Gastropod Abundance in Vegetated Habitats: The Importance of Specifying Null Models

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Limnology and Oceanography, Vol. 38, No. 1 (Jan., 1993), 217-225.

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Submitted: 31 January 1992
Accepted: 21 July 1992
Revised: 25 August 1992

Limnol. Oceanogr., 38(1), 1993, 217–225

Gastropod abundance in vegetated habitats: The importance of specifying null models

Abstract—We compared gastropod diversity and abundance between areas of high and low macrophyte biomass in Trout Lake, Wisconsin, and performed laboratory experiments to determine the role of substrate surface area in explaining differences. Species richness was greater in macrophytes than in cobble, and four of the six species occurring in both areas had higher abundances per unit bottom area in the macrophyte bed. In the laboratory, we provided six snails with a choice of substrates: sand, macrophytes on sand, and cobble (rocks). When results were expressed per unit bottom area, most species preferred cobble and macrophytes, but avoided sand. When snail densities were expressed per unit surface area, most species preferred cobble, and avoided macrophytes. Our results indicate that the greater abundance and diversity of invertebrates (per unit bottom area) in vegetated habitats may be explained by the greater colonizable surface area, without recourse to alternative explanations such as decreased predation risk.

Both the diversity and abundance of benthic invertebrates are positively correlated with biomass and species richness of macrophytes and macroalgae in marine (Heck and Orth 1980; Lewis and Stoner 1983; Stoner and Lewis 1985) and freshwater (Cyr and Downing 1988; Brown et al. 1988 and references therein) communities. Three main explanations have been offered for this pattern.

First, vegetation offers a refuge from predation in both freshwater (Crowder and Cooper 1982; Savino and Stein 1982; Rozas and Odum 1988) and marine (Heck and Thoman 1981; Leber 1985; Holmlund et al. 1990) habitats. Second, vegetation reduces water velocity, a situation preferred by some invertebrates (Statzner et al. 1988). Third, many invertebrate species colonize vegetation (and other physical structures) in higher densities than unvegetated habitats, even in the absence of predation (Bell and Westoby 1986). The relative importance of these processes probably differs for different invertebrate taxa, and probably also varies among different ecological communities.

However, many of these studies and explanations assume a pattern that may not exist. Although there are greater numbers of invertebrates *per unit bottom area* in vegetated relative to unvegetated habitats, this pattern hardly requires explanation because vegetation clearly adds colonizable surface area to the bottom of a lake, stream, or marine habitat. The fact that invertebrates colonize vegetation

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Acknowledgments

We gratefully acknowledge the support of NSF grants BSR 85-00775 and BSR 89-07407 to D.M.L. and BSR 85-00774 and BSR 89-07690 to K.M.B. Ouida Williams and Carolyn Sheild helped in the collection of field and laboratory data.

in higher densities per unit bottom area even in the absence of predation is thus not at all surprising. The focus of this note is to test some quantitative aspects of this pattern, which have not been addressed by previous studies.

Specifically, we first test for the occurrence of the common vegetation-invertebrate pattern for gastropods in Trout Lake, Wisconsin, and find results consistent with previously published studies. Second, we compare results of laboratory experiments providing six species of snails a choice of habitats (in the absence of both predators and substantial water movements) to two null models: null model of equal numbers of invertebrates *per unit total surface area* (surface area null model); and the more widely used model of equal numbers of invertebrates per unit bottom area (habitat null model).

Trout Lake (Vilas County, Wisconsin, 46°N, 89°W) is a mesotropic lake with surface area of 1.61×10^3 ha. Benthic samples were taken in the southeast bay (site description and map given by Weber and Lodge 1990) in two different habitats. The first was in a mixed species macrophyte bed at ~1.0-m depth. Samples were collected with a corer constructed from 15-cm-diameter PVC pipe (sample area, 0.0177 m^2) which was lowered in the substrate until a bottom could be inserted to collect the top 2–3 cm of substrate, macrophytes, and associated snails (Lodge et al. 1987). This sampling technique gives less biased estimates of snail abundance than Ekman grabs (Brown 1991). Samples were collected on 20 May ($N = 10$), 10 June ($N = 5$), 27 June ($N = 6$), 26 July ($N = 5$), and 11 August ($N = 5$) 1986. Over the course of the study the total bottom area sampled was 0.55 m^2. The range of macrophyte biomass was 100–1,000 g wet mass m^{-2} (Lodge et al. 1987). Sediments were washed through a 0.5-mm sieve, which retained all snails, and snail densities were converted to No. m^{-2}.

