Diel patterns of active vertical migration in seagrass meiofauna

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ABSTRACT: Patterns of active vertical migration exhibited by sediment-associated meiofauna were examined in a subtropical seagrass meadow. Total numbers, species composition and percentage of sediment meiofauna found to migrate were examined during two 24 h studies. Large numbers ($> 20\,000\,h^{-1}\,m^{-2}$) of harpacticoid copepods representing a substantial proportion ($> 50\,\%$) of the total benthic harpacticoid community migrated from the sediment into the water column. Nineteen of 36 harpacticoid species identified migrated actively. Migration was greatest during nighttime. Results indicate the importance of vertical migration to benthic-pelagic interactions in shallow seagrass environments.

INTRODUCTION

Benthic invertebrates in the meiofaunal size range (63 to 500 μm, Coull & Bell 1979) occur regularly in the water column (e.g. Bell & Sherman 1980, Hagerman & Rieger 1981, Sibert 1981). The pelagic occurrence of these sediment-associated organisms may result from passive resuspension (current mediated erosion), active migration (behaviorally directed emergence), or a combination of both. Passive resuspension and active migration may involve meiofaunal behavior. Although meiofauna can be resuspended when current velocities exceed critical values, sediment surface activity may make organisms more susceptible to resuspension (Waters 1972). Recent laboratory experiments and field studies on meiofauna from estuarine mud flats suggest that a few taxa enter the water column only when resuspended by currents (Palmer 1984, Palmer & Gust 1985). In contrast, active vertical migration entails the 'swimming' of organisms into the water column and is distinctly different from passive resuspension, including resuspension of surficially active organisms. Active migration of predominantly macrofaunal taxa from a subtidal sand flat has been documented by Alldredge & King (1980). Other field studies have reported the emergence of macrofauna and meiofauna from sediments (Alldredge & King 1977, Porter & Porter 1977, Hobson & Chess 1979, Robichaux et al. 1981, Ohlhorst 1982, Youngbluth 1982), but the sampling design in each of these studies does not allow one to distinguish

between passive resuspension or active migration. However, Hicks (1986) has documented active emergence of phytal harpacticoids in a New Zealand seagrass bed.

In Tampa Bay, Florida (USA), meiofauna are found in a number of subhabitats within seagrass beds: uppermost sediment layers (as in estuarine mud flats), seagrass blade surfaces and water column. Combined densities of at least one meiofaunal taxon, harpacticoid copepods, from all 3 subhabitats rank among the highest reported in the world (Bell et al. 1984). The movement of meiofauna among sediment, blade and water column subhabitats and its effects on the community dynamics of fauna inhabiting shallow vegetated systems are unknown. This investigation was initiated to determine specifically if sediment-associated meiofauna in a Tampa Bay seagrass habitat actively move into the overlying water column. We asked: (1) What fraction of the meiobenthic community migrates actively from sediment to water column? (2) Is this fraction consistent on different dates? (3) Does a daily periodicity to meiobenthic migration exist?

MATERIAL AND METHODS

Samples were collected on 19–20 November 1981 and 16–17 April 1982 at a shallow subtidal seagrass *(Thalassia testudinum)* site located near the mouth of Tampa Bay, Florida, USA (27° 38′ N, 82° 42′ W). The

seagrass bed was bordered on the landward side by a fringe of the shoal grass *Halodule wrightii* and extended >100 m from the shore. All sampling was conducted in an area approximately 10 × 10 m, 30 m from shore in a dense stand of *T. testudinum*. Water depth varied between 0.5 to 2 m depending on tides and wind direction.

