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Site-to-site variability in abundance of meiobenthic copepods along a tidal gradient over 24 hours[1]

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Abstract

As part of a larger study on the effects of juvenile fish predation on meiobenthic copepods, we collected meiofauna every two hours for 24 hours at three muddy sites along a transect through vegetated marsh, to unvegetated intertidal to unvegetated subtidal habitats. The vegetated marsh (*Spartina alterniflora*) site harbored significantly more copepods over the combined sampling period than the other two sites. Some species were distributed along the entire transect, but several species were much more abundant at one site than the others. For example, *Microarthridion littorale* was most abundant at the intertidal site, and *Enhydrosoma propinquum* was most abundant at the unvegetated sites. The most abundant subtidal species included *Pseudobradya pulchella* and *Paronychocamptus wilsoni.* Three species were most abundant in the vegetated marsh (*Stenhelia* (*D.*) *bifidia, Nannopus palustris,* and *Diarthrodes aegidius*). Maximum total copepod abundance occurred during the daytime low tide at all three sites. Of the four species more abundant in the light than at night, three were subtidal. Most of the time there were no detectable differences between high and low tide abundances, suggesting that there was little exchange of individuals between habitats as tidal levels changed. Without samples from additional transects or the ability to obtain samples for all possible combinations of light and tide levels, we could not detect significant interactions between these two environmental factors. Based upon the species composition of copepods in the gut contents of motile fish predators, the existence of distinct copepod species assemblages at sites along the transect may allow inferences about where fish had fed.

Introduction

As part of an intensive study on benthic copepods as food for juvenile fish in a South Carolina saltmarsh ecosystem, we wanted to determine: 1) if certain copepod species are 'marker' species of different habitats along a tidal gradient and, 2) whether these copepod assemblages remained constant in both species composition and abundance as light conditions and tidal coverage changed over time. There have been numerous studies on the zonation and migration of benthic copepods in sandy habitats, particularly sandy beaches (see Hicks & Coull 1983 for summary), but the question of whether copepod distribution changes over time on muddy substrates is less

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well known. Previous studies indicated that benthic copepod species were zoned along a muddy tidal gradient in South Carolina saltmarshes (Coull *et al.*, 1979) and that copepod abundance varies with the degree of tidal coverage (Palmer & Brandt, 1981; Fleeger *et al.*, 1984). The present study was designed to test the effects of light, habitat and tidal elevation on abundance and distribution simultaneously.

Because the predator of interest in the larger study, a juvenile fish (spot, *Leiostomus xanthurus* Lacepède), feeds almost exclusively in muddy substrata (Smith & Coull, 1987), our gradient-time series was conducted across muddy sediments at three locations: 1) unvegetated subtidal, 2) unvegetated intertidal and; 3) vegetated (*Spartina*) intertidal. We report here the distribution and abundance of the benthic copepods along this habitat gradient and how these copepod assemblages varied as tide and light levels changed over 24 hours.

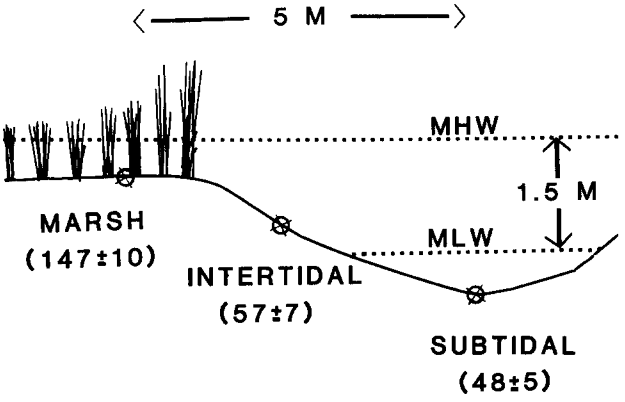

Fig. 1. Schematic of the habitat sampled. The numeric value under each habitat is the mean total number of copepods (± SE) per 10 cm^2 at each habitat averaged over 24 hours.