The second habitat was an area of cobble substrate in ~0.5 m of water midway between the macrophyte bed and shore in the same bay. (Cobble and macrophytes did not both occur at any one depth.) The rock prevented use of corers, and densities of snails were therefore estimated by haphazardly throwing out a 0.04-m^2 quadrat and carefully searching the area (using mask and snorkel) for snails. This technique is the most appropriate for estimating snail densities in cobble substrata (Brown 1991). Snails were clearly visible on rock surfaces. Samples were taken on 26 May ($N = 25$), 13 June ($N = 10$), 27 June ($N = 10$), 26 July ($N = 9$), and 13 August ($N = 9$) 1986. Over the course of the study, the total bottom area tested was 2.52 m^2. Significant differences in the average abundance (per unit lake bottom area over all dates) of all co-occurring snail species between the two substrata were determined with t-tests.

In laboratory experiments, we tested habitat and substrate selection by six of the species of snails common in Trout Lake: *Amnicola* sp., *Campeloma decisum* (Say), *Gyraulus parva* (Say), *Helisoma anceps* (Menke), *Physella* sp., and *Lymnaea emarginata* (Say) during June–August 1985 (Table 1). Each experimental arena was circular and provided snails with a choice among three equal-area, wedge-shaped habitats: unvegetated sand (~4 cm deep); sand covered with one layer of cobble (10-cm diam; range, 7–12 cm); and vegetated sand. These three habitats mimic the range of substrata and spatial scales available to snails in Trout Lake and other northern Wisconsin lakes (Lodge et al. 1989). Sand (top 3–5 cm collected from areas 0.5 to 1.5 m deep) and macrophytes (from 1 to 2 m deep) were collected from the southeast shore, and cobble (from 0.5 to 1.5 m deep) from the northeast shore of the south basin of the lake. All naturally occurring snails were carefully removed. Care was taken not to disturb the natural periphyton from sand, cobble, and macrophytes (*see* Weber and Lodge 1990), all of which were used within 24 h of collection.

Two arena sizes were used, a small (39-cm diam, 19 cm deep) epoxy-coated metal pan, and a large (91-cm diam, 24 cm deep) plastic wading pool. Small arenas were used primarily for small snails and large arenas primarily for large snails (Table 1). Small arenas were used inside under natural window lighting; large arenas were used outside under partial shade. Water temperature in the experiments was 14–21°C, except for 13 July when temperatures rose to 28°C. All temperatures are within the range of summer epilimnetic temperatures in this region (J. J. Magnuson pers. comm.).

Four (range, 3–5) and 20 (range, 19–23) rocks were used in the small and large arenas. For the vegetated habitat, haphazardly selected

Table 1. Schedule and methods of experiments testing habitat and substrate selection by six species of snails.

	Set*	1985	Source lake†	Mean size (mm)	Size range (mm)	Arena size‡	Snails per arena	Exp duration (h)	*N*
Amnicola	1	8 Jun	T	4	3.0–4.2	S	50	8	5
	2	2 Jul	M	4	2.5–4.5	S	50	6	2
	3	7 Aug	M	3	2.7–3.5	S	50	6	3
Campeloma	1	2 Jul	T	10	6–13	S	50	8	1
	2	2 Jul	G	8	5–10	S	50	8	1
	3	13 Jul	G	23	17–31	L	50	18	3
	4	7 Aug	G	9	6–10	S	50	6	2
	5	14 Aug	G	22	15–31	L	90	20	2
	6	14 Aug	G	10	9–14	L	100	20	1
Gyraulus	1	6 Jun	T	6	4.9–6.2	S	50	6	5
	2	2 Jul	T	5	4.8–6.0	S	50	7	1
	3	2 Jul	M	3	2.9–3.5	S	50	7	1
Helisoma	1	18 Jun	T	9	8–10	S	50	7	5
	2	2 Jul	T	8	8–9	S	50	7	2
	3	13 Jul	T	10	9–11	L	50	8	3
Physella	1	2 Jul	M	7	4–8	S	50	8	2
	2	7 Aug	T	7	6–8	S	50	7	2
	3	14 Aug	T	7	6–8	L	100	8	2
Lymnaea	1	12 Jun	T	11	8–12	S	50	7	5
	2	2 Jul	T	12	12–13	S	50	6	2
	3	13 Jul	T	18	15–20	L	50	7	3
	4	7 Aug	T	9	8–11	S	50	7	3
	5	14 Aug	T	14	10–20	L	100	6	3

