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Diel variation in the abundance of epifauna associated with seagrasses of the Indian River, Florida, USA

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Abstract

Day-night comparisons of the motile epifauna in the canopy of seagrass beds in the Indian River lagoon, Florida revealed that abundances were not stable over the diel period. Collections were made between February and June, 1982. Higher densities of epifauna occurred on seagrasses at night. For both of the numerically-dominant gastropod and crustacean groups, four of the five top ranked species followed this diel pattern. Crustaceans showed particularly large changes in abundance, averaging a twofold increase in nocturnal samples. Faunal similarity between day and night collections remained high, however, indicating that community structure was preserved during diel abundance changes. Equating epifauna collected from seagrass blades with those associated with the seagrass habitat in general therefore may be erroneous, particularly if collections are made during daylight. Changes in prey availability due to the diel pattern are likely to extend to important community trophic functions.

Introduction

In seagrass systems, the motile epifauna are recognized as key links in the transfer of energy to higher consumers (Nelson, 1981; Livingston, 1982; Howard, 1984; Robertson, 1984; Leber, 1985). High abundances of epifauna and their relative accessibility to epibenthic predators enhance their trophic role. Attempts at generalizations concerning the role of predation often have been frustrated by finding very different effects of predation pressure on the various available prey taxa (Nelson, 1979; Robertson, 1984; Leber, 1985). Such results suggest that behavioural and/or mor-

phological attributes of individual species are important. Differences in microhabitat-preference, behavioural rhythms and crypsis are factors which clearly can influence the outcome of trophic interactions. In most quantitative studies of seagrass faunas the macrofauna above and below the sediment-water interface have been collected using grab or coring devices. Inevitably, any spatial separation of organisms in the samples is lost in subsequent sieving and sorting. Allocation of species to microhabitats usually extends only to the broad categories of "infaunal" or "epifaunal", and this allocation is done indirectly and *a posteriori*.

Nagle (1968) isolated above-ground portions of *Zostera marina* plants in the field and identified three main distributional patterns: species which increase in abundance up the stem; those which reflect the distribution of epiphytes; and those which decrease in abundance up the stem. Samples of adjacent sediment indicated that these latter species were abundant there also, and Nagle concluded that those individuals on plants were a spillover from normally benthic populations. However, these samples were collected only during daylight hours. Many epifaunal species are: (a) non-specific with respect to plant species (Virnstein and Curran, 1986; Virnstein and Howard, in press) and (b) highly mobile and may alter their vertical distribution on a daily basis (Robertson and Howard, 1978; Bauer, 1985a, b; Howard, 1985). Although various authors have pointed out the danger of accepting daylight-only collections as representative of the epibenthic community (Heck, 1977; Greening and Livingston, 1982), the great majority of seagrass faunal studies rely on diurnal data only.

The present study examines diel patterns in the use of vertical space by mobile epifauna by comparing day and night abundances within the seagrass canopy. Three main questions are addressed by the study: Do abundances of canopy-associated macrofauna differ significantly between day and night? Are diel patterns consistent (over a period of months)? And does the quantitative structure of the fauna change along with any diel abundance changes?

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Materials and methods

Sampling was carried out at Link Port (Lat. 27°32.2'N; Long. 80°20.9'W) in the Indian River lagoon, Florida. Seagrass meadows are extensive, with *Halodule wrightii* dominating in shallow water (to 0.4 m). *Syringodium filiforme* is more abundant in deeper water (0.5 to 1.5 m). The study area has been described in detail elsewhere (Gore *et al.*, 1981; Virnstein and Carbonara, 1985). The macrofauna at this location has been studied extensively (Young *et al.*, 1976; Young and Young, 1978; Nelson, 1981; Nelson *et al.*, 1982; Stoner, 1983; Howard, 1985; Virnstein and Howard, in press).

The main sampling site was in a *Halodule wrightii* bed, ~50 m from shore. A second site was ~50 m further from shore, in a contiguous *Syringodium filiforme* bed. Sediment characteristics and physico-chemical conditions were similar (see Stoner, 1983), and similar suites of epifaunal species occurred at the two sites (Virnstein and Howard, in press).

