persist under more severe conditions than we observed, so some dense, anoxic macrophyte beds probably are poor habitats for invertebrates.

Whatever the mechanisms that allow invertebrates to tolerate the hypoxia of the *Trapa* beds, it appears that these habitats are valuable habitats in the Hudson River, supporting dense populations of invertebrates, many species of which are rare in other habitats in the river (Strayer et al. 2003). However, if hypoxia prevents fish from freely using *Trapa* beds, there may be a weak link in the food web between this rich invertebrate production and fish. There are at least three ways in which the invertebrates produced in *Trapa* beds might contribute to fish production in the Hudson. First, fish may enter the *Trapa* bed and feed there on invertebrates. This must occur at least early in the growing season, when hypoxia is still moderate. Coote et al. (2001) found that many species of fish were in the same water-chestnut bed that we studied as late in the season as August and September, and that their guts were filled with invertebrates from the bed (especially chironomids). Second, invertebrates may drift from the water-chestnut bed into adjoining, well ox-

xygenated habitats where fish live. Third, *Trapa* is an annual plant that disappears rapidly at the end of the growing season in September and October (Findlay et al. 1990). When this happens, the invertebrates it harbored must become available to fish, whether they stay in place in the newly denuded sediments or drift to other habitats in the river. Thus, it appears likely that *Trapa* beds might contribute substantially to fish production, as well as invertebrate production and biodiversity, in the Hudson, in spite of their hypoxia.

Acknowledgements

We thank Heather Malcom, Adam Głazaczow, Edyta Buczyńska, and Robert Stryjecki for technical help, and NSF DEB-0414574 for financial support. Ryszard Kornijów is grateful to the Fulbright Scholarship program for financial support.

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Submitted: 28 May 2009; accepted: 1 April 2010.