* Group of replicates with all measured experimental conditions the same.
† Trout Lake—T; Mann Lake—M; Grassy Lake—G.
‡ Small arena—S; large arena—L.

shoots of four common submersed macrophytes, *Elodea canadensis* (Michx.), *Myriophyllum exalbescens* (Fernald.), *Ceratophyllum demersum* (Linn.), and *Megalodonta beckii* (Torr.) Greene, were anchored in sand. Equal wet weights of each of the four species were used, 10 and 55 g of each in small and large arenas. Total macrophyte densities were 1,000 and 920 g m^{-2} (wet wt) in small and large arenas. These biomasses are near the high end of the range (100–1,000 g m^{-2}) in macrophyte beds in the southeast bay that were sampled for the snail density estimates, but are in the middle of the range (10–2,900 g m^{-2}) in most other mesotrophic Vilas County lakes (Lodge et al. 1989).

Snails were collected from the lake (southeast shore sand habitat, *see* Weber and Lodge 1990), and two other Vilas County lakes, Mann Lake (0.5 km south of Trout Lake, submersed macrophytes) or Grassy Lake (20 km northeast of Trout Lake, sand), as indicated in Table 1. Snails were held in laboratory aquaria and used within 1–4 d of collection. No snail was used more than once. To start each experiment, 50–100 snails (as indicated in Table 1) of one species were released from a cup placed in the center of each arena. Experiments were conducted on eight summer dates, with experiments on each species replicated through time (Table 1), as availability of snails and other logistical considerations allowed. The resulting set of experiments is not balanced for source lake, time, or number of replicates per species (Table 1), but does allow evaluation of general species-specific patterns of habitat and substrate choice.

Observations of *Amnicola,* the smallest snail, were aided by lightly spray-painting each snail orange before use. In a preliminary test in which 50 unpainted and 50 painted snails were monitored for 5 d, one unpainted and no painted snails died. There were no obvious sublethal effects of painting.

For each arena, the number of snails in the following places was recorded hourly: 1—on arena side or water surface film (these data were excluded from the statistical analysis);

Table 2. Estimated absolute area (cm^2) and percentage area of three habitats and substrata available to snails in small (S) and large (L) arenas in laboratory choice experiments.

	Habitat null model				Surface area null model			
	S		L		S		L	
	(cm^2)	(%)	(cm^2	(%)	(cm^2)	(%)	(cm^2)	(%)
Sand	398	33	2,168	33	398	11	2,168	11
Cobble	398	33	2,168	33	597	17	3,252	17
Macrophyte	398	33	2,168	33	2,577	72	13,578	72
Elodea					908		4,979	
Myriophyllum					217		1,072	
Ceratophyllum					1,051		6,136	
Megalodonta					401		1,391	
Total	1,194	100	6,504	100	3,572	100	18,998	100

2—in the sand habitat third; 3—in the cobble habitat third; 4—in the vegetated habitat third; 5—on cobble (but not including snails on the small areas of sand between rocks); and 6—on macrophytes (but not including snails on sand under macrophytes). Responses 2–4 were used to test habitat selection against the null model that equal snail numbers would occur in each habitat (habitat null model, Table 2). Responses 2, 5, and 6 were used to test substrate selection against the null model that snails would be distributed proportionately to surface area (surface area null model, Table 2).

Surface area of sand was estimated as if the sand third were a planar surface. Surface area of cobble was estimated as if each rock were spherical and as if half of each rock were available for colonization (the other half buried in the sand). Surface area of macrophytes was estimated from wet weight–surface area regressions derived from linear measurements of macrophyte parts and the application of standard geometric formulae for surface area (Cattaneo and Carignan 1983).

