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Environmental Factors Affecting Nocturnal Migrations of Macrobenthos

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ENVIRONMENTAL FACTORS AFFECTING NOCTURNAL MIGRATIONS OF MACROBENTHOS

by

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ABSTRACT

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C. Timothy Morris
Old Dominion University, 1986
Director: Dr. Daniel M. Dauer

Nocturnally dispersing macrobenthic invertebrates of the Lafayette River, Norfolk, Virginia were collected from September 4 to October 4, 1982 to determine environmental factors affecting migrations. A total of 55 taxa were identified from 325 surface and bottom nocturnal plankton tows. Peracaridan crustaceans were the dominant (99.0% of the total density) group collected. Six of the commonly collected species showed a significant ($P<0.05$) difference in vertical distribution. Nocturnal migrations of seven species were associated with tidal periodicity and many migrating species were significantly ($P<0.05$) less abundant during moonlit periods regardless of cloud cover. The significance of dispersal by postlarval macrobenthos is the ability to rapidly recolonize disturbed benthic habitats.

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INTRODUCTION

Nocturnal migrations of macrobenthic invertebrates (commonly referred to as demersal zooplankton) into the water column are well known. Much speculation concerning nocturnal movements exists; however, the activity is still poorly understood. These nightly migrations occur in a variety of marine and estuarine habitats (see Hammer, 1981; Stepien and Brusca, 1985, for examples and a list of references).

Several hypotheses have been formulated to explain nocturnal migrations of demersal zooplankton (see Alldredge and King, 1980; Dauer _et_ _al_., 1982; Hammer, 1981). Potential advantages include (1) feeding, (2) reproduction, (3) avoidance of nocturnal predators foraging in the benthos, and (4) dispersal to more favorable locations. Dispersal by postlarval macrobenthos may be an important mode for recolonization of disturbed benthic habitats (Bell and Devlin, 1983; Dauer, 1984; Dauer and Simon, 1976; Dobbs and Vozarik, 1983). Potential disadvantages include (1) predation in the water column and (2) dispersal to unfavorable habitats. Obviously, the potential advantages must supersede the disadvantages since this phenomenon is prevalent (Hammer, 1981).

A number of nocturnal migratory patterns have been described. Recently, workers have begun to relate nocturnal migratory patterns of demersal zooplankton and environmental components (e.g. Alldredge and King, 1980; Ohlhorst, 1982). Alldredge and King (1980), Dauer _et_ _al_. (1982), and Hammer (1981) have demonstrated that the migrations of demersal zooplankton are primarily nocturnal. For example, Dauer et al. (1982) reported that 99.8% of all individuals were collected nocturnally. Thus, the principal environmental factor cueing emergence from the benthos is the absence of sunlight. In addition to sunlight, lunar phase or moonlight appears to influence the nocturnal migrations of some demersal zooplankton (Alldredge and King, 1980). However, the evidence is not compelling. A myriad of biotic and abiotic factors (operating separately or synergistically) probably influence the migration of each individual or species.

The purpose of this study was to determine environmental factors affecting the nocturnal movements of macrobenthos. My objectives were (1) to quantify dispersing macrobenthic invertebrates, (2) to assess the vertical distribution of each species, and (3) to relate environmental factors to peaks of migratory activity of each species.

MATERIALS AND METHODS

Study Area

The Lafayette River, Norfolk, Virginia, is a small tributary of the lower Chesapeake Bay (Blair *et al*., 1976). The Lafayette River is one of four main branches of the Elizabeth River and the mouth of the estuary is ca. two miles south of Hampton Roads. Some characteristics of the Lafayette River are listed in Table 1. Typically, the upper reaches of the estuary are oligohaline whereas the lower portions are mesohaline. The vertical salinity profile is nearly homogeneous during periods of normal rainfall (Blair *et al*., 1976). Thus, the Lafayette River conforms to Pritchard's type III (well-mixed) category of estuarine classification.

Table 1. Some characteristics of the Lafayette River (modified from Blair *et al*., 1976).