Actively migrating and nonmigrating meiofauna were collected using a cylindrical emergence trap (Fig. 1). The trap was designed to eliminate planktonic contamination and minimize mesh size problems
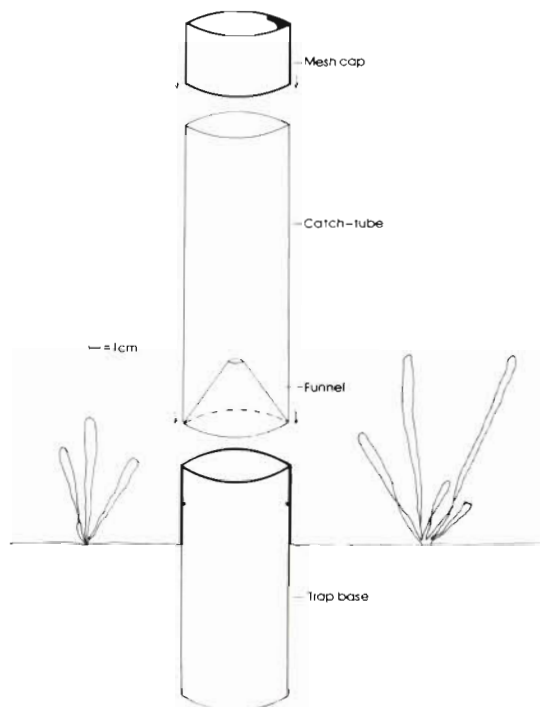

Fig. 1. Emergence trap employed in studies of 19–20 Nov 1981 and 16–17 Apr 1982 in Tampa Bay, Florida, USA. See text for description

(Youngbluth 1982). It consisted of 2 parts: a 10.2 cm diameter trap base (total area of 82 cm^2) of polyvinyl chloride 25 cm in length, and a clear acrylic catch-tube 10.1 cm in diameter and 30 cm in length. Each catch-tube had a translucent inverted funnel on one end and a removable, 63 μm mesh screen cap on the other. Traps were deployed by pushing the trap base approximately 15 cm into the sediment and then connecting the catch-tube. To avoid contamination the catch-tube funnel was corked and the catch-tube filled with seawater filtered through its mesh cap prior to placement. When the trap was in place, exchange of water between the trap and its surroundings occurred only through the mesh cap.

Organisms migrating at least 12 cm from the sediment or sediment-water interface through the inverted funnel were trapped in the catch-tube. The trap base and catch-tube restricted water flow by design so that organisms collected in the catch-tube had to have migrated actively. Previous observations that some meiofauna are more active on the sediment surface in the absence of currents (Palmer 1984) may indirectly suggest a behavioral connection between flow and an organism's probability of resuspension. However, surface activity has not been correlated to active migration or 'swimming' 12 cm, the distance required by our trap for an organism to be considered a migrator, into the water column. We do not suspect that our traps resulted in the stimulation of migration due to reduced flow conditions because many of the taxa sampled in traps have been observed in flow-through laboratory cultures actively swimming into the water column. Also, if a reduction in flow were the only factor stimulating migration within our traps then we would expect no difference in the percentage of migrating fauna during 24 h (see 'Results').

To determine the percentage of the sediment fauna which migrated, organisms remaining in the sediment within the trap base were subsampled. Three sediment subsamples were taken per trap in November and 2 sediment subsamples per trap in April using a 2.8 cm diameter syringe to a depth of 4.5 cm. One sediment subsample per trap base was processed completely after preliminary determination that ca 70 % of the adult harpacticoid species recorded from multiple subsamples within a trap base could be found in a single subsample.

Five emergence traps were haphazardly (not statistically random) positioned in the field between seagrass culms at the beginning of a sampling period and collected 6 h after placement. An *a posteriori* test, based on the coefficient of variation calculated from November's samples, indicated that 5 samples were adequate to detect differences in migration between sampling periods (e.g. Box 9.13, Sokal & Rohlf 1981). The length of a sampling period was chosen to maximize the number of organisms captured because earlier studies had shown relatively low numbers of meiofauna entering the water column on an hourly basis (Alldredge & King 1977, 1980, Robichaux et al. 1981). Differences in water chemistry between the water column inside and outside traps over the sampling period were minimized by the porous mesh cap which allowed water exchange between catch-tube and water column. Revsbech et al. (1980) found that in 5.4 cm diameter cores studied in the lab oxygen levels can become partially depleted in water immediately above the sediment, but even after 260 min of incubation in the dark oxygen was still present in the sediments. In our study, available data on dissolved oxygen concentrations, determined by Winkler titration of water over-

lying the sediment within traps, indicated that oxygen was available to sediment fauna (K. Walters unpubl.). Changes in other sediment ions within our traps should occur slowly (K. Fanning pers. comm.). After each sampling period traps were replaced in an undisturbed section of the seagrass bed to avoid resampling a trap base from which 2 to 3 sediment samples had been destructively taken.

