

Macroinvertebrates associated with water hyacinth roots and a root analog

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Abstract: The ecological effects of water hyacinth (*Eichhornia crassipes*), an introduced macrophyte, in freshwater systems depend on the growth and extent of floating mats. We studied macroinvertebrates associated with roots of water hyacinth in the Waccamaw River, a blackwater, tidal river in northeastern South Carolina, USA. In this system, water hyacinth is limited to a few protected bays and backwaters where the ecological effect is unknown. Our goal was to assess whether water hyacinth roots provided unique habitat. Plants representing ambient conditions, plants with defaunated roots, and a root analog (cotton mop strands = mop) were secured to floating frames in open water adjacent to water hyacinth mats. Samples were collected every 2 wk for 2 mo, and invertebrates were identified and quantified. Colonization of defaunated roots began within 2 wk, and invertebrate assemblages differed between roots and mops. The most common taxa on water hyacinth roots were Branchiopoda, Oligochaeta, Talitridae, and Chironomidae (Diptera), whereas Oligochaeta and Chironomidae were predominant on mops. *Berosus* sp. (Hydrophilidae) was the top-ranked taxon by proportional biomass on roots and mops. Total abundance and taxon richness of macroinvertebrates were greater on roots than on mops. Collector-gatherers were the most abundant functional feeding group (FFG) on mops, whereas distributions of abundance were relatively even among FFGs on ambient and defaunated roots. Predators dominated invertebrate biomass of all treatments, and shredder biomass was higher on roots than on mops. These data suggest that water hyacinth roots provide habitat for a diverse assemblage of macroinvertebrates, a function that should be weighed and assessed with other impacts before management actions are initiated.

Key words: *Eichhornia crassipes*, macroinvertebrates, assemblage, blackwater river, invasive plant, roots, water hyacinth

Aquatic macrophytes influence community development and ecosystem function by providing food, habitat, and refugia for other organisms and by modifying the physical and chemical properties of aquatic environments (Newman 1991, Sharitz and Batzer 1999, Cronk and Fennessy 2001). These effects vary depending on plant species, plant abundance, and community type (Rooke 1986, Lalonde and Downing 1992, Feldman 2001, Strayer et al. 2003, Hutchens et al. 2004). Regardless of whether an aquatic system supports aquatic macrophytes, potential exists for introductions of new macrophytes and, depending on the outcomes of these introductions, corresponding changes may occur in aquatic systems (Theel et al. 2008, Villamagna and Murphy 2010).

Most research on effects of introduced macrophytes in aquatic systems in the USA has focused on a few species known to influence commerce, fisheries, and recreation in situations where the plants assume dominance (Madsen

1997, Cronk and Fennessy 2001). By extension, these same species often are considered undesirable components of all aquatic communities because of their nonindigenous status. However, an emerging paradigm for invasion ecology places less emphasis on the geographic origin of species (i.e., indigenous vs nonindigenous) and more emphasis on measured effects (Davis et al. 2011, Martin 2011, Valinoti et al. 2011). This shift in emphasis has increased the need for research on introduced macrophytes across a broad range of conditions and levels of invasion.

Water hyacinth, *Eichhornia crassipes*, is a floating aquatic plant native to the Amazon River basin, Brazil, that is invasive in subtropical and warm temperate areas of the USA (Penfound and Earle 1948, Villamagna and Murphy 2010). It affects aquatic systems via floating leaves and an extensive root system suspended in the water column (Madsen 1997, Toft et al. 2003). Aquatic invertebrate assemblages can differ depending on their

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position in or near water hyacinth mats because of variation in light, O₂, and nutrient levels associated with the mats (Bailey and Litterick 1993, Masifwa et al. 2001, Brendonck et al. 2003, Midgley et al. 2006). Water hyacinth roots can support diverse invertebrate assemblages (Poi de Neiff and Carignan 1997, Ekelemu et al. 1999) and significantly greater invertebrate densities than sediments (O'Hara 1967) probably because of habitat, food, or structure provided by the roots. Hansen et al. (1971) documented an entire community associated with water hyacinth roots in Florida. This community included the shredder *Hyalella azteca* and the crayfish *Procambarus fallax* as primary herbivores, the snail *Pomacea paludosa* and tadpoles of *Hyla cinerea cinerea* as consumers of periphyton growing on water hyacinth roots, and juvenile fishes as predators of root-dwelling herbivores. Invertebrates found on water hyacinth roots occurred less frequently in fish diets than did invertebrates associated with the native pennywort, providing evidence that water hyacinth roots functioned as a refuge (Toft et al. 2003). Authors of a recent review concluded that water hyacinth invasions may entail both positive and negative ecological effects (Villamagna and Murphy 2010).