Samples were collected with an epifaunal grab sampler (illustrated in Virnstein and Howard, in press), a horizontal hand-operated modification of benthic grab samplers. The sampler collects a small quantity (~5 to 10 g dry wt) of seagrass blades and associated animals. A sample was collected by positioning the sampler among the seagrass blades and resting against the sediment, then gradually opening the jaws to a gape of about 20 cm, while moving the sampler gently forward to enclose a sample of appropriate size. The jaws were then quickly squeezed shut and enclosed seagrass blades snipped off along the lower edge of the sampler and wherever they protruded from the grab. Opposing edges of the sampler were lined by compressible rubber so that they formed a tight seal when clamped around the seagrass blades. The grab was 25-cm-tall and enclosed the entire length of most upright seagrass blades. Walls of the sampler were 0.5-mm mesh nylon. Unlike previous diel collections of seagrass fauna which have utilized trawls, pushnets and handnets of variable and unknown sampling efficiencies, this method provides direct, quantitative counts of epifauna and avoids disturbance of the sediment surface during sampling.

The contained sample was washed out of the sampler and preserved in 5% formalin-seawater. In the laboratory, seagrass blades were washed thoroughly onto a 0.5-mm mesh sieve. Material retained on the sieve was sorted by hand and the macrofauna was stored in 70% ethanol. For each sample, seagrass and algal material were separated before drying for one week at 60°C and weighing. The latter category was mostly drift algae which was always <5% of the total plant material in any one sample and usually was <1%. On all sampling dates the proportion of algae in samples was not significantly different between day and night collections (Student's *t*-test, $p < 0.05$).

Collections were made at intervals of approximately two months (19 February, 19 April and 25 June, 1982) at the *Halodule wrightii* site, whereas the *Syringodium filiforme* site was sampled only in April. On each sampling

date, six replicate samples were obtained in daylight and six during darkness. Collecting corresponded with low tide. Day collections were followed by night collections at the following low tide, a period of about 12 h. All collections were made during calm weather. Night collections were obtained before moonrise and 3 to 4 h after sunset.

Only the motile macroepifauna were considered, excluding sessile species and those taxa normally considered meiofaunal. Abundances were calculated as the number of individuals per gram plant weight.

Day versus night abundances of dominant species were compared at each sampling date using Student's *t*-tests. The presence of diel patterns across all sampling dates at the *Halodule wrightii* site was tested using 2-factor analysis of variance (ANOVA). Data were first log-transformed to achieve homogeneity of variances.

Faunal similarity between sampling dates and between day and night at the *Halodule wrightii* site was measured using the relative-dominance index, rho (van Belle and Ahmad, 1974), which considers the relative proportion of species in two samples. Replicate abundance means were used for the analysis, and a group-average clustering strategy was applied in the construction of a dendrogram from the indices.

Results

The motile epifauna was dominated by gastropod molluscs (Table 1). Peracarid and decapod crustaceans comprised the remainder of the more abundant taxa. The epifaunal abundance (all species combined) and gastropod and crustacean abundance for all collections were consistently higher at night (Fig. 1, Table 2). Only for the gastropods in April (both sites) was the abundance not significantly higher at night.

Individual species generally conformed to this diel pattern (Figs. 2, 3, Table 2). All significant differences in abundance were due to higher nocturnal values. The high proportion of non-significant interaction terms in ANOVAs, with time of day and sampling date as factors, is indicative of the stability of the diel pattern across sampling dates. An exception was the gastropod *Cerithium muscarum*, which was more abundant at night in February and April, yet showed no such diel difference in June (Fig. 2). Of the ten most abundant species, only the gastropod *Astryis lunata*, the isopod *Erichsonella attenuata* and the shrimp *Palaemonetes intermedius* did not show significant diel variation in abundance (Table 2, Figs. 2, 3).

Diel abundances at the *Syringodium filiforme* site in April reflected the pattern at the *Halodule wrightii* site (Figs. 1, 2, 3). The large diel change in the abundance of total epifauna at the *S. filiforme* site was due mainly to the influence of crustaceans, which were more abundant at that site.

Community similarity, as measured by the dominance-weighted index rho, was high among all collections from the *Halodule wrightii* site, ranging from 0.80 to 0.98

Table 1. Ranked overall abundance of dominant Indian River epifauna, sites and sampling dates combined. Species comprising 0.2% are omitted. (G = gastropod, A = amphipod, I = isopod, M = mysid, T = tanaid, D = decapod)