More specifically, for the range of shoot sizes used in our experiments, three to five shoots of plants from the southeast bay of Trout Lake were collected in bags and weighed individually after gentle blotting on paper towels. For each shoot of each species, the number of leaf whorls and the number of leaves per whorl (for at least 10 whorls) were counted, stem length was measured with a millimeter ruler, and stem diameter (at three to seven points) was measured with an ocular micrometer. For all species, we assumed the stem was cylindrical. For *Elodea,* we measured the length and maximum width of 10 leaves. Leaf area was estimated as the mean of the area calculated as if the leaf were a rectangle and that calculated as if it were a triangle. For *Myriophyllum,* we measured, for each of 10 leaves, the length and midleaflet width of three leaflets, and the length and midrachis width of the central leaf rachis. Leaflets and the central rachis were then assumed to be rectangular. For *Ceratophyllum,* for 10 leaves, we measured the length and width of the basal part of the leaf, and the length and midfork width of both upper forks of each leaf. Each part of each leaf was then assumed to be rectangular. For *Megalodonta,* we measured, for 10 leaves, the total length of leaflet forks, and the midfork width of at least five forks. Each part of each leaf was then assumed to be rectangular.

For all macrophyte species, when plant parts did not obviously conform to a geometric shape, we were conservative, that is, we used the shape that produced a lower surface area estimate (e.g. rectangular instead of cylindrical). Regressions of calculated surface area (A, cm^2) on shoot wet weight (W, g) were: *Elodea,* $A = 91W - 3$ ($r = 0.98$, $N = 5$ shoots); *Myriophyllum,* $A = 19W + 27$ ($r = 0.99$, $N = 3$ shoots); *Ceratophyllum,* $A = 113W - 79$ ($r = 0.96$, $N = 4$ shoots); and *Megalodonta,* $A = 22W + 181$ ($r = 0.77$, $N = 4$ shoots).

Numbers of snails on each substrate increased rapidly at first and then reached an asymptote after 4–15 h, depending on the species. The experiments were ended after snail numbers on each substrate changed little (mean of 21%) for 2–3 h, and after no change in rank order of snails on each of the substrates oc-