In our study, aquatic macroinvertebrates associated with water hyacinth roots were studied in a tidally influenced blackwater river in South Carolina, USA. In this ecosystem, water hyacinth invasion is limited by several factors (Rotella and Luken 2012). Our objective was to investigate whether small, isolated water hyacinth mats have negative or positive effects in this river system. Abundance, biomass, taxon richness, and functional feeding groups of fauna residing on ambient roots, defaunated roots, and artificial substrates were documented every 2 wk for 2 mo in an effort to address the following questions: 1) What macroinvertebrates are associated with water hyacinth roots and an artificial substrate? 2) How quickly do macroinvertebrates colonize water hyacinth roots and an artificial substrate? and, 3) Do water hyacinth roots have function beyond providing structure for colonization?

METHOD

Study area

The Waccamaw River is an unregulated tidal blackwater river flowing ~225 km from Lake Waccamaw in North Carolina to Winyah Bay and the Atlantic Ocean in South Carolina. It is a slow-moving, blackwater river with dissolved O₂ (DO) levels usually <5 mg/L. It drains ~2900 km², and its width varies from 10 m at the headwaters to 1400 m at the mouth. Our study sites were in South Carolina along a 10-km stretch upriver from the confluence with the Atlantic Intracoastal Waterway (AICW) in the freshwater forest/marsh zone (Conner et al. 2007) where tidal fluctuation is ~60 cm. Water hyacinth per-

sists and forms mats in backwaters and bays where plants are relatively protected from current. Plants also can be found as transient populations floating downriver or snagged on trees. DO levels measured adjacent to floating mats at a depth of 25 cm during the study ranged from 3.0 to 5.5 mg/L, and surface water temperatures ranged from 22 to 32°C (USGS 2012). The Waccamaw River is considered relatively nutrient poor (Hupp 2000).

Field experiment

Three persistent populations of water hyacinth were chosen as sites for a field experiment: Millpond (lat 33° 43.366"N, long 79°2.996"W), Peach Tree (lat 33°42.141"N, long 79°2.666"W), and Alligator (lat 33°41.274'N, long 79°3.719'W). Six floating 1-m² polyvinyl chloride (PVC) frames were deployed and anchored to the river bottom adjacent to the leading edge of each population in open water that was ≥1 m deep at low tide. At each site, 2 frames were allocated to each of 3 treatments: ambient roots, defaunated roots, and root analogs. The ambient roots treatment was established by removing individual plants from the floating mats and tethering them inside the frames. The defaunated roots treatment was similar except that the roots of the plants were rinsed in 10% isopropyl alcohol for 10 s before the plants were tethered inside the frames (Toft et al. 2003). Rinsing removed 69.8 ± 4.7% of the individuals and 83.3 ± 3.2% of the taxa on the roots (*n* = 6 samples). Defaunation allowed us to measure subsequent colonization by invertebrates. Root analogs (mops) consisted of 20 strands (25 cm long, 3 mm in diameter) from an industrial cotton mop secured together and weighted with a 170-g Pb shot. When tethered inside the frames, these structures mimicked suspended water hyacinth roots and provided biologically inert substrate for invertebrate colonization.

Invertebrate sampling and processing

At each site, 5 individual plants or mops were sampled randomly from each frame at the start of the experiment on 26 May 2010 (wk 0) and every 2 wk thereafter for 8 wk: 9 June 2010 (wk 2), 22 June 2010 (wk 4), 7 July 2010 (wk 6), and 21 July 2010 (wk 8) (total *n* = 90). On each date, plants and mops were removed from the frame with a 1-mm mesh net and immediately preserved in 70% ethanol. In the laboratory, roots were rinsed and brushed with a comb over a 500-μm sieve. The rinsed roots and retained residue of 3 samples were examined separately to estimate removal efficiency of this procedure. Rinsing removed 91.5 ± 2.8% of the organisms on the roots. Thereafter, only retained residues were examined for invertebrates. Samples were sorted under a dissecting microscope at 10× magnification. Mops were not combed, but invertebrates were sorted under a dissecting microscope at 10× magnification. All invertebrates were removed and mea-