Collections were made during 2 sampling periods in November (I [1200 to 1800 h], IV [0800 to 1400 h]) and 4 periods in April (I [1300 to 1900 h], II [1900 to 0100 h], III [0100 to 0700 h], IV [0700 to 1300 h]). These sampling periods were selected so that a period would bracket either sunset (I) or sunrise (III) on each date. Sampling periods approximately corresponded to dusk (I), nighttime (II), dawn (III) and daytime (IV). The moon was in its last quarter and clear weather conditions persisted on both sampling dates except briefly during Sampling Period I in November when a rapidly moving storm caused a premature reduction in daylight.

Twenty-nine catch-tube samples and 67 trap base subsamples were collected during the 2 sampling dates; one trap was lost during Period IV in November. All samples were preserved with 10 % formalin in the field and taxa retained on a 63 µm sieve were counted in the lab. Adult harpacticoid copepods were identified to species. Catch-tube samples which contained more than 500 harpacticoids were subsampled to facilitate taxonomic identification using the procedure of Sherman et al. (1984). More than 15 000 adult harpacticoids were identified.

Data were classified into 4 categories: migration (migrators = catch-tube organisms; nonmigrators = trap base organisms); period (I, II, III, IV); date (Nov, Apr); and dominant species (for harpacticoids only). The resulting contingency tables were analysed using a hierarchical loglinear model and the SPSSX (Nie 1983) package of statistical procedures. For theoretical and analytical descriptions see Bishop et al. (1975), Haberman (1978), Fienberg (1980); for biological applications see Sokal & Rohlf (1981), Whittam & Siegel-Causey (1981), Okamura (1984). Log-linear analyses were used because data consisted of counts classified into multidimensional contingency tables. Problems associated with heteroscedasticity, interpreting transformed data and the lack of independence between estimates of migration and nonmigration were avoided by using log-linear analyses (Haberman pers. comm.). All models analysed were corrected for missing periods (in November there are no Periods II and III) or missing samples (in November Period IV is missing data from one complete trap). Numbers of migrators in catch-tubes and nonmigrators in trap bases were summed separately to meet design requirements of the log-linear model (Bishop et al. 1975,

Haberman 1978, Fienberg 1980). In the absence of generally accepted procedures, summing of samples represents a practical approach to dealing with complex sampling designs (Fingleton 1984), as in this study.

RESULTS

Harpacticoid copepods numerically dominated the taxa which actively migrated. During times of increased migration (Periods I, II, III) harpacticoids were the most common migrating fauna and comprised more than 50 % of all individuals found in the water column (Fig. 2). Other meiofaunal and macrofaunal taxa were collected in the water column and included cyclopoid and calanoid copepods, amphipods, ostracods, barnacle nauplii, larval and adult polychaetes, and turbellarians. In November, polychaete larvae constituted between 8 and 22 % of all individuals migrating during Period I, but most macrofaunal taxa represented less than 1 % of either sediment or water column samples and were not considered further (Fig. 2). Gastropods, bivalves and oligochaetes were never found in the water column but occurred in sediment samples. Nematodes, the dominant sediment taxon, were a small fraction of the total migrating fauna (Fig. 2).

Active vertical migration of harpacticoid copepods was substantial. From 13 to 67 % of all benthic harpacticoids migrated into the water column (Table 1). In April, more than 60 % of all harpacticoid individuals within traps were found in the water column during each of Periods I, II, and III. No other taxon exhibited as large a percentage of its benthic population migrating vertically.

