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HABITAT HETEROGENEITY AND INVERTEBRATE SPECIES RICHNESS
AND ABUNDANCE IN TROPICAL SEAGRASS MEADOWS

Gregory S. Wetstone and Kenneth L. Heck Jr.¹

Department of Biological Science
Florida State University
Tallahassee, Florida 32306

Running Head: Habitat heterogeneity in seagrass meadows

¹Order of authorship was determined by the flip of a coin

ABSTRACT

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Two measures of habitat heterogeneity, plant species number and plant biomass, are considered in relation to the species richness and abundance of invertebrates inhabiting tropical sea-grass (Thalassia testudinum) meadows. Plant biomass is significantly correlated with both invertebrate species number and abundance, while the number of plant species is not significantly related to either of these factors. The significant correlation between plant biomass and invertebrate species number is probably a result of the additional [sheltered] ? ^{defun?} habitats that are formed among the foliose branches of certain plant species when they are very dense. The significant plant biomass-invertebrate abundance correlation is most likely due to the protection from predators that thick ← vegetation provides, as well as the greater plant surface area that is available for habitation in heavily vegetated areas. The lack of correlation between plant species number and either invertebrate species number or abundance supports the thesis that these tropical marine species are not specialized feeders on macroplants. This stands in sharp contrast to the highly specialized feeding habits ascribed to many terrestrial herbivores in the tropics.

increased food from detritus? —

A primary concern of ecology is to determine why different areas support different numbers of species. One of the earliest explanations involves differing structural characteristics of the environment (Wallace 1890); intuition dictates that a more complex environment will support more species. In recent years this idea has been termed the theory of spatial heterogeneity (Simpson 1964; Connell and Orias 1964). Mechanistically, complex environments could support a diverse array of species because they would contain many resources capable of sustaining large numbers of species. (cf. MacArthur 1972, pp. 177-179).

The correlation between habitat complexity and species number has been documented for a wide variety of terrestrial organisms including birds (MacArthur and MacArthur 1961), mammals (Simpson 1964), lizards (Planka 1967), insects (Murdoch et al. 1972), and plants (Johnson and Simberloff 1974). In the marine environment Abele (1974) demonstrated that over a wide geographical range the number of shallow water decapod species is a function of substrate complexity. Kohn (1967) found a similar relationship for gastropods of the genus Conus. In general, however, marine habitats have been poorly investigated with regard to this phenomenon, especially when the habitat complexity is comprised of living organisms.

The seagrass habitat, which is widespread throughout tropical and temperate latitudes and exhibits varying degrees of complexity in relatively small areas, is a convenient system for investigating habitat heterogeneity in marine environments. In this study we discuss the relationship between habitat complexity and both the number of species and the number of individuals of epibenthic invertebrates living in subtidal seagrass meadows.

METHODS

A quantification of habitat heterogeneity should reflect those aspects of the environment which are important to the organisms being considered. In a given area, heterogeneity is usually defined in terms of the structural (physical) complexity

of the environment (e.g. MacArthur and MacArthur's (1961) "foliage height diversity" and Abele's (1974) "number of substrates"). Here we consider two measures of heterogeneity: plant biomass and plant species number.

Plant biomass should represent structural complexity because the dense stands of seagrasses and algae, which provide habitable spaces for invertebrates below and between their leaves, are heavy (i.e., contain more plant biomass) relative to structurally simpler stands. Plant species number would be a reasonable measure of habitat heterogeneity if tropical plant-eating invertebrates behave similarly to many tropical phytophagous insects, which are specialized on only one or a few plant species (Janzen 1970).

Study Areas

Six sites off the coast of the Republic of Panama, located less than one km from the Smithsonian Tropical Research Institute's Galeta Marine Lab, were chosen in an effort to sample a spectrum of shallow water vegetative habitats (Figure 1). Plant species which exceeded one gram of wet weight per 0.25m^2 sample at any of the six sites included the marine spermatophytes Thalassia testudinum and Syringodium filiforme; the calcareous green algae Halimeda opuntia, H. incrassata, Penicillus pyriformis, and Udotea flabellum; and the filamentous green alga Cladophora fascicularia. The following is a brief description of the vegetational characteristics at each site:

Site 1 - A mixed stand of dense growths of T. testudinum and H. opuntia, with a small amount of P. pyriformis.