sured to the nearest 0.5 mm to estimate macroinvertebrate biomass using length–mass regressions in Benke et al. (1999) and other sources. Any taxon found only once during collection was excluded from further analyses. Invertebrates were identified to the lowest practical taxonomic level with the assistance of keys provided by Brigham et al. (1982), Epler (1996), Wiggins (1996), Merritt et al. (2008), and Rogers and Hill (2008) and were classified by functional feeding group (FFG) according to Merritt et al. (2008). After invertebrates were removed, all roots were rinsed and left to air dry for 24 h, oven-dried at 70°C for 48 h, and weighed. Stems and leaves were oven-dried at 70°C for 48 h, and then weighed. Volume of roots was estimated with the displacement method (Rocha-Ramírez et al. 2007).

Statistical analyses

Data were checked for assumptions of normality and equal variance. Two-way blocked (by site) analyses of variance (ANOVA) were used to compare macroinvertebrate abundance (invertebrates/L and invertebrates/g root or mop, including and excluding cladocerans) over time (wk 2–8 only) and across treatments. ANOVAs were run with and without cladocerans because of the possible overriding influence of their high abundance on the analysis and because they are more planktonic than epiphytic. Two-way blocked (by site) ANOVAs also were used to compare expected species richness (calculated using EcoSim, version 7.0; Gotelli and Entsminger 2011) and biomass over time (wk 2–8 only) and across treatments. When ANOVAs showed significant effects, Tukey's Honestly Significant Difference (HSD) tests with $\alpha = 0.05$ were used to identify treatments that differed. Cumulative abundance (invertebrates/L) and biomass of functional feeding groups were compared among treatments with a cross-tabs χ^2 test (Pearson χ^2 test). ANOVAs and cross-tabs χ^2 tests were run in SPSS (version 18; IBM, Armonk, New York). A 1-way factorial permutation-based multivariate ANOVA (PERMANOVA) was used to compare assemblage composition among treatments based on abundance (invertebrates/L) and biomass values at wk 2 and 8 (Sørensen [Bray–Curtis] distance measure; McCune and Mefford 2011). PERMANOVA was run in PC-ORD (version 6.0; MjM Software, Gleneden Beach, Oregon).

RESULTS

Invertebrate abundance

A total of 108,080 invertebrates were extracted, identified, and measured from the 3 treatments during the study. The 3 most abundant taxonomic groups on water hyacinth roots were Oligochaeta, Branchiopoda, and Chironomidae. *Hyalella* sp. (Hyaellidae) and *Caenis* sp. (Caenidae) were important genera (Table 1). Ambient and defaunated roots generally supported a similar tax-

onomic distribution of macroinvertebrates. Invertebrate abundance on mops was dominated by Oligochaeta and Chironomidae. *Berosus* sp. had the highest biomass in all 3 treatments, and *Berosus* biomass was higher on mops than on ambient or defaunated roots (Table 2).

Total abundance/L root volume differed among treatments ($F_{2,57} = 3.250$, $p < 0.05$) but not among times ($F_{3,57} = 0.682$, $p = 0.566$) or sites ($F_{2,57} = 2.431$, $p = 0.097$), and the treatment \times time interaction was significant ($F_{6,57} = 2.835$, $p = 0.017$). Total abundance/L decreased over time in the ambient treatment and increased over time in the mop treatment. At wk 2 and 4, total abundance/L was greater on ambient roots than on defaunated roots or mops, but at wk 6, total abundance/L was similar among all treatments (Fig. 1). When cladocerans were removed from the analysis, total abundance/L did not differ among treatments ($F_{2,57} = 0.723$, $p = 0.490$), but the treatment \times time interaction was significant ($F_{6,57} = 2.583$, $p = 0.028$). When cladocerans were removed from the analysis and abundance was expressed as invertebrates/g root mass, total abundance/g differed among treatments ($F_{2,57} = 15.164$, $p < 0.05$) but not among times ($F_{3,57} = 1.668$, $p = 0.184$) or sites ($F_{2,57} = 2.397$, $p = 0.100$), and the treatment \times time interaction was not significant ($F_{6,57} = 1.370$, $p = 0.242$). Total abundance/g was greater on ambient and defaunated roots than on mops.