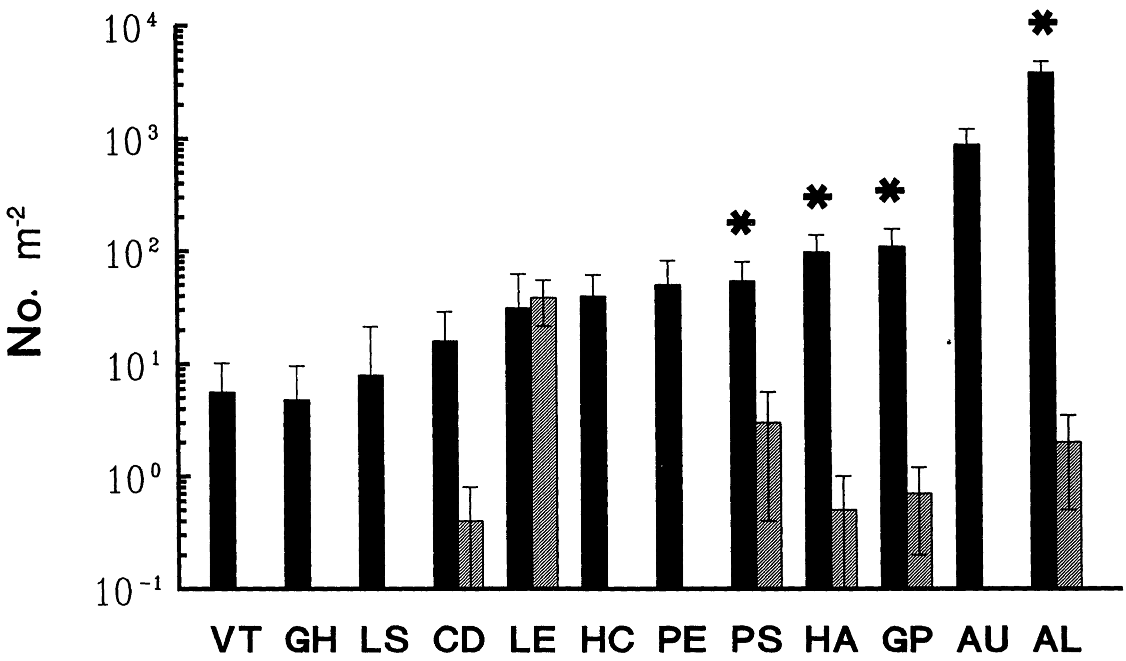

Fig. 1. Semilogarithmic plot of average abundances (± SE) for gastropods in two habitats in Trout Lake. Shaded bars—cobble; solid bars—macrophyte habitat. VT—*Valvata tricarinata*; GH—*Gyraulus hirsutus*; LS—*Lymnaea stagnalis*; CD—*Campeloma decisum*; LE—*Lymnaea emarginata*; HC—*Helisoma companulatum*; PE—*Promonetus exacuous*; PS—*Physella* sp.; HA—*Helisoma anceps*; GP—*Gyraulus parva*; AU—*Amnicola lustrica*; AL—*Amnicola limosa*. Asterisks indicate a significant difference in density between substrata (*t*-test). Species are arrayed in order of increasing abundance. Sample sizes and sampling dates are given in text.

curred. Only the final observation was analyzed. This approach has been successful in previous behavioral experiments with gastropod habitat choice (Lodge 1985; Kershner and Lodge 1990; *see* Brown 1991).

We used replicated G-tests (Sokal and Rohlf 1981) to test both habitat and surface area null models. The G_T (total) statistic tests the overall fit of the data to the null model and is the sum of the G_P (pooled) and G_H (heterogeneity) statistics. The relative magnitudes of the latter two statistics reveal much about the preference for different substrata relative to variation in preference among replicates, analogous to an ANOVA. For example, if the G_P statistic is relatively large, then snails showed the same preference in all replicates. However, if the G_H statistic is large, snails showed different preferences across replicates (e.g. analogous to an interaction affect in an ANOVA). Note that either result could produce a significant G_T statistic.

Twelve gastropod species were collected in the macrophyte habitat vs. only six species in the cobble (Fig. 1), despite the fact that the bottom area sampled in cobble was 4.6 times that sampled in macrophytes. *Helisoma companulatum* (Say), *Amnicola lustrica* (Say), *Valvata tricarinata* (Say), *Promonetus exacuous* (Say), *Lymnaea stagnalis* (Say), and *Gyraulus hirsutus* (Say) were absent in the cobble samples. Of the six species that co-occurred in both habitats, four had significantly higher abundances in the macrophyte bed: *Physella* sp. ($t = 2.0, P = 0.04$), *H. anceps* ($t = 2.4, P = 0.03$), *G. parva* ($t = 2.3$, $P = 0.02$), and *Amnicola limosa* ($t = 4.0$, $P < 0.001$). *L. emarginata* ($t = 1.0, P = 0.25$) and *C. decisum* ($t = 1.8, P = 0.08$) did not differ in abundance between the two habitats.

Our field results thus suggest gastropod species richness was clearly lower in a habitat with less macrophyte cover. Further, most of the co-occurring species had reduced abundances in cobble, with 67% of the species significantly more abundant in the macrophyte bed. Given the patchy distributions of freshwater snails in general (Brown 1991), we believe these data

Table 3. Results of laboratory selection experiments. Pooled results for each species are plotted in Fig. 2. N refers to the number of experimental sets (*see Table 1*), numbers in parentheses are the error degrees of freedom for each G value. No G-test was performed when any expected value was <5 (Sokal and Rohlf 1981). Asterisks: **—$P < 0.01$; ***—$P < 0.001$.