Methods and materials

Three locations at Oyster Landing, North Inlet Estuary, South Carolina, USA (33° 19.0′ N, 79° 11.6′ W), were sampled for meiobenthos from 1000 hrs 22 May 1986 to, and including, 1000 hrs 23 May 1986. The three sites were a subtidal creek bottom (unvegetated), an intertidal creek bank (unvegetated), and a low marsh (tall *Spartina alterniflora* Loisel) levee (Fig. 1). The transect spanned a horizontal distance of 5 m and was perpendicular to the direction of tidal flow. Four replicate core samples (2.66 cm inner diameter) were taken at each of the three sites every 2 h (i.e., 12 samples every 2 hours × 13 time periods = 156 total samples). The tidal height and light cycles over the 24 h are illustrated in Fig. 2.

All sites were marked by plastic stakes and all samples were collected randomly within a meter of the stake. A boardwalk over the marsh was used for access to sample the *Spartina* marsh site by hand at every tidal level. At low tide, the intertidal and subtidal sites were accessible by walking; thus, all the low-tide cores were taken by hand. At high tide, the subtidal and intertidal sites were accessible only by a boat which was paddled to the sites. The core tube was attached to an adjustable 1.5 m steel rod to collect the samples from the boat.

Upon collection, the samples were immediately fixed in 10% buffered formalin with Rose Bengal. The samples were later sorted to major taxon and counted under a dissecting microscope. Every adult copepod and copepodite was enumerated and identified to species and sex where possible.

All quantitative data were stored as SAS data sets (Freund & Littell, 1981) on the University of South Carolina mainframe computer. For all

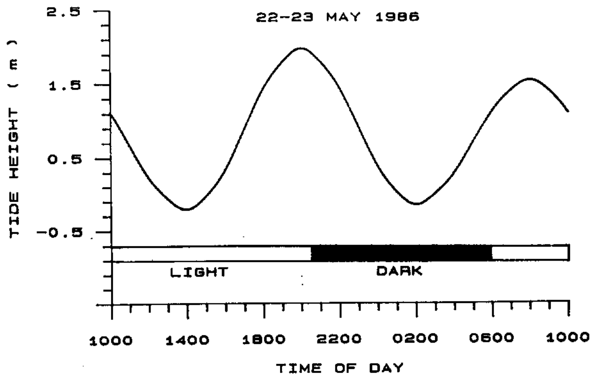

Fig. 2. Tide curve and light/dark periods over the 24 hour sampling regime.

analyses the count data were $\log_{10}$ transformed to meet the assumptions of analysis of variance. One-way analysis of variance (ANOVA) tested for differences in abundance of the taxon or individual copepod species between sites and between time periods at each site. Two-way ANOVA was used to test the main effects of tide (4 levels–high, falling, rising, low) and light (2 levels–light, dark). All significance levels were set at $p < 0.05$.

Results

A total of 17 benthic copepod species were identified from the three sites over the 24 hours. Eight species comprised >90% of the total copepod fauna and there were significantly more copepods at the marsh site than at the intertidal or subtidal sites. Several of the species were restricted to particular habitats and as such are regarded as 'markers' of that habitat (Table 1). *Stenhelia (D.) bifidia, Nannopus palustris* and *Diarthrodes aegidius* were clearly marsh species, whereas *Pseudobradya pulchella* and *Paronychocamptus wilsoni* were almost entirely restricted to the subtidal (Table 1). *Enhydrosoma propinquum*, while significantly more abundant intertidally and subtidally, occupied the entire gradient, whereas *Halicyclops coulli* and *Microarthridion littorale* did not occur abundantly in the marsh (Table 1). *Halicyclops* is typically a subtidal species that occurred abundantly ($60 \cdot 10\,\text{cm}^{-2}$) in only one of 52 marsh samples and thus, the mean abundance value of $2 \cdot 10\,\text{cm}^{-2}$ is strongly biased by this particular sample. There were significant differences in abundance of total copepods over time at all 3 locations ($p = 0.0001$ intertidal, $p = 0.05$ marsh, and $p = 0.0001$ subtidal, Fig. 3). We have plotted the abundance of some abundant individual species in Figures 4 and 5 over the 24 hour period but have not plotted every species, nor every location for each species except for *Enhydrosoma propinquum*.