Biomass

Total invertebrate biomass did not differ among treatments ($F_{2,57} = 1.600$, $p = 0.211$). Biomass differed among times ($F_{3,57} = 4.736$, $p < 0.05$), with a pronounced increase on mops (Fig. 2). The treatment \times time interaction was not significant ($F_{6,57} = 2.099$, $p = 0.067$). Results of the biomass analyses should be viewed conservatively because the assumption of equality of error of variances was not met for raw or transformed data.

Taxon richness

Both rarefied and unaltered taxon richness data were analyzed. The results did not differ, so results based on raw values are reported. Ambient and defaunated roots supported more taxa than mops ($F_{2,57} = 15.618$, $p < 0.05$; Fig. 3). Taxon richness differed among times ($F_{3,57} = 4.591$, $p < 0.05$). In general, richness increased and then decreased, but the time \times treatment interaction was not significant ($F_{6,57} = 1.666$, $p = 0.146$).

FFGs

Distribution of FFG abundance differed among treatments (Pearson $\chi^2 = 333,413.9$, $df = 8$, $p < 0.05$). The abundances of all FFGs were relatively similar on ambient and defaunated roots except that filterers (mainly cladocerans) were more abundant than other FFGs on

Table 1. All taxa with cumulative total counts ≥ 5 that were collected during the experiment and the cumulative total count collected from each treatment. Each taxon was classified into a functional feeding group (FFG). An asterisk indicates a tribe. (A) indicates an adult. N/A indicates the organism was not included in the FFG analysis. P = predator, F = filterer, C/G = collector-gatherer, Sc = Scraper, and Sh = Shredder.

Class (Subclass)	Order (Suborder)	Family (Subfamily)	Genus species	FFG	Ambient	Defaunated	Mop	Total count	
Arachnida	Oribatida			P	44	64	12	120	
	Trombidiformes (Clade: Hydracarina)			P	337	334	27	698	
Branchiopoda				F	14,234	5703	2491	22,428	
Clitellata (Hirudinea) (Oligochaeta)				P	19	29	5	54	
				C/G	3700	3000	21,049	27,749	
Gastropoda		Hydrobiidae		Sc	453	294	93	840	
		Physidae		Sc	993	658	1255	2906	
		Planorbidae (Planorbinae)		Sc	1543	953	169	2665	
		Ancylini*		Sc	47	17	9	73	
		Sphaeromatidae		F	6	7	0	13	
		Unknown 1		Sc	118	105	100	323	
		Unknown 2		Sc	16	2	4	22	
	Insecta	Coleoptera	Curculionidae		Sh	13	9	0	22
			Dytiscidae	<i>Hydrovatus</i> sp.	P	0	6	0	6
			Elmidae		Sc	3	11	0	14
			<i>Macronychus</i> sp.	C/G	7	5	0	12	
Hydrophilidae			<i>Berosus</i> sp. <i>Berosus</i> sp. (A)	P P	581 14	324 9	128 0	1033 23	
Diptera		Ceratopogonidae			P	10	20	6	36
			<i>Bezzia</i> sp.		P	139	98	235	472
		Chironomidae			C/G	2441	2333	15,051	19,825
		Tanypodinae			P	1494	1598	1378	4470
		Ephemeroptera				C/G	21	14	37
Baetidae					C/G	60	40	17	117
Caenidae			<i>Caenis</i> sp.		C/G	609	559	470	1638
Heptageniidae					C/G	4	3	25	32
			<i>Maccaffertium</i> / <i>Stenonema</i> sp.		C/G	3	4	23	30
Hemiptera		Leptophlebiidae			C/G	16	6	2	24
		Aphididae			N/A	21	7	0	28
		Belostomatidae			P	1	4	0	5
		Mesoveliidae	<i>Mesovelia</i> sp.		P	31	26	2	59
		Naucoridae	<i>Pelocoris</i> sp.		P	16	20	0	36
		Veliidae			P	1	14	0	15
		<i>Microvelia</i> sp.		P	0	10	1	11	
	Lepidoptera			Sh	3	9	0	12	
Neuroptera	Sisyridae	<i>Climacia</i> sp.		P	44	45	0	89	
	Odonata (Anisoptera)			P	126	174	24	324	
Corduliidae				P	27	41	29	97	
		<i>Somatochlora</i> sp.		P	1	6	2	9	
Libellulidae				P	22	84	3	109	
	<i>Erythemis</i> sp.		P	25	24	2	51		
	<i>Pachydiplax</i> sp.		P	1	6	3	10		