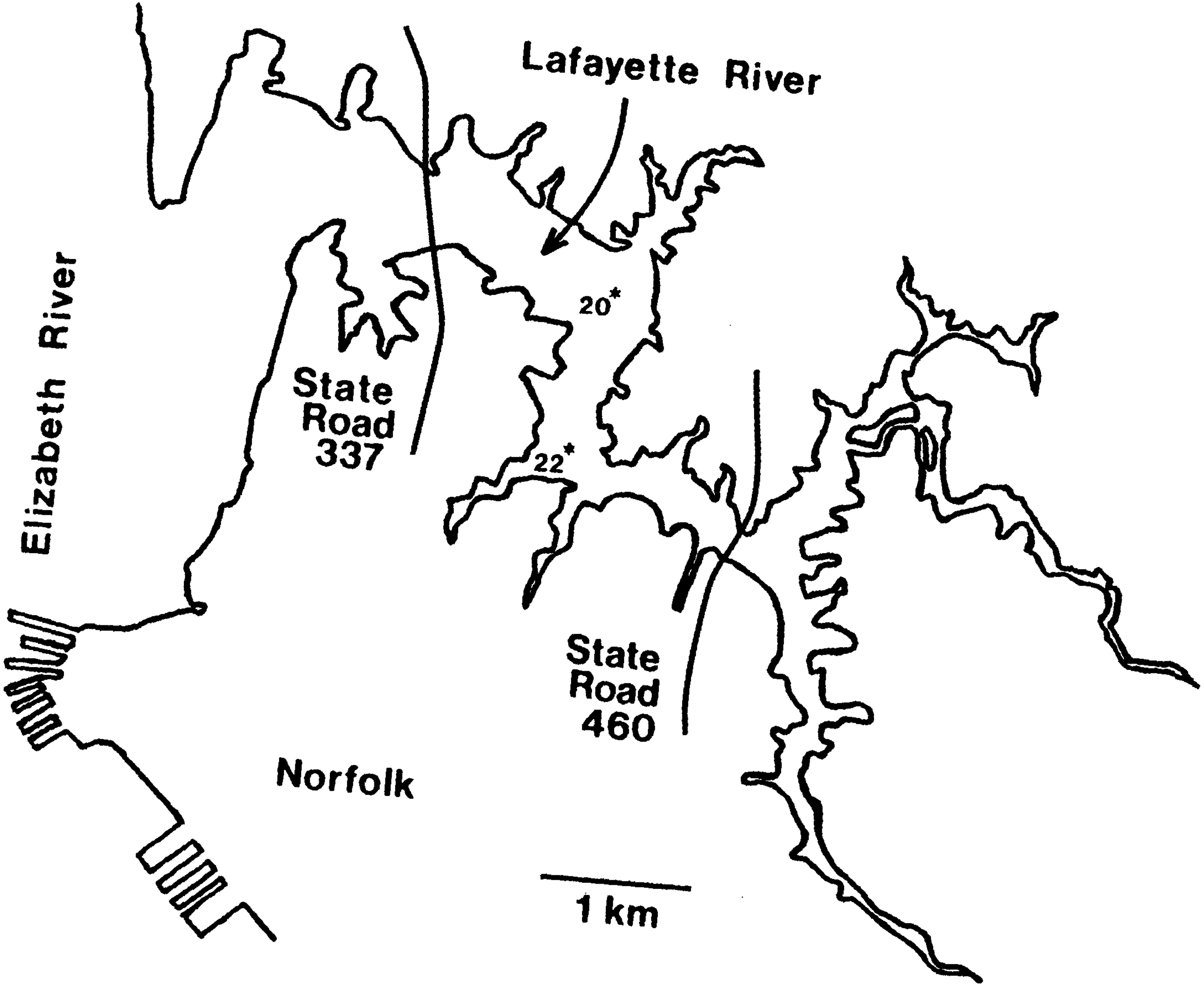
Parameter	Measurement
Channel Length	11 km
Maximum Width	800 m
Maximum Depth Below MLW	5.9 m
Mean Depth Below MLW	1.2 m
Mean Tidal Range	0.8 m
Maximum Current Velocity	30.5 cm/s

Sampling Procedure

Migrating macrobenthic invertebrates of the Lafayette River were collected at night with two 0.5 m plankton nets (351 and 363 mesh) from September 4 to October 4, 1982. Samples were collected from a small boat along a transect between navigational markers 20 and 22 (Fig. 1). The bottom contour along the transect was uniform and the depth was ca. 3 m below MLW. For easier maneuverability, tows were taken with the direction of current flow at an estimated speed of 2.5 knots. One net was positioned at the water's surface and the other ca. 0.5 m from the bottom. Flowmeters with low-speed rotors were attached to each net to quantify the volume of water sampled. Usually, ten hourly samples were taken every other night. Sampling commenced at dusk and concluded near dawn.