Table 1. Mean abundance (number per 10 cm^2) of the eight dominant copepods at the 3 sites. Abundances of a species are not significantly different at sites having a common underline (Tukey's multiple comparison procedure; experiment-wise error rate $p < 0.05$).

Species	March	Intertidal	Subtidal
Stenhelia (D.) bifidia (Coull)	100	1	0
Enhydrosoma propinquum (Brady)	9	26	18
Microarthridion littorale (Poppe)	3	20	8
Nannopus palustris (Brady)	16	1	0
Halicyclops coulli (Herbst)	2	5	8
Pseudobradya pulchella (Sars)	0	2	10
Diarthrodes aegidius (Brian)	9	0	0
Paronychocamptus wilsoni (Coull)	1	1	6
Total Copepods	147	57	48

The two-way ANOVA indicated little effect of tide or light on abundance of a particular species or total copepods. Of a total of 27 two-way ANOVA's (9 taxa × 3 sites), there were only 9 significant differences (Table 2) and only one significant interaction (*Halicyclops coulli*) between light and tide. Tide affected the abundance of only *E. propinquum* intertidally and total copepods in the intertidal and in the marsh; in all three cases abundance was significantly higher at low tide than at high tide. Abundances during rising and falling tides were not significantly different from high or low tide abundances for these three cases (Tukey's multiple comparison procedure; experiment-wise error rate $p < 0.05$). Tests for the effects of light found 4 of the 5 significant differences occurring subtidally, wherein abundance was significantly higher in the light than in the dark (Table 2).

Discussion

We were not surprised to find that individual copepod species occupied particular habitats along the short 5 m transect since Coull *et al.*

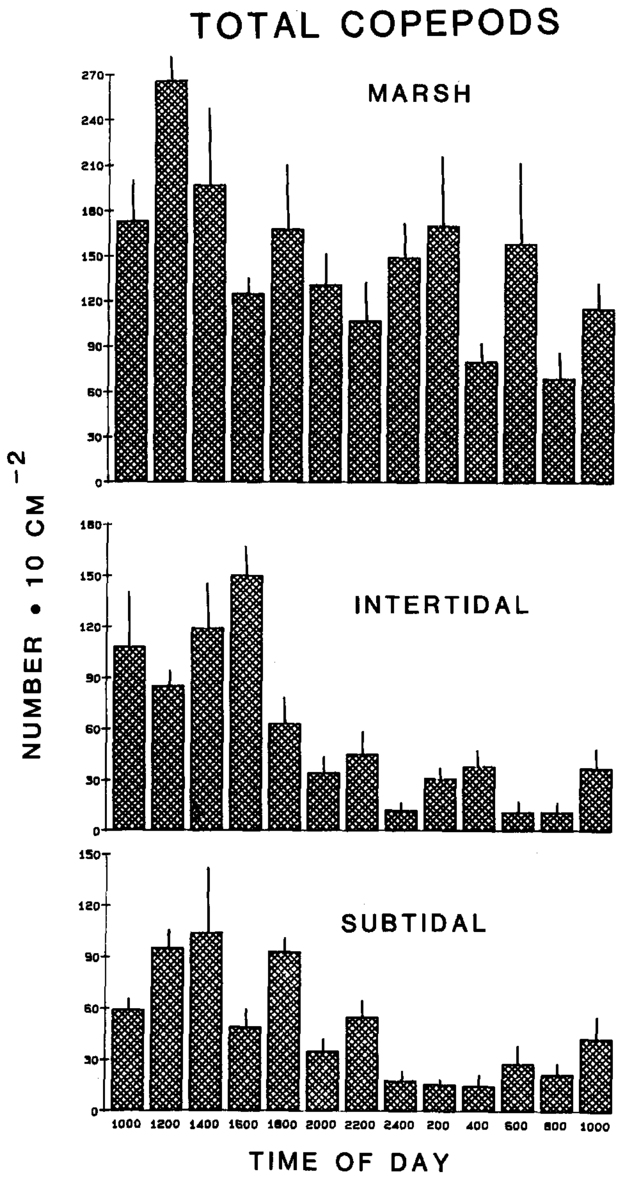

Fig. 3. Mean abundance (± SE) of total copepods at the three sites over 24 hours (samples were taken every 2 h from 1000–1000 hrs).