	Habitat H_0			Surface Area H_0		
	G_H	G_P	G_T	G_H	G_P	G_T
Amnicola spp.	405.0***	17.0***	422***	109.0***	118.5***	228.0**
($N = 3$)	(18)	(2)	(20)	(18)	(2)	(20)
Campeloma decisum	36.7**	23.0***	59.7***	142.0***	948.9***	1,090.9***
($N = 6$)	(18)	(2)	(20)	(18)	(2)	(20)
Gyraulus spp.	31.8**	170***	202***	33.6**	129.9***	163.5***
($N = 3$)	(12)	(2)	(14)	(12)	(2)	(14)
Helisoma anceps	66.1***	268.0***	334***	61.7***	315.7***	377.4***
($N = 3$)	(18)	(2)	(20)	(18)	(2)	(20)
Physella spp.	36.1***	172.0***	208.0***	42.3***	185.0***	227.3***
($N = 3$)	(10)	(2)	(12)	(10)	(2)	(12)
Lymnaea emarginata	11.0***	374.0***	484.0***	137***	915.1***	1,052.1***
($N = 5$)	(30)	(2)	(32)	(30)	(2)	(32)

clearly indicate greater gastropod abundances and diversities in areas with higher macrophyte biomass. Our results thus agree with earlier studies indicating that gastropod abundance, along with other groups of the phytomacrofauna, is correlated with macrophyte biomass and other macrophyte bed characteristics (Cyr and Downing 1988).

For all six snail species used in the laboratory substrate selection experiments, both the habitat and surface area null models were rejected. When results were pooled over all replicates for each species (G_P statistics, Table 3), with the exception of *Campeloma,* all species exhibited similar trends in habitat and substrate selection (Fig. 2). For the habitat model, five of the six species colonized cobble more than expected and avoided sand, while *Campeloma* had the opposite preference. All species except *Lymnaea* colonized macrophytes at least slightly more than predicted by the habitat model. For the surface area null model, macrophytes were however colonized far less than expected by all six species. All species except *Campeloma* showed the most positive response to cobble and had a near null response to sand. *Campeloma* again differed strongly from the other species in having a very positive response to sand. *Campeloma* was the only species in which individuals spent most of their time buried or half-buried in the sand, and this species is known to be a deposit feeder (Brown 1991).

As indicated by the many significant G_H values for both null models (Table 3), there was substantial variation between sets of replicates that differed in experimental details. Heterogeneity among replicates was particularly high for *Amnicola* and *Campeloma* for the data testing the habitat model. The major trends reflected in Fig. 2, however, are robust, because G_P statistics are highly significant in all cases and because little of the variation between sets can be attributed to any of the major variables that differed between sets of replicates—source lake, snail size, or arena size.

The similarity in response of all the snails except *Campeloma* is striking in regard to both the habitat and surface area models. If snail habitat preference determines snail distribution in the field, we would expect from these experiments that rank order of abundance (taken from the habitat model results) of *Helisoma, Physella* sp., and *Lymnaea* would be cobble $\geq$ macrophytes $>$ sand; for *Amnicola* sp., m $>$ c $>$ s; and for *Campeloma,* s $>$ m $>$ c. Our sampling data indicate these expectations are correct for *Amnicola* sp. only. *Gyraulus* showed no clear preference for macrophytes over cobble in the habitat model, but is clearly more abundant in the Trout Lake macrophyte habitat. Although *Helisoma, Lymnaea,* and *Physella* sp. preferred cobble habitat in the experiments, they were not more abundant in cobble in the field. For these latter three species, some other factor may have caused the lower than expected abundances in cobble.