Tidal range, low and high tide times, moon rise and set times, and lunar phase (i.e. new, full, first quarter, and third quarter) were obtained from NOAA tidal charts for each sampling night. Tidal data were not corrected for winds. For each collection, sampling time, surface water salinity and temperature, tidal height, surface and bottom current velocity, and relative cloud cover (i.e. clear, partly cloudy, and cloudy) were recorded. Current velocity was not measured on the first night of sampling. Salinity and temperature were measured with a Beckman salinometer. Tidal height was calculated from a computer program written by N. A. Chamberlain. This calculation utilized sampling time, low and high tide times, and tidal range data. A flowmeter with a low-speed rotor was used to estimate surface and bottom current velocity. The flowmeter was attached 0.5 m from the bottom of a weighted line and suspended in the water column for 90 s. Current velocity was calculated using the formula provided in the General Oceanics, Inc. flowmeter instruction manual. Because lowering and raising the flowmeter to the bottom during current measurements increases the number of revolutions or counts, a correction factor for

Figure 1. Location of sampling transect in the Lafayette River (modified from Dauer _et al_., 1982). * = navigational marker.



Lafayette River
Elizabeth River
20*
22*
State Road 337
State Road 460
Norfolk
1 km

each bottom measurement was calculated. This was done by lowering the flowmeter to the bottom and immediately raising it a second time and subtracting the correction factor from the bottom current measurement. Salinity, temperature, and current velocity measurements were taken at navigational marker 22 before each tow.

To eliminate scyphozoans (*Chrysaora quinquecirrha* and *Aurelia aurita*) and ctenophores (*Mnemiopsis leidyi*) from the samples, the contents of each tow were transferred to a 4.76 mm sieve and rinsed with riverwater. The effluent (sample) and large macroinvertebrates retained on the sieve were transferred to geological sand sample bags. The samples were preserved in 20 l buckets containing a 5% formalin-Rose Bengal riverwater solution and transported to the laboratory.

In the laboratory, samples were sieved (0.5 mm mesh) and all macrobenthic invertebrates were removed (except mysids), identified, enumerated, and stored in 1 dram vials of 70% isopropanol-deionized water solution. Because mysids were so numerous, a Folsom plankton splitter was used to estimate their abundance. The abundance of all macrobenthos was converted to individuals per unit volume of water sampled.

Statistical Procedure

Only those species that occurred in at least 5% of the samples (a total of 19 species) were used for data analysis. Four plankton tows were omitted from data analysis because the flowmeter attached to the plankton net malfunctioned during sampling. A t-test was used to assess the vertical distribution of each species. For those species (i.e. 6 of the 19 species shown in Table 4) that showed a significant ($P<0.05$) difference in vertical distribution, only surface or bottom data were used for further data analysis (see below). Both surface and bottom data were considered for all other species.

Environmental factors affecting the nocturnal migrations of macrobenthos were determined by (1) qualitative data synthesis, (2) univariate statistical analysis, and (3) multivariate statistical analysis. A Statistical Analysis System (SAS) plotting procedure was used to determine if there was a relationship between the abundance of commonly collected species and the tidal cycle. Each sample or plankton tow was rearranged with reference to the time of high tide so that all surface and bottom tows conformed to a single tidal cycle. For three species (i.e. flood tide dominant - *Leptocheirus plumulosus*; ebb tide dominants - *Eteone heteropoda* and *Parahesione luteola*), only flood or ebb tide data were considered for further data analysis (see below). Both flood and ebb tide data were used for all other species.