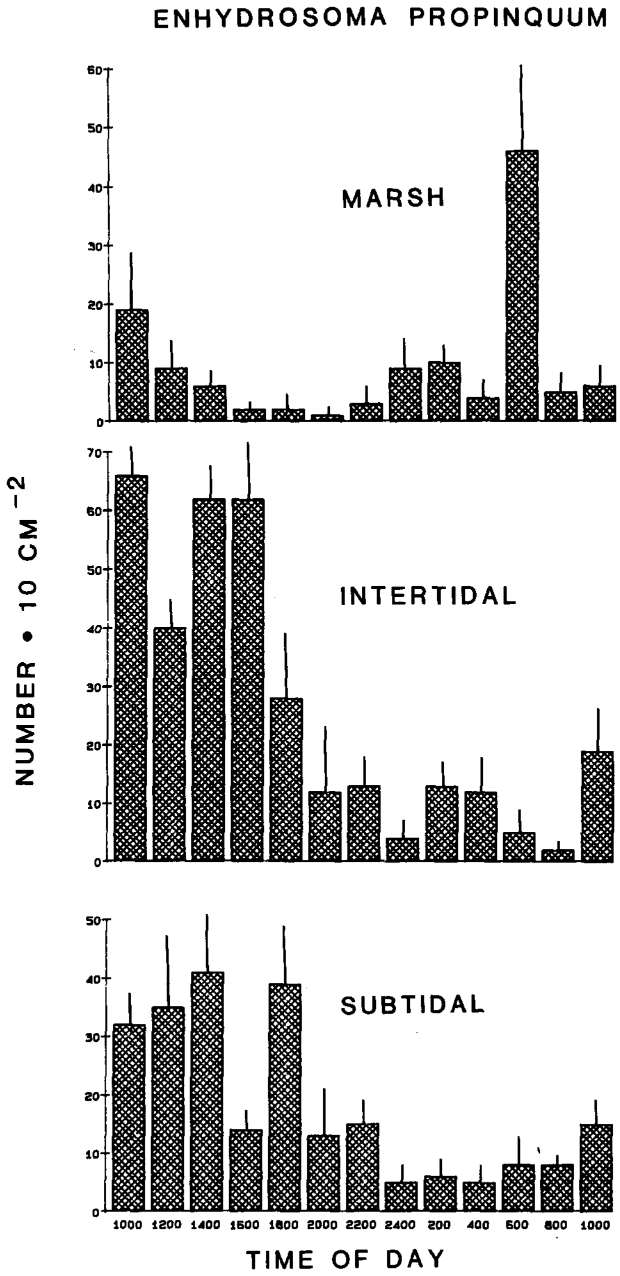

Fig. 4. Mean abundance (± SE) of *Enhydrosoma propinquum* at the three sites over 24 hours.

(1979) had reported copepod species zonation across a similar habitat. The samples collected by Coull *et al.* (1979), however, were all taken at low tide over a period of several years in several locations. Since there was evidence that copepod abundance in mud in southeastern US estuaries varied with the tide (Palmer & Brandt, 1981; Fleeger *et al.*, 1984; Palmer & Gust, 1985) and species exhibited different behavior in light vs dark (Palmer, 1984), we *a priori* expected there to be differences in abundance related to daylight and tidal level. There were certainly abundance differences over the 24 hours (Figs. 3–5), but few of these were due to the effects of tide or light