Rank	Species		Number of individuals	% of total collection
1	<i>Crepidula convexa</i>	(G)	5 974	38.3
2	<i>Bittium varium</i>	(G)	4 445	28.5
3	<i>Cerithium muscarum</i>	(G)	1 181	7.6
4	<i>Modulus modulus</i>	(G)	1 158	7.4
5	<i>Cymadusa compta</i>	(A)	990	6.4
6	<i>Astyris lunata</i>	(G)	341	2.2
7	<i>Mysidopsis bigelowi</i>	(M)	222	1.4
8	<i>Hyppolyte pleuracanthus</i>	(D)	214	1.4
9	<i>Erichsonella attenuata</i>	(I)	204	1.3
10	<i>Ampithoe longimana</i>	(A)	127	0.8
11	<i>Cymodoce faxoni</i>	(I)	103	0.7
12	<i>Palaemonetes intermedius</i>	(D)	95	0.6
13	<i>Crepidula plana</i>	(G)	75	0.5
14	<i>Turbonilla incisa</i>	(G)	72	0.5
15	<i>Corophium</i> spp.	(A)	55	0.4
16	<i>Hargeria rapax</i>	(T)	43	0.3
17	<i>Ercolania fuscata</i>	(G)	37	0.2
18	<i>Odostomia engonia</i>	(G)	37	0.2
19	<i>Pagurus macLaughlinae</i>	(D)	33	0.2
20	<i>Prunum apicinum</i>	(G)	31	0.2
Total:			15 437	99.0

Table 2. Results of 2-factor analysis of variance on abundances of Indian River epifauna (no. of individuals/g plant); factors are time of day (i.e. day or night) and sampling dates. * $0.05 > p > 0.01$, ** $0.01 > p > 0.001$, *** $p < 0.001$

Source of variation:	F ratio		
	Time of day	Sampling dates	Interaction
df	1	2	2
Total epifauna	26.60***	15.14***	2.45
Total Gastropoda	24.00***	17.19***	4.28*
Total Crustacea	54.68***	1.06***	1.30
<i>Crepidula convexa</i>	12.59**	0.86	2.05
<i>Bittium muscarum</i>	38.9***	47.56***	9.57***
<i>Bittium varium</i>	10.75*	99.80***	1.65
<i>Modulus modulus</i>	13.56**	55.15***	2.93
<i>Astyris lunata</i>	0.02	37.63***	4.59*
<i>Cymadusa compta</i>	37.93***	9.12***	2.34
<i>Erichsonella attenuata</i>	0.71	3.26	1.03
<i>Hyppolyte pleuracanthus</i>	4.73*	3.59*	2.40
<i>Ampithoe longimana</i>	5.84*	8.79**	1.56
<i>Palaemonetes intermedius</i>	2.96***	37.42***	0.62

Fig. 4). Collections made on the same date, i.e. within-date, day versus night, had values of 0.95 to 0.97. Among-date comparisons of collections produced indices of 0.83 to 0.87 for day collections and 0.86 to 0.93 for night collections. Hence, the among-date similarity was lower than the within-date similarity, indicating a smaller effect of diel variability on community composition than that due to long-term (2 to 4 months) changes.