A t-test was used to determine if there was a difference between the abundance of each species and the presence or absence of moonlight for each level of cloud cover. A one-way ANOVA was used to determine if there was a difference between the abundance of commonly collected species and lunar phase. The ANOVA utilized Duncan's multiple range test to test for significant ($P<0.05$) differences between groups. Spearman's correlation coefficients were used to correlate the density of each species to current velocity, tidal height, tidal range, water temperature, and water salinity.

A Principal Component Analysis (PCA) was used to determine if there was a relationship between the eight environmental variables (e.g. current velocity, tidal height, tidal range, water salinity and temperature, moonlight, lunar phase, and cloud cover) and the nocturnal migrations of macrobenthos. This was performed by regressing the principal component scores of the first three principal axes of the environmental data and the abundance of each species. To examine linear as well as non-linear relationships, PCA's were performed on both transformed and untransformed environmental variables.

Two tidal cycle variables (e.g. Tidal height and current velocity) were transformed because these variables were curvilinear over time. Tidal height was transformed by subtracting all flood tide height measurements from a value of 2.1 m. The value 2.1 m was chosen because this value was approximately twice the greatest tidal height measurement. Current velocity was transformed by substracting current measurements taken between slack low water and peak flood tide from a value of 40 cm/s. Likewise, current measurements taken between peak ebb tide and slack low water were subtracted from a value of 50 cm/s. The values 40 cm/s and 50 cm/s were chosen because these values were approximately twice the greatest flood and ebb tide current measurements, respectively. Finally, flood and ebb tides were differenciated by multiplying flood currents by +1 and ebb currents by -1.

RESULTS

Descriptive Statistics

A total of 55 taxa were identified from 325 nocturnal plankton tows (Table 2). Peracaridan crustaceans were the dominant (99.0% of the total density) group collected. Table 3 shows the mean density and percentage of the total density of commonly collected species. Mysids (*Mysidopsis bigelowi* and *Neomysis americana*) were the most numerous (87.6% of the total abundance) group collected. Only mysids were collected in every tow. Amphipods (*Corophium lacustre*, *Gammarus* spp., *Gitanopsis* sp., *Leptocheirus plumulosus*, *Melita nitida*, *Paracaprella tenuis*, and *Stenothoe minuta*) were the next most numerous (9.8% of the total density) group collected.

Vertical Distribution

Six taxa showed a significant difference in vertical distribution (Table 4). *Palaemonetes pugio* was significantly more abundant in surface plankton tows while *Corophium lacustre*, *Leptocheirus plumulosus*, *Mysidopsis bigelowi*, *Paracaprella tenuis*, and *Parahesione luteola* were significantly more numerous in bottom tows.

Tidal Stage

Only seven species showed easily identifiable migratory patterns associated with the tidal cycle (Figs. 2-5). Four principal migratory patterns were identified: (1) dispersal during flood tides, (2) dispersal during ebb tides, (3) dispersal during both ebb and flood tides, and (4) swimming activity correlated with high tides.

Table 2. List of macrobenthos collected from 325 nocturnal plankton tows.