Site 2 - An almost pure stand of T. testudinum with a small amount of P. pyriformis.

Site 3 - An almost pure stand of S. filiforme with a small amount of C. fascicularia.

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of species

Site 4 - A mixed stand containing T. testudinum, H. opuntia, H. incrassata, P. pyriformis, with small amounts of S. filiforme and U. flabellum.

Site 5 - A pure stand of mat-like growths of H. opuntia.

Site 6 - A mixed stand of H. opuntia, H. incrassata, P. pyriformis, and a small amount of U. flabellum.

Each site was located between 20 and 50 meters offshore in one to two meters of water. The substrate at all sites was composed of muddy sand with fragments of Halimeda spp. leaves. The tidal range in this part of the Caribbean is small (less than 0.5 m, Dept. of Commerce Tide Tables, 1975) and none of the sites is ever exposed at low tide. Salinity fluctuated between 18 and 34 ppt during the sampling period due to the influence of seasonally heavy rains. These fluctuations in salinity did not noticeably correlate with species changes during the period of this study.

Sampling procedure

Four samples were taken at each of the six sites during October-November 1974. Each sample consisted of all the epibenthic macro-invertebrates and vegetation in a 0.25m^2 area, randomly selected within sites. At the time of sampling each area was sealed off with a covered 0.25m^2 wooden box. The legs of the box were driven into the substrate to prevent the escape of any animals, and a small mesh net (ca. 5mm.) was inserted through an opening in the top of the box and swept through the water column to obtain any natant invertebrates. The cover of the box was then removed and the vegetation and remaining invertebrates were removed by hand. Only those animals and plant parts which were on or above the substrate were collected: Infaunal invertebrates were not taken nor was any of the root or rhizome system of the plants.

In initial sampling efforts, large quantities of formaldehyde were released inside the sampling box to disable the invertebrates and ensure their capture. However, replicate samples indicated that the formaldehyde did not enhance sampling

effectiveness and since this technique was both cumbersome and expensive, it was discontinued.

RESULTS

The biomass of plant species and the abundances of invertebrate species taken in each sample are shown in Tables 1 and 2. Both parametric and nonparametric correlation coefficients and their levels of significance, determined for all meaningful combinations of the variables plant species number, plant biomass, invertebrate species number, and invertebrate abundance, are shown in Table 3. Figures 2 and 3 illustrate the relationships among the variables that are significantly correlated.

The correlations in Table 3 indicate that one measure of habitat heterogeneity, plant species number, is very weakly related to invertebrate species number and abundance, whereas plant biomass is very strongly and highly significantly related to both these factors (see also Figures 2 and 3).

DISCUSSION

One potentially confounding effect in this study, that numbers of invertebrate species might be differentially available among sites, can be dismissed at the outset. Data collected over a one year sampling period have shown that all of the species collected in this study are present at all the sites during some part of the year (Heck, in preparation). Accordingly, we now assess the different aspects of habitat complexity as they relate to the invertebrate fauna.

Plant Species Number

If tropical herbivorous marine invertebrates specialize on one or a few plant species the species richness of invertebrates in a given area should be roughly proportional to the number of plant species in that area. Although it is widely