Adult harpacticoids exhibited both diel and sampling date differences in migration (Table 1). On both dates, differences in migration existed between Period IV and all other periods. In November, only 33 % of the adult harpacticoids migrated during Period I in comparison to 61 % for the same period in April. When the association between sampling date, period (I and IV), and numbers of migrating or nonmigrating adult harpacticoids was examined using the log-linear model, the 3-way interaction was highly significant (likelihood ratio $\chi^2 = 905.3$, df = 1, p < 0.0001). The significance of the 3-way interaction indicated that the association between any 2 variables was dependent on the specific level of the third variable (e.g. the association between migration and period may be dependent on the date when samples were taken). Examination of the parameter estimates for the log-linear model (Bishop et al. 1975, Haberman 1978, Fienberg 1980) suggested that sampling period had the most important effect on the migration of adult harpacticoids.
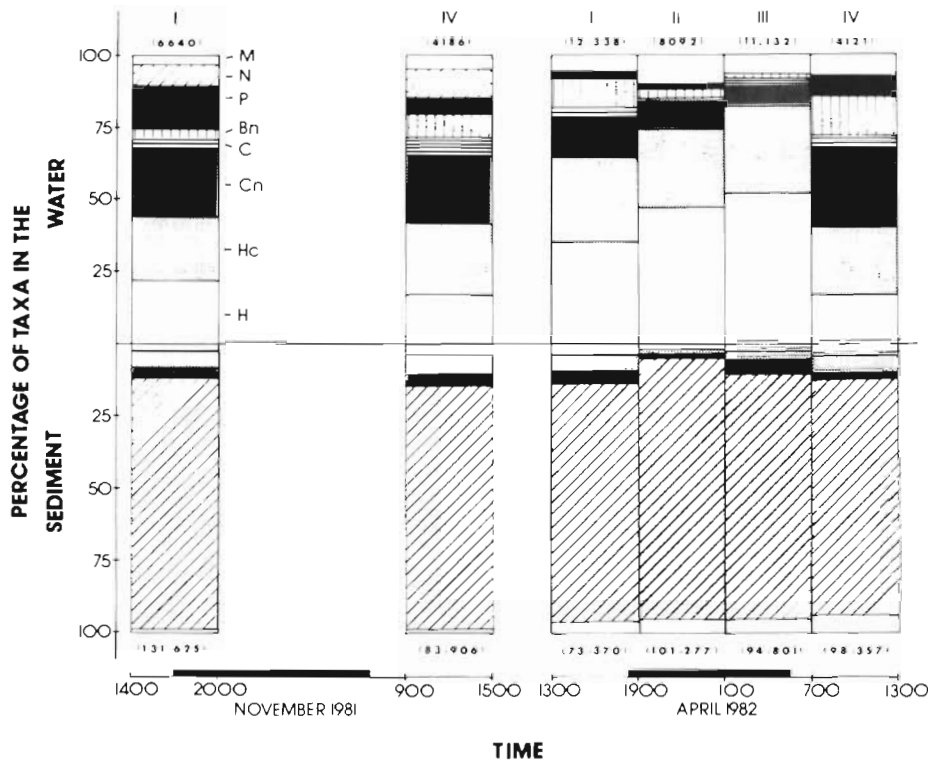
Fig. 2. Proprotional abundance for sediment and water-column taxa sampled in Nov 1981 and Apr 1982. Taxa representing less than 1 % of the total are combined into the miscellaneous category. Sunset and sunrise are represented as endpoints of the blackened time scale. H: harpacticoids; Hc: harpacticoid copepodites; Cn: copepod nauplii; C: cyclopoids; Bn: barnacle nauplii; P: polychaetes; N: nematodes; M: miscellaneous

Table 1. Total number (per 82 cm^2) and percent of adult harpacticoid copepods migrating from the bottom at different times of the day during 2 field studies at a shallow subtidal seagrass site near the mouth of Tampa Bay, Florida, USA

Date	Period	Time	Migration Migrators (catch-tube)	Migration Nonmigrators (trap base)	Percent migrating
19–20 Nov 1981	I	1200–1800	1473	2967	33
	IV	0800–1400	721	3271	18
16–17 Apr 1982	I	1300–1900	4318	2720	61
	II	1900–0100	3828	2277	63
	III	0100–0700	5772	2816	67
	IV	0700–1300	679	4678	13

Over twice the number of individuals, based on odds ratios (e.g. Nie 1983, p. 550), were likely to migrate at dusk compared to day on both dates.