- Cnidaria
  - Anemone sp.
- Polychaeta
  - *Autolytus* sp. stolons
  - Cirratulidae sp.
  - *Eteone heteropoda* Hartman
  - *Glycera americana* Leidy
  - *Leitoscoloplos fragilis* (Verrill)
  - Maldanidae sp.
  - *Nereis succinea* (Frey & Leuckart)
  - *Nereis succinea* heteronereids
  - *Parahesione luteola* (Webster)
  - *Paraprionospio pinnata* (Ehlers)
  - *Podarkeopsis levifuscina* Perkins
  - Sabellidae sp.
  - Spionidae sp.
  - *Streblospio benedicti* Webster
- Oligochaeta
  - Oligochaeta sp.
- Bivalvia
  - *Gemma gemma* (Totten)
  - *Macoma* sp.
- Pycnogonida
  - *Callipallene brevirostris* (Johnston)
- Mysidacea
  - *Mysidopsis bigelowi* Tattersall
  - *Neomysis americana* (Smith)
- Cumacea
  - *Cyclaspis varians* Calman
  - *Leucon americanus* Zimmer
  - *Oxyurostylis smithi* Calman
- Tanaidacea
  - *Leptochelia savignyi* (Krøyer)
- Isopoda
  - *Cassidinidea lunifrons* (Richardson)
  - *Cyathura polita* (Stimpson)
  - *Edotea triloba* (Say)
  - *Idotea balthica* (Pallas)
  - *Ptilanthura tenuis* Harger
  - *Sphaeroma quadridentatum* (Say)
- Amphipoda
  - *Ampelisca abdita* Mills
  - *Ampelisca vadorum* Mills
  - *Cerapus tubularis* Say
  - Corophiidae sp.
  - *Corophium lacustre* Vanhoffen
  - *Cymadusa compta* (Smith)
  - *Elasmopus laevis* Smith
  - *Gammarus* spp.*
  - *Gitanopsis* sp.
  - *Leptocheirus plumulosus* Shoemaker
  - *Melita dentata* (Krøyer)
  - *Melita nitida* Smith
  - *Monoculodes edwardsi* Holmes
  - *Orchestia grillus* Bosc
  - *Paracaprella tenuis* Mayer
  - *Parapleustes aestuarius* Watling & Maurer
  - *Protohaustorius* cf. *deichmannae* Bousfield
  - *Stenothoe minuta* Holmes
- Decapoda
  - *Callinectes sapidus* Rathbun
  - *Crangon septemspinosa* (Say)
  - *Libinia dubia* Milne Edwards
  - *Ogyrides alphaerostris* (Kingsley)
  - *Palaemonetes intermedius* Holthuis
  - *Palaemonetes pugio* Holthuis

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* *Gammarus palustris* Bousfield and *Mucrogammarus mucronatus* (Say) were not differenciated

Table 3. Mean density (individuals/1000 m^3) and percentage of the total density of those species occurring in at least 5% of the samples.

Species	Mean Density	Percentage of the Total Density
Eteone heteropoda	0.92	0.03
Nereis succinea atokes	1.93	0.07
Nereis succinea epitokes	1.45	0.05
Parahesione luteola	17.4	0.61
Macoma sp.	1.15	0.04
Mysid spp.*	1470	9.67
Mysidopsis bigelowi	1180	33.9
Neomysis americana	1530	44.0
Cyclaspis varians	20.6	0.73
Cyathura polita	0.92	0.03
Edotea triloba	25.3	0.90
Corophium lacustre	54.6	1.93
Gammarus spp.	80.6	2.85
Gitanopsis sp.	0.48	0.02
Leptocheirus plumulosus	110	3.88
Melita nitida	23.0	0.81
Paracaprella tenuis	3.74	0.13
Stenothoe minuta	4.06	0.14
Ogyrides alphaerostris	1.05	0.04
Palaemonetes pugio	0.83	0.03
rarer taxa	0.10	0.14

* *M. bigelowi* and *N. americana* were counted together for the first three sampling nights

Table 4. Differences in the vertical distribution of those taxa occurring in at least 5% of the samples. Shown are surface and bottom mean densities (individuals/1000 m^3) for each species. * = significantly different ($P<0.05$), ** = ($P<0.01$), *** = ($P<0.001$).

Species	Mean Surface Density	Mean Bottom Density
Eteone heteropoda	1.00	0.85
Nereis succinea atokes	2.11	1.75
Nereis succinea epitokes	1.75	1.19
Parahesione luteola	3.43	31.7***
Macoma sp.	0.93	1.36
Mysidopsis bigelowi	829	1520**
Neomysis americana	1470	1610
Cyclaspis varians	20.4	21.0
Cyathura polita	0.90	0.83
Edotea triloba	20.8	29.1
Corophium lacustre	40.6	68.4***
Gammarus spp.	90.4	71.4
Gitanopsis sp.	0.47	0.51
Leptocheirus plumulosus	37.1	183*
Melita nitida	21.2	25.0
Paracaprella tenuis	1.62	5.85***
Stenothoe minuta	3.70	4.35
Ogyrides alphaerostris	0.66	1.46
Palaemonetes pugio	1.64***	0.03

Figure 2. Dispersal of Leptocheirus plumulosus during flood tides from bottom nocturnal plankton tows. Shown are the mean density (individuals/m^3) and one standard error relative to the tidal cycle (hours). HT = high tide hour, LT = approximate low tide hour.