held that marine macroscopic vegetation is not appreciably grazed (Mann 1972), detailed studies on the feeding habitats of most of the organisms considered in this study have not been done. However, using the information which is available and extrapolating from data on closely related species, we agree that the species listed in Table 2 apparently do not depend directly on rooted macroscopic vegetation for most of their food supply. Rather, they seem to be generalized detrital feeders and/or unspecialized grazers of the epibiota growing on the leaves of the macroplants. For example, our stomach analyses of the xanthid crab Panopeus occidentalis and the maill crab Mithrax forcens showed that several species of epiphytic algae, seagrass particles, and Halimeda spp. fragments are eaten. The gastropods Cerithium eburneum and Modulus modulus graze on epibiota (Jackson 1972), and the hippolytid shrimp Thor floridanus probably does also (cf. Kikuchi's (1966) stomach analyses of several species of hippolytid shrimps). We have observed the hermit crabs Pagurus bonairensis, Paguristes limonensis, and Clibinarius antillensis apparently indiscriminately grazing the epibiota of macroplants, such as T. testudinum and H. opuntia, and Calcinus tibicen is known to graze epibiota on hard surfaces (L. G. Abele, personal communication). The snapping shrimp Alpheus armillatus is known to feed on algae and to take prey (Hazlett 1962), and by analogy so would A. viridiri. These alpheidids probably are also detritivorous since some of their congeners have been found to consume detrital material (Odum and Heald 1972). The porcellanid crabs Petrolisthes armatus and P. galathinus are filter feeders and Fasciolaria hunteri and the unidentified polychaete are carnivorous and hence not relevant to this discussion.

In summary, these marine invertebrates as a group appear to feed in quite a different manner than do tropical phytophagous insects and may actually be more analogous to soil arthropods in their trophic relationships to plants. The lack of significant correlation between plant species number and invertebrate species

number agrees with the accepted idea that these organisms are not specialized on particular macroscopic plant species. We therefore discard the hypothesis that plant species number is an adequate representation of the habitat heterogeneity in the study areas.

Plant Biomass

We believe that plant biomass is a good indicator of the structural complexity of the environment with respect to the species listed in Table 1. This is due to the fact that the mat-like growths of Halimeda opuntia and thickly vegetated stands of T. testudinum provide many living spaces among their closely packed leaves and are relatively heavy compared to other structurally simple stands.

Given that plant biomass does reflect physical complexity, we conceive of four possible, although not mutually exclusive, mechanisms by which vegetational complexity might affect invertebrate species number and abundance, and consider them in turn.

(1) Food availability. If food were in short supply sites containing large plant biomasses might provide relatively high food levels, thereby allowing increased numbers of individuals and perhaps additional species to inhabit such areas. Since it is unlikely that plankton is differentially available among our sites because they are contained in such a small area, increased food availability should not be a factor influencing those two plankton feeding species in our collections. The most important estimates of food availability in the study areas would be the amount of detritus and epibiota present since, as discussed earlier, most of the invertebrates are considered to be detrital feeders and/or to graze epibiota. Previous characterizations of grass bed areas (Jackson 1972; Mann 1972) with which we agree, have held that detrital material is super-abundant. Epiphytic

algae and microorganisms thickly cover the macroscopic plants at each of our study sites, even at the site of lowest biomass. It is not possible to determine just how much of the detritus and epibiota is truly "available" to the invertebrates (cf. the Hairston et al. 1960) vs Murdoch (1966) and Ehrlich and Birch (1957) debate) and we can reach no firm conclusion on this point. It is our opinion however that food limitation is relatively unimportant to individuals of the species being considered here.

(2) Additional habitats. Densely vegetated areas can also create new habitats by providing protected living spaces for cryptic species among the foliose branches of Halimeda spp. and between and under the dense T. testudinum leaves. Thus, increased physical complexity can effectively create new habitats. Evidence that heavily vegetated areas do actually provide additional habitats is given by the presence of alpheid shrimps and porcellanid crabs only in such places within our sampling sites. These animals are cryptic and normally occur under rocks and coral rubble, or in sponges or burrows (Abele 1972; Nolan and Salmon 1970). In our densely vegetated areas they occur among the closely packed T. testudinum blades or among the Halimeda spp. branches, which are suitable substitutes for their sheltered habitat requirements.

(3) Increased living space. Populations of resident species may be larger in densely vegetated areas simply because these areas contain more habitable space than less densely vegetated sites. Thus, more plant leaves in a given area may simply provide more living space for individuals of invertebrate species to inhabit and, from the species' point of view, these areas would be larger than less heavily vegetated sites. A similar kind of effect has been found to operate among decapod crustaceans associated with several species of corals (Abele, 1976). In this case individual coral heads that were most ramose, effectively offering more living space to commensal crustaceans, supported larger populations than coral heads with fewer branches.