Table 1 (Continued)

Class (Subclass)	Order (Suborder)	Family (Subfamily)	Genus species	FFG	Ambient	Defaunated	Mop	Total count
	(Zygoptera)	Coenagrionidae		P	663	625	130	1418
			<i>Enallagma</i> sp.	P	417	390	203	1010
			<i>Ischnura</i> sp.	P	17	15	17	49
	Trichoptera	Hydroptilidae		Sc	80	124	29	233
			<i>Ochrotrichia</i> sp.	C/G	17	9	11	37
			<i>Orthotrichia</i> sp.	Sc	200	360	58	618
			<i>Oxyethira</i> sp.	Sc	93	71	7	171
		Leptoceridae		Sh	21	51	0	72
			<i>Nectopsyche</i> sp.	Sh	10	7	0	17
			<i>Oecetis</i> sp.	P	201	257	57	515
			<i>Trianodes</i> sp.	Sh	25	17	0	42
		Polycentropodidae		F	17	10	19	46
			<i>Cyrnellus</i> sp.	F	1	4	140	145
			<i>Polycentropus</i> sp.	F	81	64	70	215
Malacostraca	Amphipoda			Sh	215	421	23	659
		Gammaridae	<i>Gammarus</i> sp.	Sh	405	613	73	1091
		Hyalellidae	<i>Hyalella</i> sp.	Sh	942	878	115	1935
		Talitridae		Sh	2751	2307	305	5363
	Isopoda	Asellidae	<i>Caecidotea</i>	C/G	7	3	2	12
Maxillopoda (Copepoda)				F	809	534	53	1,396
Ostracoda				F	1541	998	1390	3929
Turbellaria				Sc	278	231	17	526
			<i>Cassidinidea ovalis</i>	C/G	159	184	26	369

ambient roots (Fig. 4). In contrast, collector-gatherers, especially Oligochaeta and Chironomidae, dominated invertebrate abundance on mops (Fig. 4).

Distribution of FFG biomass also differed among treatments (Pearson $\chi^2 = 1,981.8$, $df = 8$, $p < 0.05$). Predators dominated the biomass on all treatments and this dominance was most evident on mops (Table 1, Fig. 5). Scraper and filterer biomass was evenly distributed among treat-

ments and contributed little to total biomass. Biomass of collector-gatherers was lower on ambient and defaunated roots than on mops, whereas biomass of shredders was lower on mops than on ambient and defaunated roots (Fig. 5).

Assemblage structure

Macroinvertebrate assemblage structure based on abundance/L varied significantly among treatments on wk 2 (PERMANOVA, $F_{2,15} = 2.963$, $p < 0.05$) and wk 8 ($F_{2,15} = 3.6146$, $p < 0.05$). Assemblage structure did not differ between ambient and defaunated roots (T1: $t = 0.731$, $p = 0.809$; T4: $t = 0.733$, $p = 0.901$) but did differ between ambient roots and mops (T1: $t = 2.157$, $p < 0.05$; T4: $t = 2.580$, $p < 0.05$) and between defaunated roots and mops (T1: $t = 2.134$, $p < 0.05$; T4: $t = 2.032$, $p < 0.05$). Results were similar when PERMANOVAs were based on biomass.

DISCUSSION

Macroinvertebrates and colonization

Water hyacinth roots often function as novel habitat that can increase the diversity and abundance of macro-

Table 2. Eight taxa with highest biomass (% of total) found on water hyacinth roots (ambient and defaunated) and a root analog (mop).