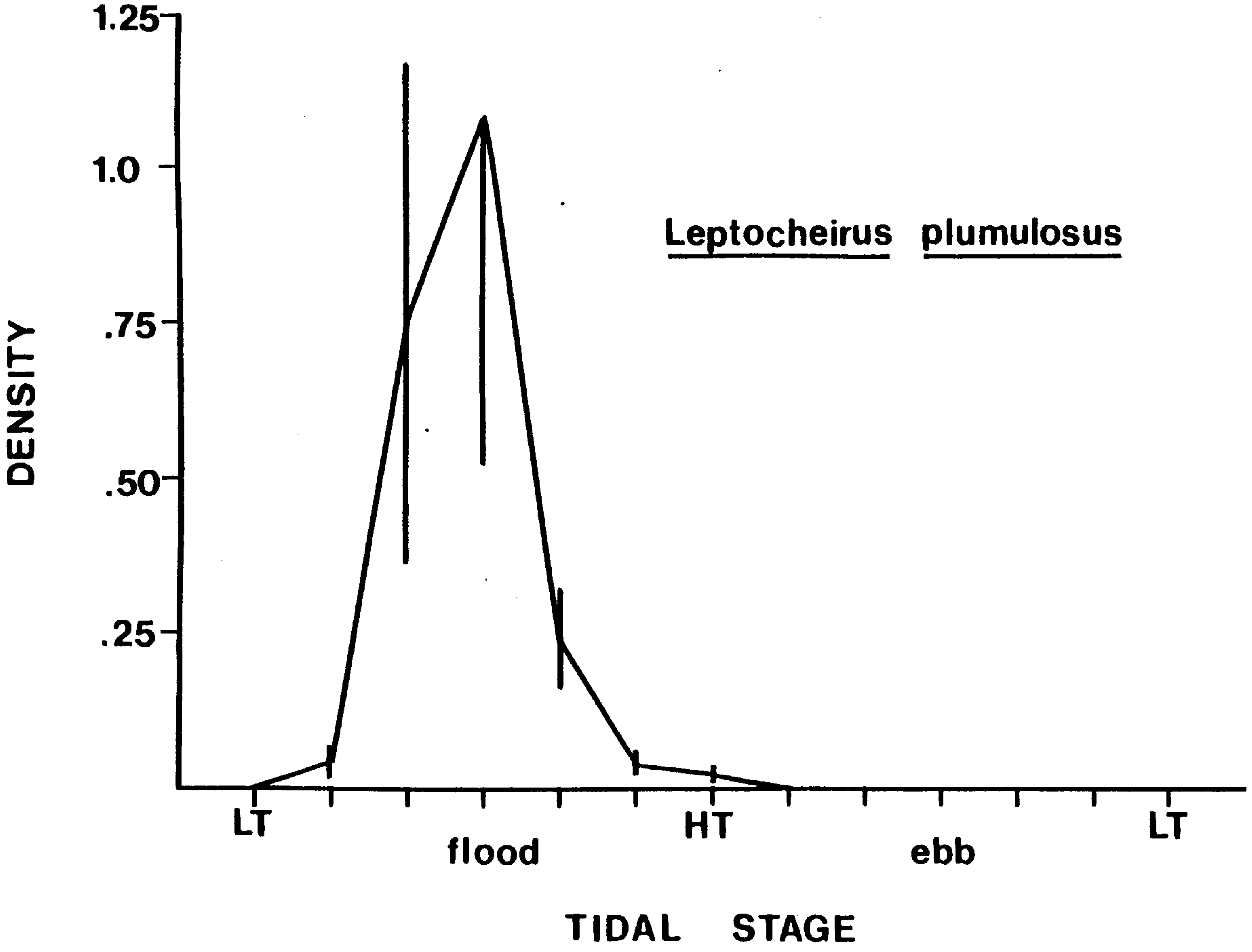

1.25
1.0
.75
.50
.25
DENSITY
Leptocheirus plumulosus
LT
flood
HT
ebb
LT
TIDAL STAGE

Figure 3. Movements of _Parahesione luteola_ during ebb tides from bottom nocturnal plankton tows. See explanation of Fig. 2.