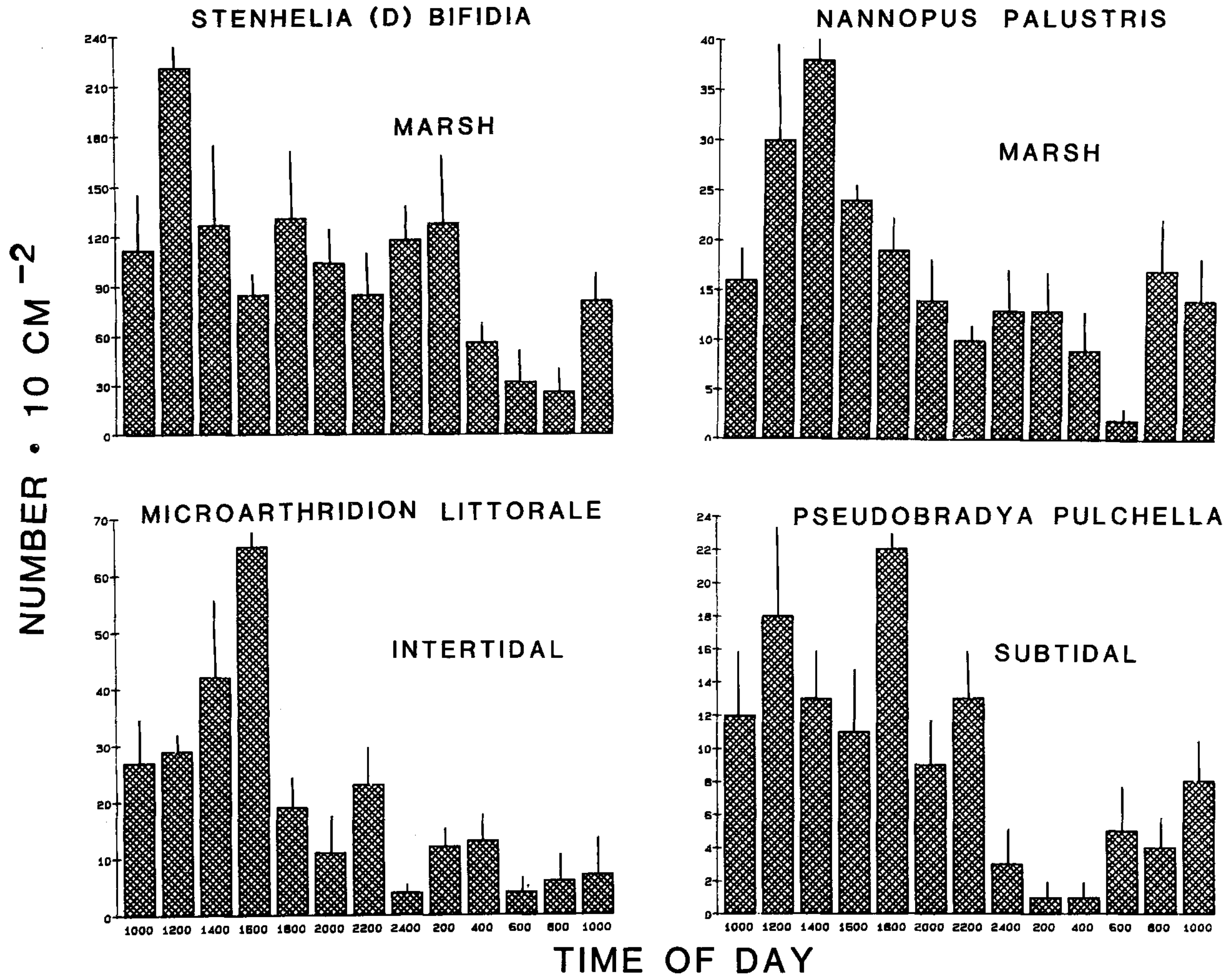

Fig. 5. Mean abundance (± SE) of 4 species over 24 hours. These 4 species are figured only for the sites where they were abundant.

Table 2. Summary of the results of 2-way ANOVA's testing the effects of light (vs. dark) and tide levels (high, falling, low, rising) on the abundance of copepods at each habitat. Only results significant at $p < 0.05$ are listed. For tide, LT = Low tide, HT = high tide; for light, L = light; D = dark. (* = a light × tide interaction at $p = 0.0115$, df = 4.94; ** = insufficient abundance).