(4) Fish predation. Coral reefs adjacent to seagrass meadows harbor a group of predaceous fishes that routinely forage over the grass flats at night, but shelter on the reefs during the day (Randall 1963; Earle 1972). Thus, in addition to a resident grass bed fish fauna there is another group of species that preys heavily on many common grass bed invertebrates, including those collected in this study (Randall 1967; Starck and Schroeder 1971). Because there are several reefs adjacent to our sampling sites (Figure 1), we expect that heavily vegetated areas would provide more protection from visually searching fish predators than would sparsely covered areas, thereby accounting for larger population sizes in areas of plant biomass. The large number of cryptically colored species in the sea grass meadows, including several species of decorator crabs, indicates, albeit indirectly, that predation may be important there. The importance of predation by reef fishes in shallow tropical seas has been previously stressed by Bakus (1964, 1969) in relation to the preponderance of toxic and unpalatable marine invertebrates in the tropics.

SUMMARY AND CONCLUSIONS

We have shown that the number of plant species in a given area is unrelated to epibenthic invertebrate species number or abundance. Plant biomass is significantly correlated with invertebrate species number, most likely because of the additional sheltered habitat types that are formed in densely vegetated areas. The significant plant biomass-invertebrate abundance relationship appears to be both a result of the protection from fish predators that dense vegetation provides and of the additional living space available in such areas.

Presently we are designing experiments to test directly the mechanisms generating the strong correlations between plant biomass and invertebrates species number and abundance. The necessary experiments are conceptually straight forward but will be both time consuming and logistically difficult to carry out.

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Biomass (wet weight) of plant species collected at each of the sampling sites

[illegible]

TABLE 2

Abundance of invertebrate species collected at each of the sampling sites

Site:	1				2				3				4				5				6			
Sample:	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
<i>Alpheus armillatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	3	0	0	0	0	0
<i>Alpheus viridiri</i>	0	1	1	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Calcinus tibicen</i>	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cerithium eburneum</i>	118	0	4	0	45	15	6	9	25	8	23	12	28	31	18	12	0	0	0	0	1	2	3	4
<i>Clibinarius antillensis</i>	23	0	1	5	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Fasciolaria tulipa</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Megalobrachium poeyi</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mithrax forceps</i>	5	5	2	7	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	4	0	0	0	1
<i>Modulus modulus</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Paguristes limonensis</i>	106	5	20	32	33	7	2	3	0	0	0	0	6	11	3	1	0	0	0	0	0	0	0	0
<i>Pagurus bonaiensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	5	11	0	0	0	0
<i>Panopeus occidentalis</i>	10	7	5	15	0	0	0	0	0	0	0	0	4	0	6	11	4	8	4	4	0	0	0	0
<i>Petrolisthes armatus</i>	0	1	0	9	0	0	0	0	0	0	0	0	0	0	0	0	11	4	3	5	0	0	0	0
<i>Petrolisthes galathinus</i>	24	24	7	41	0	0	0	0	0	0	3	0	0	0	0	0	3	5	8	5	0	0	0	0
<i>Thor manningi</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified polychaete	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0

Table 3

		Untransformed		Log-transformed	
		INV SP #	INV ABUN	INV SP #	INV ABUN
Pearson "r"	PLANT BIOM	.8593 ***	.6383 ***	.8435 ***	.6430 ***
	PLANT SP #	.0957 N.S.	.2133 N.S.	.0526 N.S.	.0355 N.S.
Kendall "τ"	PLANT BIOM	.6134 ***	.4762 **	.6134 ***	.4762 **
	PLANT SP #	.1432 N.S.	.279 N.S.	.1432 N.S.	.279 N.S.

** = $p < .02$

*** = $P < .001$

N = 24

Table 3. Parametric and nonparametric correlation coefficients and their levels of significance for both untransformed and log-transformed data.

LEGEND FOR FIGURES

- Figure 1. Map of Panama (inset) and the study sites. The location of coral reefs is indicated by scalloped lines just seaward of the land boundary.
- Figure 2. Plot of the logarithms of invertebrate species number (ordinate) vs plant biomass (abscissa).
- Figure 3. Plot of the logarithms of invertebrate abundance (ordinate) vs plant biomass (abscissa).