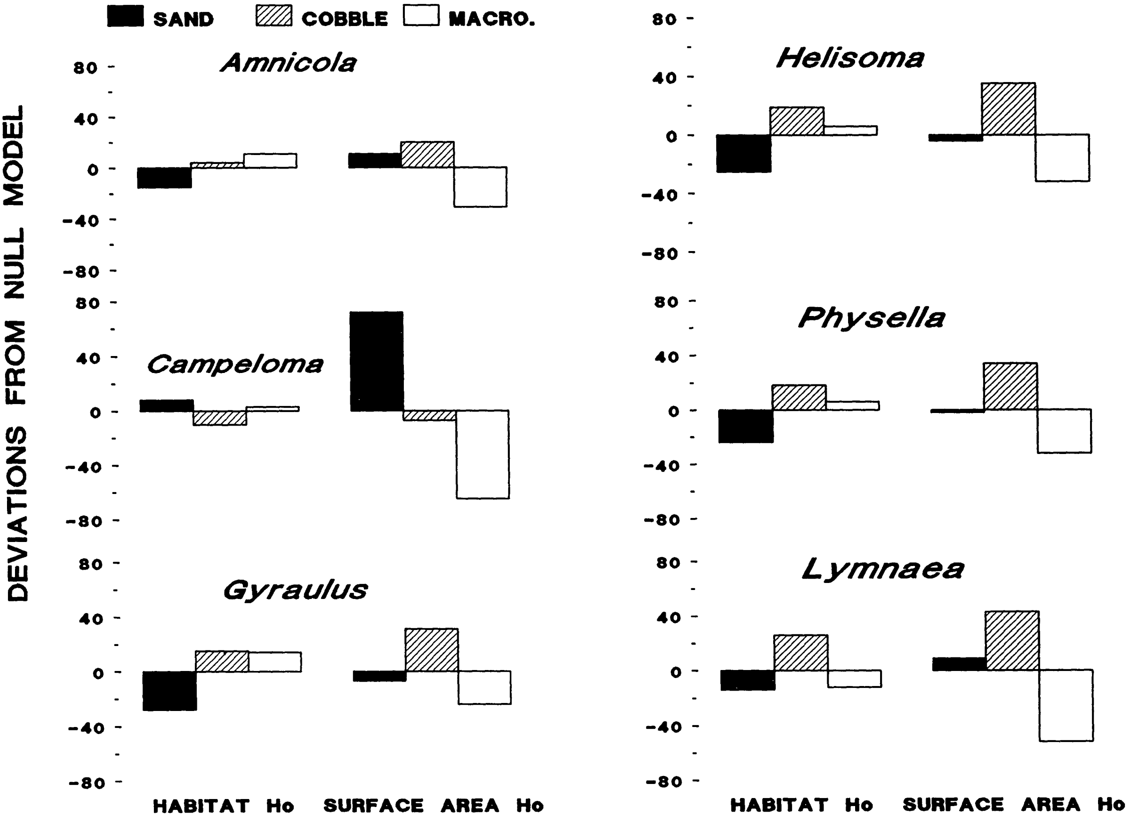

Fig. 2. Observed minus expected number of snails on the habitat null model (left) and on the surface area null model (right) for six snail species. The habitat model is based on equal bottom area in each substrate while the surface area model takes substrate surface area into account (*see text*). Data were pooled across all replicates within a species, and total number of snails was normalized to 100 for each species. For all species, the null models for both habitat and surface area selection were rejected (*see Table 3*).

Comparing results for the habitat and surface area models, however, suggests that the apparently positive habitat responses to macrophytes are a function of the much larger colonizable surface area provided by plants. When that is controlled for (surface area model), all species avoided macrophytes, and, except for *Campeloma,* strongly preferred cobble. The preference for cobble probably results from a positive response to the higher periphyton abundance (*see* Weber and Lodge 1990), essentially because this substrate (unlike most macrophytes) is available for periphyton colonization and growth throughout the field season. For example, Weber and Lodge (1990) found that *Amnicola* sp., *H. anceps, L. emarginata,* and *Physa* sp. all respond positively to periphyton abundance, and that choice by *Lymnaea* among sand, rocks, and macrophytes is largely a function of periphyton abundance (estimated by chlorophyll concentration).

The southeast bay cobble sampled for snails has much lower periphyton chlorophyll (~0–2 μg cm^{-2}) than the northeast shore cobble (0–6 μg cm^{2}) studied by Weber and Lodge (1990). Yet, because that is still considerably higher than on the southeast bay macrophytes (0.1 μg cm^{-2}, figure 3 of Weber and Lodge 1990), part of the discrepancy between laboratory substrate preferences and field distributions remains unexplained. Undescribed temporal dynamics of periphyton on the three substrates may be substantial and may contribute to the discrepancy. Alternately, crayfish predation may reduce snail densities in cobble but not in macrophytes (Weber and Lodge 1990).