To examine further the interaction between the emergence of harpacticoids and sampling period, individual 2-way log-linear analyses were run separately on each date (e.g. Sokal & Rohlf 1981, p. 749). Interaction between period and migration for adult harpacticoids was highly significant in both November (likelihood ratio χ^2 = 177.5, df = 1, p < 0.0001) and April (likelihood ratio χ^2 = 4993.7, df = 3, p < 0.0001). Interactions between period and migration were the result of increases in water column densities during Periods I, II, and III and reciprocal decreases in sediment densities during these periods. Periods I, II and III

all sampled the time between sunset and sunrise, and the pattern of migration contrasted strikingly with that of Period IV, the only complete daytime sampling period (Table 1). Since samples collected numbers of individuals moving into the water column over an entire 6 h period, it is impossible at this time to be more precise than to state that increased migration occurred at night. Further examination to determine when peak migration occurs, i.e. whether there are crepuscular maxima, will require modification of the sampling regime.

Thirty-six harpacticoid species from 15 families were identified and subsequently classified by their pattern of migration (Table 2). Five species were collected on only 1 of the 2 dates, usually in very low numbers

Table 2. Classification of seagrass harpacticoid species identified from November and April studies into 4 groups based on overall abundance and behavior. (Group 1 = rare species; Group 2 = nonmigrators; Group 3 = found only in water column; Group 4 = migrators) Within each group, species are listed in decreasing order of abundance on both dates

Group 1	Group 3
Diosaccid sp. D	Laophontid sp.
Diosaccid sp. E	Dactylopusoides sp.
Cyllindropsyllid sp.	Tisbe sp.
Zaus sp.	
Porcellidium sp.	
Group 2	**Group 4**
Enhydrosoma herrerai	Ectinosomatid spp.
Nitocra sp.	Paralaophonte sp.
Leptomesochra sp.	Heterolaophonte sp.
Mesochra sp.	Mesochra pygmea
Tegastid sp.	Diosaccid sp. B
Dactylopodella sp.	Dactylopodia tisboides
Paramphiascella	Diosaccid sp. A
sirbonica	Zausodes arenicolus
Cletoid sp.	Longipedia helgolandica
Thalestrid sp.	Laophonte cornuta
	Harpacticus sp.
	Halectinosoma sp.
	Robertsonia sp.
	Ameirid spp.
	Paradactylopodia brevicornis
	Metis holothuriae
	Diosaccid sp. C
	Lourinia armata
	Scottolana canadensis

(Group 1). Examination of these rare species provided little insight into the migration process because of their extremely low densities. Nine species (Group 2) were found only in sediment samples on one or both dates. This group included burrowing forms which might not be morphologically adapted for migration (Bell et al. 1986b). Even though Mesochra sp. and Tegastid sp. were found exclusively in the sediment on one date, both migrated in large numbers on the other sampling date. A small group of species was found only in water-column samples (Group 3). At least 2 members of this group (Tisbe sp., Laophontid sp.) are normally epibenthic or found on seagrass blades and are not sampled effectively by sediment cores (Bell et al. 1986). The dominant group (Group 4), 19 species, was found in water column and sediment samples on one or both dates.

Sediment and water column densitites for the 6 dominant harpacticoid species of Group 4 (>65% of all harpacticoids) sampled in November or April are shown in Fig. 3 and 4. Many of the dominant species in November were also dominant in April, but there were differences in their patterns of emergence on the 2 dates. Both Heterolaophonte sp. and Paralaophonte sp. exhibited greater migration into the water column du-

ring Period I in April when compared to November (Fig. 3 & 4). Mesochra pygmea and Dactylopodia tisboides did not exhibit a major difference between dates in the numbers that enter the water column and demonstrated a consistent pattern of migration (high dusk and low daytime water-column densities) on both dates (Fig. 3 & 4). The differences in migration for these 4 dominant species resulted in a highly significant 4-way interaction when species (Heterolaophonte sp., Paralaophonte sp., M. pygmea, D. tisboides), date (Nov, Apr), period (I, IV), and migration were examined in a hierarchical log-linear model (likelihood ratio χ^2 = 26.7, df = 3, p < 0.0005). Species, period and date interacted to determine the overall observed pattern of migration.