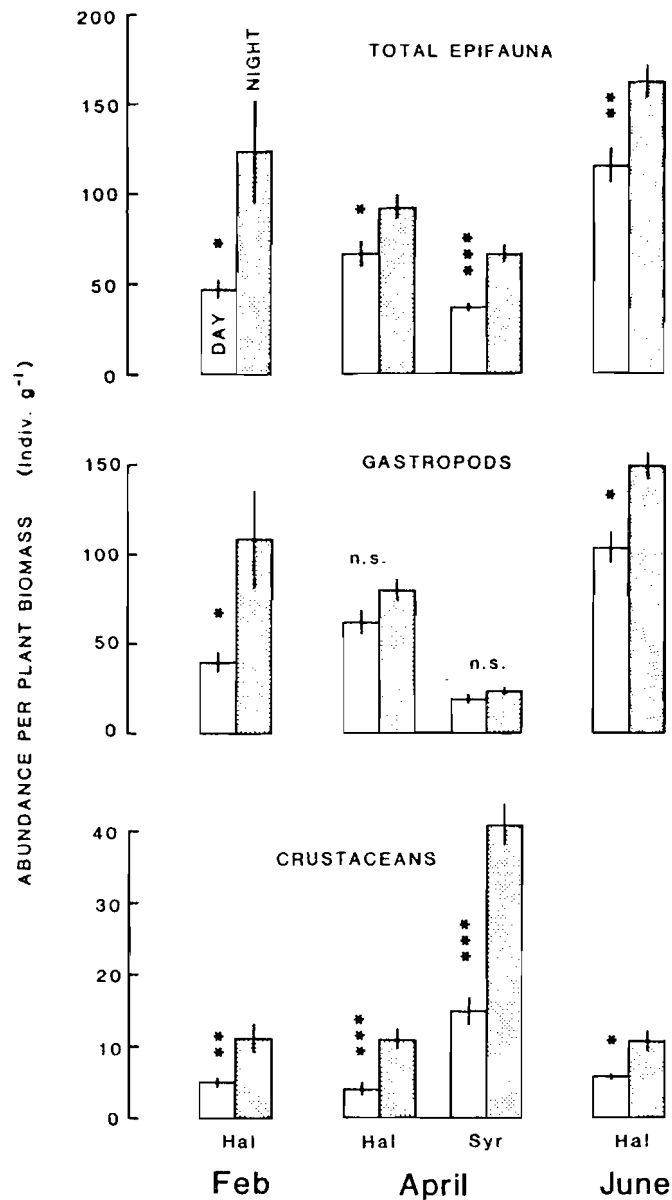


Fig. 1. Day and night abundances of Indian River epifauna: total (all species combined), total gastropods and total crustaceans. (Mean $[\pm SE]$ number of individuals per g dry wt of plant). Hal = *Halodule wrightii* site, Syr = *Syringodium filiforme* site; * $0.05 > p > 0.01$, ** $0.01 > p > 0.001$, *** $p < 0.001$

Discussion

The abundance of motile epifauna on seagrass blades was always greater at night. This was true for the majority of dominant gastropod and crustacean species. The diel changes in abundance were particularly large for crustaceans, with average nighttime abundances being about twice those of the day. These quantitative data confirm diel patterns suggested by qualitative studies of the macroepifauna of European seagrass beds (Ledoyer, 1964, 1969) and of the larger epibenthic fauna of American, Caribbean and Australian seagrass beds (Heck, 1977; Howard, 1981; Greening and Livingston, 1982; Bauer, 1985 a, b). Marked