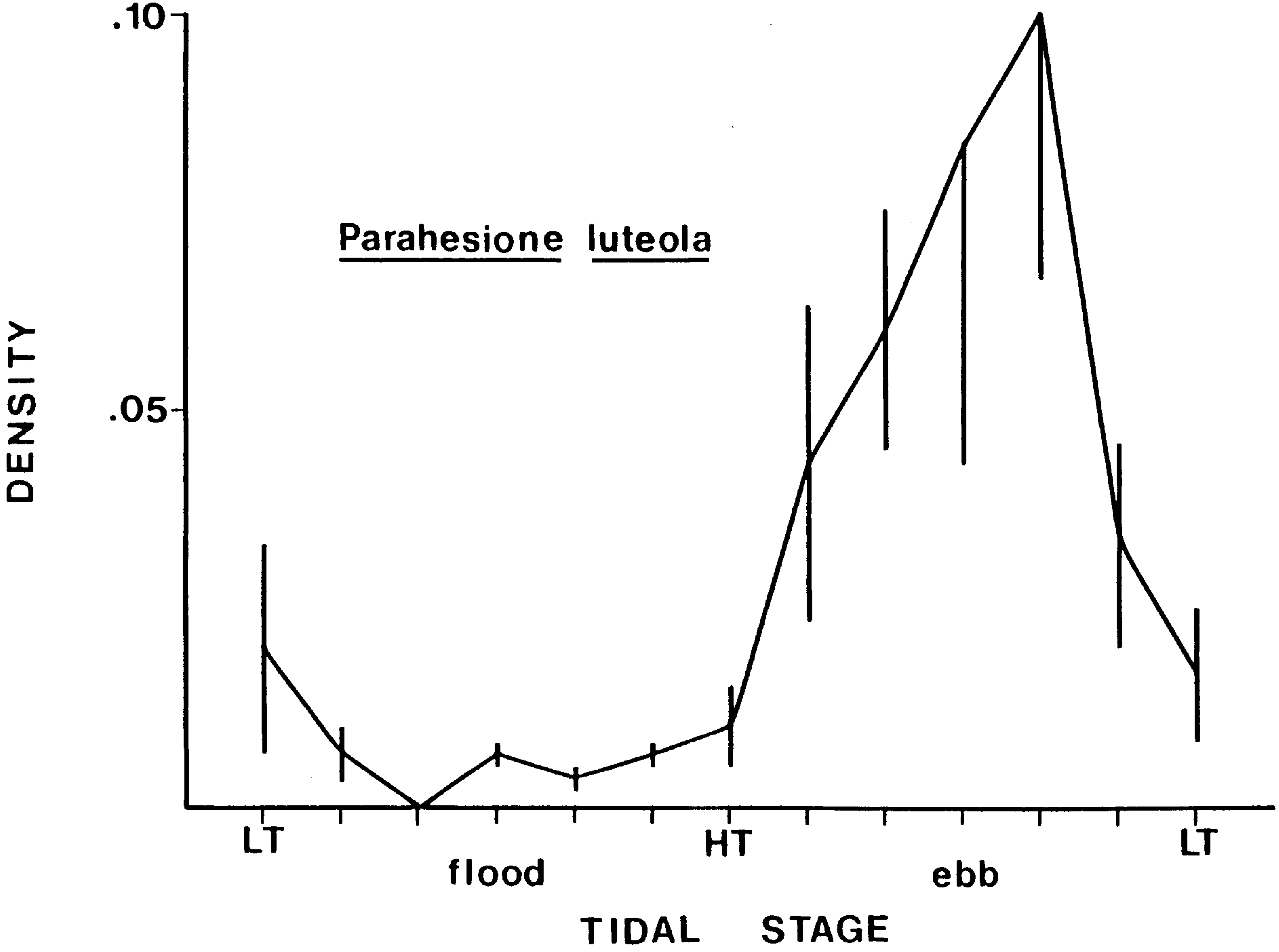

Parahesione luteola
DENSITY
.10
.05
LT
flood
HT
ebb
LT
TIDAL STAGE

Figure 4. Dispersal of *Mysidopsis bigelowi* during both ebb and flood tides from bottom nocturnal plankton tows. See explanation of Fig. 2.