Taxon	Ambient	Defaunated	Mop
<i>Berosus</i> sp.	7.2	4.9	20.9
<i>Enallagma</i> sp.	3.5	2.8	3.0
Astacoidea	3.0	1.4	1.0
<i>Gammarus</i>	2.8	3.9	0.6
<i>Erythemis</i> sp.	2.8	1.1	0.1
Talitridae	1.6	1.7	0.3
<i>Hyalella</i> sp.	1.5	1.7	0.2
Tanypodinae	0.6	0.6	0.9

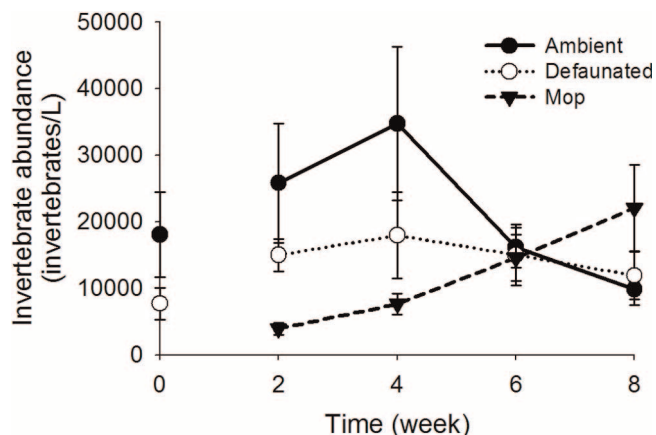


Figure 1. Mean (± 1 SE, $n = 6$) invertebrate abundance (invertebrates/L root or analog volume) associated with ambient and defaunated water hyacinth roots and root analogs (mop) through the study duration. Abundance differed among treatments, and the treatment \times time interaction was significant. Week 0 data were not included in the analyses.

invertebrates (Villamagna and Murphy 2010). Macroinvertebrate assemblage structure on water hyacinth roots in shallow, protected waters of the Waccamaw River was similar to assemblage structure reported by other investigators (Villamagna and Murphy 2010) and in studies conducted under similar environmental conditions (O’Hara 1967, Hansen et al. 1971, Toft et al. 2003). For example, *Hyalella* are closely associated with water hyacinth roots in blackwater or tidal systems, presumably because the roots provide a food source (Hansen et al. 1971).

Colonization of water hyacinth roots in the Waccamaw River probably reflected proximity to existing floating mats and tidal fluctuations of the Waccamaw River. The

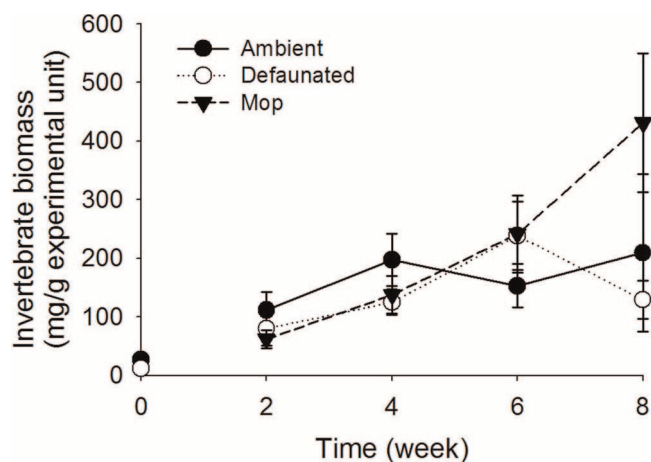


Figure 2. Mean (± 1 SE, $n = 6$) invertebrate biomass (biomass/g root or analog dry mass) associated with ambient and defaunated water hyacinth roots and root analogs (mop) through the study duration. Taxa found only once during collection were excluded from analysis. Biomass differed among times. Week 0 data were not included in the analyses.

short travel distance probably explains the high abundances of chironomids, oligochaetes, amphipods, and the mayfly *Caenis* sp. *Hyalella* may have reached treatments by swimming, whereas insect taxa may have hatched from eggs, flown, or drifted (Mackay 1992). Chironomids drift at high rates in southeastern USA Coastal Plain rivers (Benke et al. 1986), and oligochaetes could have been transported from the large hyacinth mats to the experimental frames by daily tidal fluctuation (Williams and Hynes 1976, Mackay 1992). Amphipods, such as *Gammarus*, are strong swimmers and are often one of the earliest taxa to colonize new habitat (Mackay 1992). Mayflies, which crawl at faster speeds when a habitat has high periphyton levels, also are early colonizers (Mackay 1992). Cladocerans (e.g., *Daphnia*) were abundant and rapid colonizers of hyacinth roots. *Daphnia* primarily inhabit the pelagic zone, but they migrate to the littoral zone during daylight to seek refuge in aquatic macrophytes from pelagic predators (Van de Meutter et al. 2004), and samples were collected during daylight when *Daphnia* would have been taking refuge among the roots.