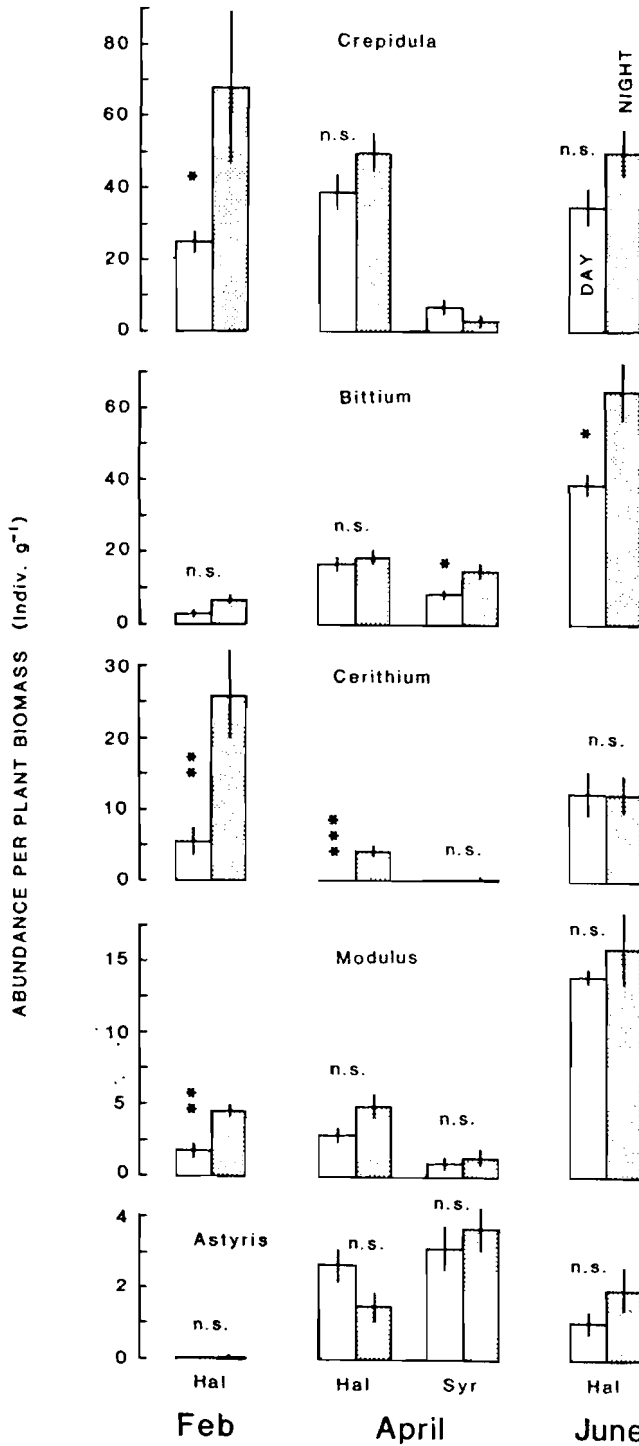


Fig. 2. Day and night abundance of Indian River epifauna: the five most abundant gastropod species. (Mean \pm SE) number of individuals per g dry wt of plant). Hal = *Halodule wrightii* site, Syr = *Syringodium filiforme* site; * $0.05 > p > 0.01$, † $0.01 > p > 0.001$, ‡ $0.01 > p > 0.001$, § $p < 0.001$

diel variation in abundance may be typical of a wide range of taxa of most seagrass systems.

Diel abundance changes were comparable in magnitude to the abundance changes seen between sampling dates. However, the order and magnitude of species dominance tended to be preserved between day and night samples. Hence, diel differences were primarily quantitative.

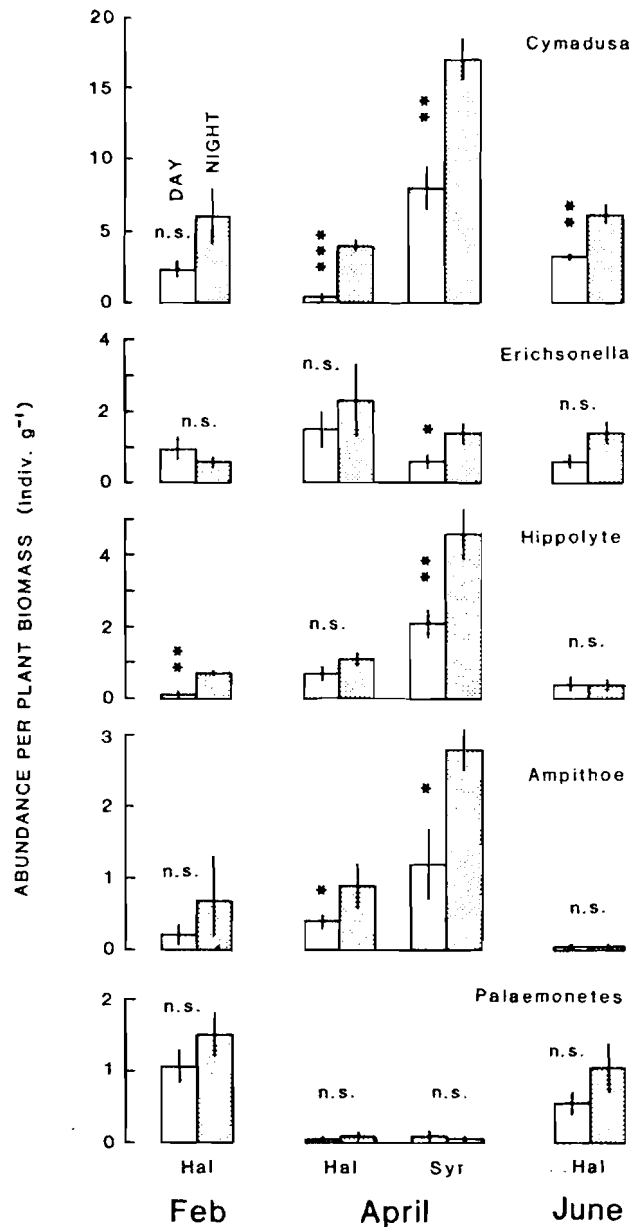


Fig. 3. Day and night abundances of Indian River epifauna: the five most abundant crustacean species. (Mean \pm SE) number of individuals per g dry wt of plant). Hal = *Halodule wrightii* site, Syr = *Syringodium filiforme* site; * $0.05 > p > 0.01$, † $0.01 > p > 0.001$, ‡ $0.01 > p > 0.001$, § $p < 0.001$

A vertical migration between the sediment surface and the seagrass canopy is most probably responsible for the daily pattern. Horizontal migration of epifauna to and from the study sites, perhaps from deeper habitats farther from shore, is unlikely to account for abundance changes. Although crustacean species can be highly mobile (Howard, 1985; Virnstein and Curran, 1986), the gastropod component of the fauna clearly is not capable of the rapid daily migrations over the required distances (of 10s to 100s of metres). Furthermore, a very similar pattern of diel epifaunal abundance occurred at both the nearshore (*Halodule wrightii*) site and the deeper (*Syringodium filiforme*) site.