We are not the first to consider the importance of surface area to the number of invertebrates colonizing different biomasses, species, or architectures of macrophytes (e.g. Lodge 1986; Kershner and Lodge 1990). Yet few, if any, previous workers have used experiments controlling for other factors (e.g. predation) and quantitatively compared densities of invertebrates (per unit surface area) on vegetation vs. other submersed substrata. The previous data allowing comparisons of invertebrate densities (per unit surface area) on vegetation and other substrates do not control for predation's effects; with that caveat, they do however suggest that our finding of low densities on plants is general. For example, invertebrate densities (per unit surface area) were 10 times and 2–3 times more abundant on unvegetated sediments than on vegetation in a stream (figure 3 of Gregg and Rose 1985) and shallow marine community (calculated from figure 2 of Stoner and Lewis 1985).

Taken together, our field and laboratory results suggest caution in attributing increased phytomacrofaunal abundances in macrophyte beds to habitat selection or refuge from predation. Snails actually colonized macrophytes at lower densities than either cobble or sand. The higher snail densities per unit bottom area in the field simply reflect the greater surface area of macrophytes. Future investigations seeking to explain substrate preference should incorporate substrate surface area into expected frequencies to rule out this simpler hypothesis. Such estimates are not that difficult to derive, as illustrated by our work. Taking surface area into account is particularly important for periphyton grazers, whose resources are surface-dependent.

We do not mean to conclude that predators cannot affect the abundance of gastropod grazers; indeed we have argued elsewhere that they can be quite important (Lodge et al. 1987; Weber and Lodge 1990). However, the relative importance of causal forces for phytomacrofauna-macrophyte relationships may differ among taxa and habitats, and assigning importance will require experiments in each system. In our particular case, colonizable surface area in macrophyte beds can explain greater snail numbers, without any recourse to habitat selection or refuge from predators. We suggest that the interesting question is not the conventional one of why there are so many invertebrates (per unit bottom area) in vegetated habitats, but why are there so few invertebrates (per unit surface area) on vegetation?

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Submitted: 28 February 1992
Accepted: 6 August 1992
Revised: 11 September 1992

Limnol. Oceanogr., 38(1), 1993, 225–231

An ecological cascade effect: Migratory birds affect stability of intertidal sediments

Abstract—A comprehensive study of factors controlling the erodibility of fine-grained intertidal sediments found that sediment strength increased with the arrival of large numbers of migratory shorebirds. Before the birds came, sediment cohesion resulted in part from secretion of polysaccharides by benthic diatoms whose production was controlled mainly by a grazing amphipod, *Corophium volutator*. When the birds arrived, *Corophium* behavior and abundance changed, bioturbation and grazing pressure on the diatoms decreased, and production of cohesion-inducing carbohydrates rose. The results emphasize the importance of biological processes in affecting sediment stability and the limitations of laboratory-based measurements of sediment properties used in models of cohesive sediment behavior.

It is a commonplace of ecology that in simple ecosystems the effects of the activities of organisms in the topmost trophic level(s) can be traced through much or all of the food chain, so that the structure of the ecosystem can be said to be largely derived from this top-down influence. Organisms at the bottom of the chain are assumed to be closely tied to features of their physical environment. Sometimes this relationship is reciprocal in that the organisms themselves exert a detectable influence on the abiotic world. We present evidence here suggesting that the foraging activities of a top predator cascade down through lower trophic levels to affect the dynamic properties of estuarine sediments, and thus change the relationships between those sediments and the physical (oceanographic and atmospheric) factors that normally control their distribution.

Predicting the behavior of intertidal sediments is important wherever human activities (e.g. dredging, harbor or causeway construction) effect changes in coastal and estuarine environments. Although the behavior of coarse, noncohesive sediments is reasonably well known, accurate prediction is extremely difficult in the case of fine-grained, cohesive sediments because of variations in sediment composition, atmospheric effects, and biological processes. In addition, most work on sed-

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Acknowledgments

We are grateful to our many colleagues who assisted with LISP 89 and to P. Hicklin for his shorebird records. Two referees provided comments on the manuscript.

LISP 89 was supported by contract UP A8-001 from the Department of Supply and Services, Canada, by a grant to the Acadia Centre for Estuarine Research from the Nova Scotia Tidal Power Corporation, and grant A 9679 to G. Daborn from the Natural Sciences and Engineering Research Council.