Across all treatments combined, total abundance of macroinvertebrates did not change significantly over the total duration of the experiment. Ambient roots were heavily populated at the beginning of the experiment, and no overall increase was expected in this treatment. Mops were colonized at a slow, steady rate during the experiment, and defaunated roots showed little change in abundance after the first 2 wk of colonization. After a disturbance, colonization by invertebrates commonly reaches equilibrium in 10 to 25 d, but total abundance can continue to fluctuate as the substrate accumulates detritus, the epiphytic texture changes, and the invertebrates express varying patterns in life history (Mackay 1992).

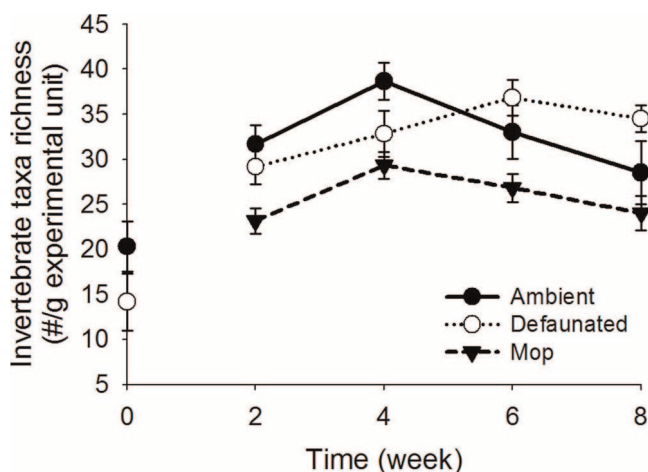


Figure 3. Mean (± 1 SE, $n = 6$) taxa richness of invertebrates associated with ambient and defaunated water hyacinth roots and root analogs (mop) through the study duration. Richness differed among treatments and among times. Week 0 data were not included in the analyses.

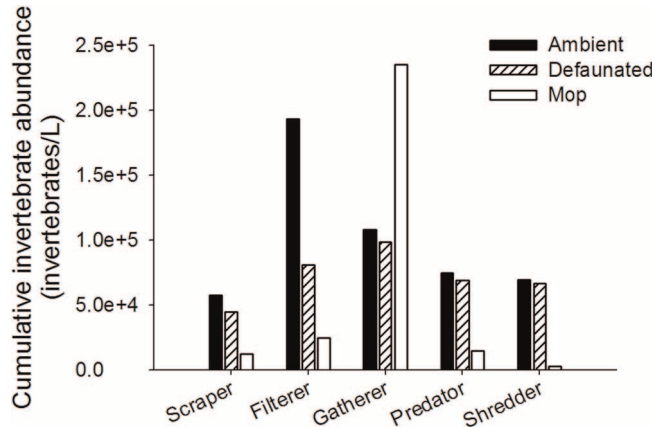


Figure 4. Cumulative (over 8 wk and all replicates) invertebrate abundance (invertebrates/L root or analog volume) in each functional feeding group (FFG) on ambient and defaunated water hyacinth roots and root analogs (mop). Distribution of abundance among FFGs differed among treatments.

Roots vs structure

Overall, invertebrate abundances were not strongly affected by time, but differences were observed in temporal patterns of abundance of invertebrates on ambient and defaunated roots and mops. At wk 2, ambient roots had significantly greater invertebrate abundance than mops, but by wk 8, invertebrate abundance was similar across treatments. The increase in abundance on mops and the early increase on defaunated roots probably reflected colonization, whereas the decrease on ambient roots might indicate seasonal changes in root quality. Invertebrate assemblage structure did not differ between ambient and defaunated roots, but did differ between roots and mops. These differences in assemblage structure probably reflect responses to the greater structural complexity of roots (Jeffries 1993, McAbendroth et al. 2005). Morphologically complex macrophytes often support greater abundance and richness of invertebrates (Wise and Molles 1979, Jeffries 1993, Villamagna and Murphy 2010). In addition, more complex structures generally have more surface area available for epiphytic growth, which provides food for colonizing invertebrates (Kelly and Hawes 2005). For example, more scrapers, especially gastropods and hydroptilid caddisflies, were found on water hyacinth roots than on mops. Hydroptilids also were abundant on hyacinth roots in a subtropical impoundment (Brendonck et al. 2003).