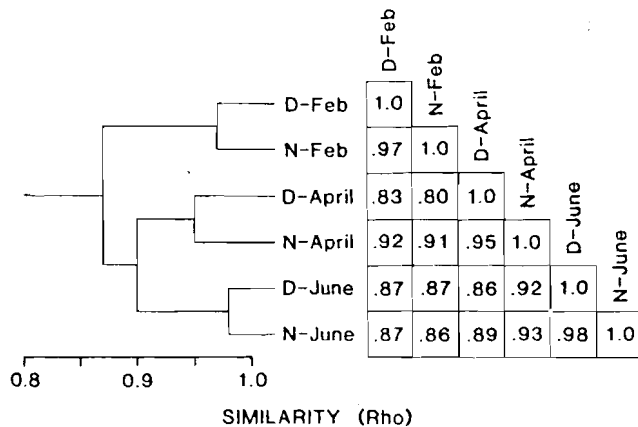


Fig. 4. Matrix of similarity coefficients (ρ), and dendrogram grouping of Indian River epifauna collections using group-average clustering strategy. D = day collection, N = night collection

The majority of mobile epifaunal species are not obligate canopy-dwellers. Surfaces of both the sediment and the seagrass leaves are apparently utilized. Some species may burrow into the sediment during daylight, e.g. penaeid, crangonid and processid shrimps (Hughes, 1968; Al-Adhub and Naylor, 1975; Bauer, 1985a, b), but these groups are not important elements of the Indian River seagrass fauna. The Indian River epifauna lack substratum specificity toward different available plants. Very similar suites of species are found on all three local seagrass species as well as on interspersed clumps of drift algae (Virnstein and Howard, in press). Experiments have shown that the surfaces of artificial seagrasses are colonized by essentially the same assemblage (Virnstein and Curran, 1986). This flexibility in microhabitat use by the majority of the fauna blurs the distinctions between "epifauna", "sediment-surface fauna" and "infauna" over the diel period.

The daily use of both sediment and seagrass canopy may not always be consistent for all size-classes of epifaunal species. Considerably higher nocturnal abundances of *Cerithium muscarum* in February and April were due to the diel movements of adults. Adults had completely disappeared from the population by June, and the newly recruited juveniles that replaced them did not differ in day and night abundances. Apparent movements of the filter-feeding slipper limpet *Crepidula convexa* in February in fact reflect the movements of larger gastropods (mainly *C. muscarum* and *Modulus modiolus*) to which they attach. Newly-settled juvenile *C. convexa* occur independently on seagrass leaves, but are extremely sedentary.

The actual function served by diel migrations of the epifauna is conjectural. Many of the arguments advanced to explain vertical migration in open-water and demersal plankton (Longhurst, 1976; Robertson and Howard, 1978) could easily apply. Avoidance of diurnal predation by visually-feeding fish in the well-illuminated and more open upper canopy, or a diel tracking of migrating food resources by epifauna are plausible functions. Analogous examples of the former are the downward movement of zooplankton

during the day to avoid planktivorous fish (Fancett and Kimmerer, 1985) or the upward movements of saltmarsh snails to avoid predatory crabs at high tide (Warren, 1985). Vertical movements in response to a changing distribution of food seems less likely, as the majority of species are grazers on attached algal or detrital material (Howard and Short, 1986).

The implications of the observed diel abundance patterns for both the practical aspects of sampling programs and conceptual views of the structure of epifaunal communities are significant. Clearly, abundance estimates of the epifaunal component of seagrass communities are sensitive to the time of day when samples of the canopy are obtained. Such a predictable source of variability should be a primary consideration in the design of epifaunal sampling programs.

In terms of ecosystem function, diel patterns in the use of vertical space by seagrass-associated macrofauna may have trophic repercussions. Predators which forage either in the seagrass canopy or on or near the sediment surface clearly are likely to face large diel variability in the availability of prey. In seagrass systems elsewhere it has been shown that nocturnal vertical migrations of benthic macrofauna into the water column are exploited by fish (Robertson and Howard, 1978; Robertson and Klumpp, 1983). Similar trophic coupling may occur within the canopy, given that: (a) many predators are restricted to well-defined vertical foraging zones e.g. syngnathid fish (Howard and Koehn, 1985), and (b) mobile epifauna are important prey groups for consumers in seagrass systems (Howard, 1984; Robertson, 1984).

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