A strong interaction between migration and period existed for the 6 dominant species when each date was examined separately. The log-linear analyses which examined this interaction between species, period, and the numbers of individuals of each species entering the water column again had highly significant 3-way interactions: November (Periods I, IV) – likelihood ratio χ^2 = 198.1, df = 5, p < 0.0001; April (Periods I, II,
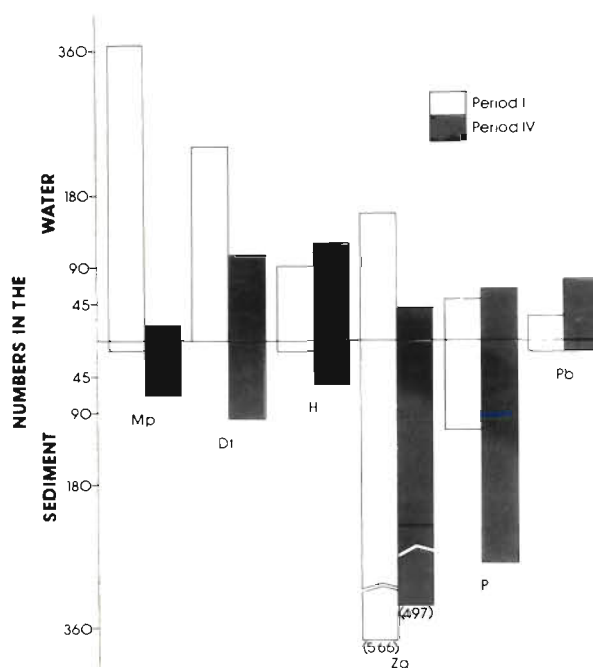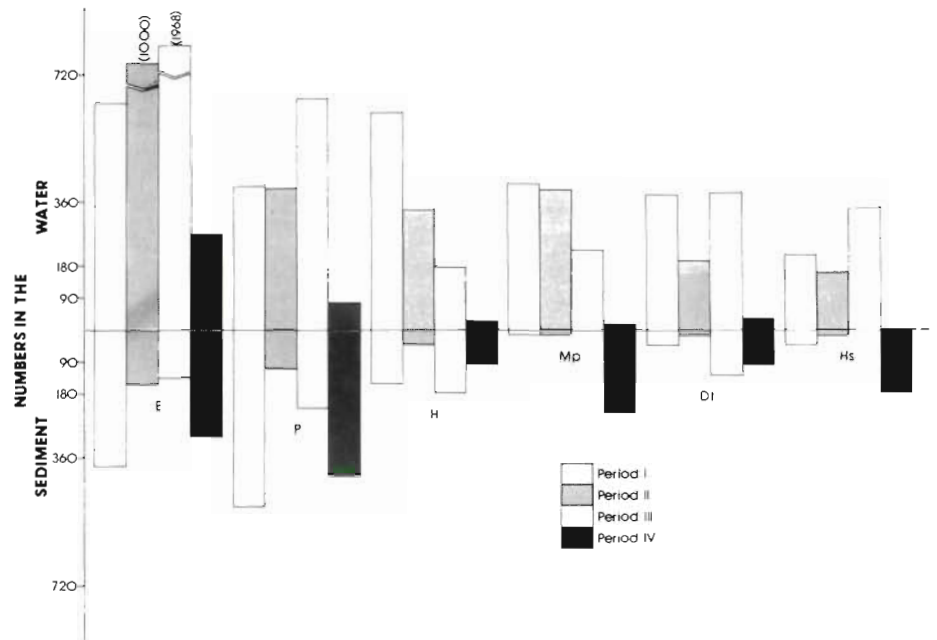