Species	Marsh Light/Tide	Intertidal Light/Tide	Subtidal Light/Tide
S. (D.) bifidia		**	**
E. propinquum		L > D/LT > HT	L > D/
M. littorale	**		
N. palustris		**	**
H. coulli	**		L > D/LT > HT*
P. pulchella	**	**	L > D/
D. aegidius		**	**
P. wilsoni	**	**	
Total copepods	/LT > HT	/LT > HT	L > D/

(Table 2) and rarely were 'marker' species from one habitat displaced into another. While only one species, *Enhydrosoma propinquum*, occurred in abundance across the entire gradient, *Microarthridion littorale* was also regularly found at all 3 sites. *Halicyclops coulli*, a true epibenthic form, occupied both the intertidal and subtidal, but not the marsh (the $2 \cdot 10\,\mathrm{cm}^{-2}$ listed in Table 2 is probably an anomaly – see results). We would have predicted *H. coulli* to move with the tide due to its natant behavior, yet the ANOVA did not indicate a significant effect of tide in the intertidal (Table 2).

Light level appears to have had its greatest effect on the subtidal species. Four of the significant effects of light on abundance occurred in the subtidal and in every case, including the significant effect of light on the intertidal *Enhydrosoma* population, there was greater abundance in the light than in the dark. One would need to replicate this 24-hour study several times under all possible combinations of tide level and light to actually separate the effects of these factors in controlling copepod abundance. However, the higher abundances found subtidally during daylight suggest that factors related to water depth (clarity?) affect abundance in this particular habitat.

The four cases where there were more individuals at low tide than at high tide (Table 2) – but recall that neither low tide nor high tide abundance was different from flooding or ebbing tides – suggests there was little horizontal displacement or movement of these species along our sampling transect with the tide. Palmer & Brandt (1981) reported higher abundances at high and low tide than at rising or falling tides at an intertidal and a subtidal site approximately 100 m from ours over a single (12.5 h) tidal cycle. This was certainly not the case over the 2 ± tidal cycles we sampled. When a difference occurred, low tide abundance was always greater than high tide abundance. Although it is difficult to establish the existence of meaningful trends with so few data, it appears that nearly all species in each of the three sites underwent a significant decline in abundance during the study, reaching maximum abundance around the daytime low tide (Figs. 3,4 & 5). We doubt that this decline was caused by human disturbance or 'overfishing', as only a very small percentage of the sediment was removed from each site; The trend was not caused by differences in sorting efficiency, as all samples were sorted and counted at random. Nor was there any large difference in tidal levels during the study (Fig. 2). Until we repeat this work over a longer sampling interval, e.g. 48 h, we will not be able to discern the cause(s) of this apparent reduction in abundance.

Palmer (1980) reported that life history patterns of *Microarthridion littorale* differed between intertidal and subtidal sites in North Inlet and speculated that the varied life histories might have been due to differences in food quality and quantity, predator exposure and differential competitive pressures in the two areas. While this may be true, the apparent lack of movement between populations in the present study suggests that the individuals at each site do not interact strongly.

This labor intensive study of copepod distribution demonstrated the existence of distinct species assemblages in particular habitats. Changes in light and/or tide levels had little effect on the distribution and abundance of a particular species. We have identified 'marker' species which, if found in the gut contents of fish collected in the vicinity of the transect, should allow us to infer at which level on the tidal gradient (subhabitat) fish had been feeding. To fully understand the dynamics of a predator/prey system where the predator moves and cannot be observed while it feeds, basic data on the distribution of the prey are requisite. We are now better able to determine where fish predators may have fed by examining the species of meiobenthic copepods in guts at any one time. Furthermore, if one wants to estimate maximum abundance of a species, samples should probably be taken at low tide (as all practical marine meiofaunologists do anyway), since we found either no difference in abundance by tide or higher abundances at low tide (Table 2).

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