Differences observed in invertebrate taxon richness and abundance among treatments were not accompanied by differences in biomass. Structural complexity of macrophytes can affect invertebrate biomass both negatively (McAbendroth et al. 2005) and positively (Lalonde and Downing 1992, Hutchens et al. 2004). In our study, mops supported a few large organisms (e.g., *Berosus* sp., *Helocombus* sp.), whereas the roots supported many small organisms. As a result, biomass was relatively similar among

treatments. This explanation is further supported by the presence of low abundance but high biomass of predators on mops.

Ambient and defaunated roots supported a fairly even abundance of organisms from all FFGs, whereas FFGs on mops were dominated by collector-gatherers, especially oligochaetes, chironomids, and mayflies. The FFG that was least prevalent on mops was shredders, such as amphipods and leptocerid caddisflies (e.g., *Trianodes*). *Trianodes* sp. (Leptoceridae) construct their cases from plant materials (Merritt et al. 2008), something not found on our artificial substrate. *Trianodes* sp. on roots appeared to use the root in construction of its case (JEB, personal observation). Roots were consumed, but root growth was not inhibited. During the experimental period, root length increased an average of 8.4 cm. As a result, the food source for these shredders increased with time, making the choice of a living habitat more beneficial than an artificial habitat.

Assessing water hyacinth invasion

Water hyacinth is considered one of the world's worst weeds (Holm et al. 1977). This characterization probably is accurate when considering impacts on recreation and DO, but might require reassessment when considering only effects on macroinvertebrates, biotic interactions, or in systems where the plant is limited (Villamagna and Murphy 2010). In the Waccamaw River, the plant occurs only in relatively protected backwaters and has relatively low biomass because of limitations imposed by tidal fluctuation, temperature, and nutrients (Rotella and Luken 2012). Water hyacinth has yet to cause widespread recreational problems on the Waccamaw River. Furthermore, DO levels in the Waccamaw River are naturally low

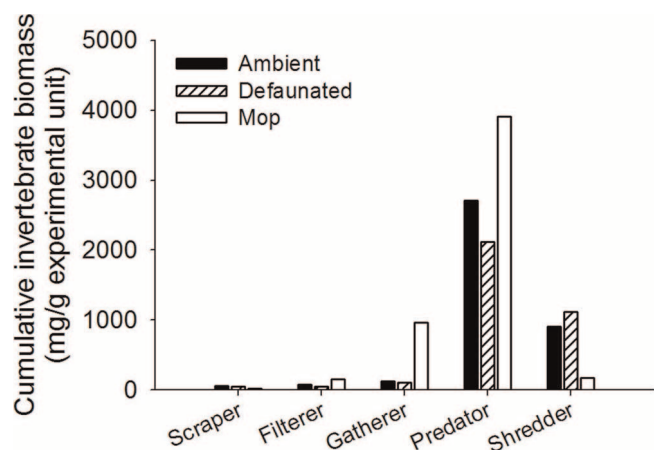


Figure 5. Cumulative (over 8 wk and all replicates) invertebrate biomass (biomass/g root or analog dry mass) in each functional feeding group (FFG) on ambient and defaunated water hyacinth roots and root analogs (mop). Distribution of biomass among FFGs differed among treatments. Taxa found only once during collection were excluded from analysis.

(~41% saturation), generally falling below the DO levels measured in water hyacinth mats in other systems (Villamagna and Murphy 2010) but above levels likely to affect macroinvertebrates negatively (Kornijów et al. 2010).

Small, isolated mats of water hyacinth may provide unique habitat that contributes to overall biotic diversity (Villamagna and Murphy 2010). Our results suggest that the suspended roots provide more than structure for colonization and support a broad range of FFGs. Other aquatic plants in the Waccamaw River grow in floating mats and produce suspended roots (e.g., *Alternanthera philoxeroides*, *Hydrocotyle umbellata*, and *Ludwigia palustris*). However, these other macrophytes do not produce roots that extend beyond 1 m in the water column. Therefore, water hyacinth provides a previously unavailable macrophytic structure for native invertebrate species. Davis et al. (2011) recommended that management of invasive species be based on measured impacts rather than species status. Our study supports that recommendation and provides the impetus for further research to understand how macrophyte additions lead to change in aquatic systems.

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