Fig. 3. Total numbers of sediment and water-column individuals during Period I (n = 5) and Period IV (n = 4) for the 6 dominant harpacticoid species sampled 19–20 November 1981. To correspond with loglinear analyses conducted, total numbers represent the sum of samples collected during a period. Lack of 1 sample in Period IV does not qualitatively change the observed relationship between Periods I and IV. Mp: Mesochra pygmea; Dt: Dactylopodia tisboides; H: Heterolaophonte sp.; Za: Zausodes arenicolus; P: Paralaophonte sp.; Pb: Paradactylopodia brevicornis

Fig. 4. Total numbers (n = 5) of sediment and water-column individuals during Periods I, II, III and IV for the 6 dominant harpacticoid species sampled on 16–17 April 1982. To correspond to analyses conducted, total numbers represent the sum of samples collected during a period. E: Ectinosomatid spp.; P: *Paralaophonte* sp.; H: *Heterolaophonte* sp.; Mp: Mesochra pygmea; Dt: *Dactylopodia tisboides*; Hs: *Harpacticus* sp.

III, IV) – likelihood ratio χ^2 = 1153.1, df = 15, p < 0.0001). In November, *Mesochra pygmea* and *Dactylopodia tisboides* were likely to migrate 4 to 6 times (odds ratio) more at dusk than during the day. *Zausodes arenicolus* did not contribute significantly to the overall 3-way interaction due to large sediment numbers during Periods I and IV (Fig. 3).

Species migration in April was more complicated than in November. While the dominant 6 species were likely to migrate 1.5 to 7 times more (odds ratio) during Periods I, II and III compared to Period IV, other effects being equal (Haberman 1978), each species exhibited a different preference within these 3 periods. Ectinosomatids were more likely to migrate during Period III, *Heterolaophonte* sp. during Period II and *Dactylopodia tisboides* during all 3 periods (Fig. 4). The migration of any of the 6 dominant species on either date was strongly associated with sampling period.

DISCUSSION

Our study shows that active vertical migration is a common behavior for a number of benthic and epibenthic meiofaunal taxa, especially harpacticoid copepods, resident in a subtidal seagrass bed. The number of migrating harpacticoids alone exceeded, often by 4 orders of magnitude, values reported in similar studies (Table 3). The results listed in Table 3 are even more striking, given that our estimates of total movement into the water column may be low. Organisms which migrate prior to trap placement and remain in the water column and organisms which may be passively resuspended are not sampled by our trap design. Alldredge & King (1980), in a comparison between emergence and reentry traps, found that emergence samplers may underestimate the numbers of migrating organisms. Estimates of the number of meiofauna

Table 3. Summary of studies which identified harpacticoid migration using traps sealed to the sediment surface

Study	Habitat	Mean number of migrating harpacticoids (no h^{-1} m^{-2})	Rank abundance of harpacticoids	Diel patterns detected
Alldredge & King (1977)	Coral sand (tropical)	15	3	No
Hobson & Chess (1979)	Sand (tropical)	2	3	Yes
Robichaux et al (1981)	Seagrass, sand (tropical)	5	1	No
Youngbluth (1982)	Sand (tropical)	170	1	No
Present study	Seagrass (subtropical)	22 635	1	Yes

Table 4. Determination of the potential carbon movement from sediments to water column. Body lengths represent the size range for harpacticoid copepods from Group 4 (Table 2). Dry weights are determined from Fig. 2 of Goodman (1980). Estimates of migration are from daytime samples for minimum and highest nighttime samples for maximum values. Carbon is assumed to be 40 % of dry weight. Maximum migration is considered to occur only 10 h d^{-1} to estimate yearly carbon movement

	Body length (mm)	Dry weight (µg)	Numbers migrating (h^{-1}m^{-2})	Rate of carbon movement from sediments to water column	
				(g h^{-1}m^{-2})	(g yr^{-1}m^{-2})
Minimum	0.4	0.3	2.7×10^3	2.8×10^{-4}	2.4
Maximum	1.2	11.4	2.3×10^4	1.0×10^{-1}	3.8×10^2

entering the water column from our study are therefore likely to be conservative.

Active migration of seagrass meiofauna in our studies (see also Hicks 1986) appears to contrast with the nonmigratory behavior of estuarine salt marsh meiofauna (Fleeger et al. 1984, Palmer 1984, Palmer & Gust 1985). Differences in faunal behavior between intertidal salt marsh systems and subtidal seagrass systems are probably due to a number of factors including hydrodynamic regimes and species composition. Behavior of salt marsh harpacticoids may be dominated by tidal and current effects (Palmer & Brandt 1981, Fleeger et al. 1984, Palmer 1984, Palmer & Gust 1985). This is not unexpected given that intertidal areas experience daily tidal flushing and currents often exceed critical erosion velocities. Reduced flow velocities caused by submerged vegetation (Fonseca et al. 1983, Madsen & Warncke 1983) and the generally slack tidal currents in the Tampa Bay seagrass bed, as indicated by the dissolving rate of salt tablets and dye studies (K. Walters unpubl.), may result in active migration being a more common behavior in seagrass habitats. Abundances of resuspended harpacticoids in salt marsh systems, although difficult to measure, are often extremely low, representing less than 1 % of the total sediment fauna, and characteristically dominated by a few copepod species (Fleeger et al. 1984, Palmer & Gust 1985). Species taxonomically similar to those resuspended in estuarine systems (Fleeger et al. 1984, Palmer & Gust 1985) were represented in our study by a small group of nonmigrating species (Table 2, Group 2). Species normally resuspended by currents in other studies showed no evidence of 'swimming' when flow was reduced in our study. The majority of seagrass harpacticoid species found to migrate (Table 2, Group 4) were either not represented or rarely occurred in studies of resuspension. Morphological studies of phytal, migrating and sediment dwelling harpacticoids indicate a distinct difference among these groups of species (Bell et al. 1987). The apparent difference in behavior between salt marsh and seagrass systems therefore is explained by differences in species com-

position and in the physical characteristics between intertidal salt marsh and subtidal seagrass habitats.

Effects of light on migration of marine organisms are well documented (Forward 1976, Forward et al. 1984, Stearns & Forward 1984) but light does not appear to be the sole stimulus for the migrations observed in our study. Large numbers of harpacticoids in the water column during nighttime Periods II and III in April (Table 1) suggest that factors other than light intensity are important in determining the migration of these seagrass organisms. Detection of differences in migration between our November and April dates could have been confounded by the premature reduction in light intensity during a Period I storm in November. However, available data do not allow for determination of the importance of changes in light levels as a proximal cause of harpacticoid migration.

While it may by convenient to consider benthic and pelagic environments as separate entities, our study shows that they continually share components. In shallow coastal seagrass beds where high densities of harpacticoids were found to migrate, vertically migrating fauna may move a significant amount of energy from the benthic to the pelagic realm. Using a typical size range for migrating harpacticoids (Table 2, Group 4) an estimate of the minimum and maximum movement of carbon into the water column can be obtained (Table 4). If the minimum estimate (daytime migration) for the rate of carbon movement is assumed to be consistant over 1 yr (migration remains constant) then 60 to 90 % of typical harpacticoid sediment production reported from other benthic habitats (Hicks & Coull 1983) can enter the pelagic environment. This energy may then be transferred to early developmental stages of fish and shrimp which frequent temperate and tropical seagrass beds and prey extensively on harpacticoids (Duka 1978, Hicks & Coull 1983, Leber 1983). In addition, vertically migrating organisms may augment physical processes and carry nutrients from the sediments to the water column, or vice versa, which may be utilized by resident bacteria and phytoplankton.

Vertical migration provides a mechanism for interac-

tion of both benthic and pelagic shallow-water systems and may directly play a role in structuring both environments. Diel migrations by a large percentage of the sediment fauna may not only introduce new members into the pelagic community that potentially interact with resident populations, but may also produce a haphazard reassortment of the benthic community. These possibilities should be addressed when proposing explanations for the structuring of seagrass assemblages. We suggest that previous views on the importance of vertical migrations to meiofaunal populations in shallow water areas in general need reassessment, given the extremely large numbers of fauna found diurnally migrating in our study.

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