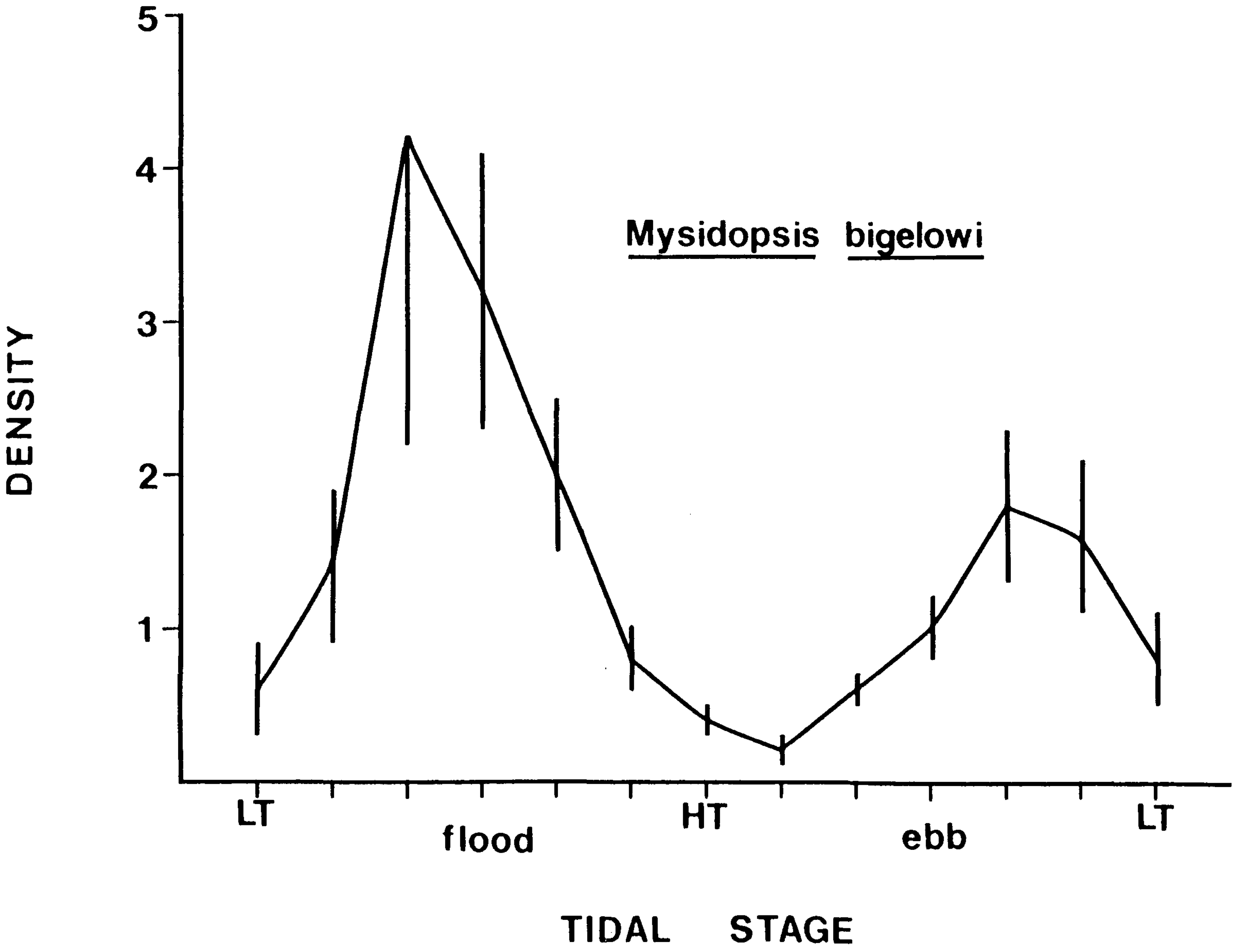
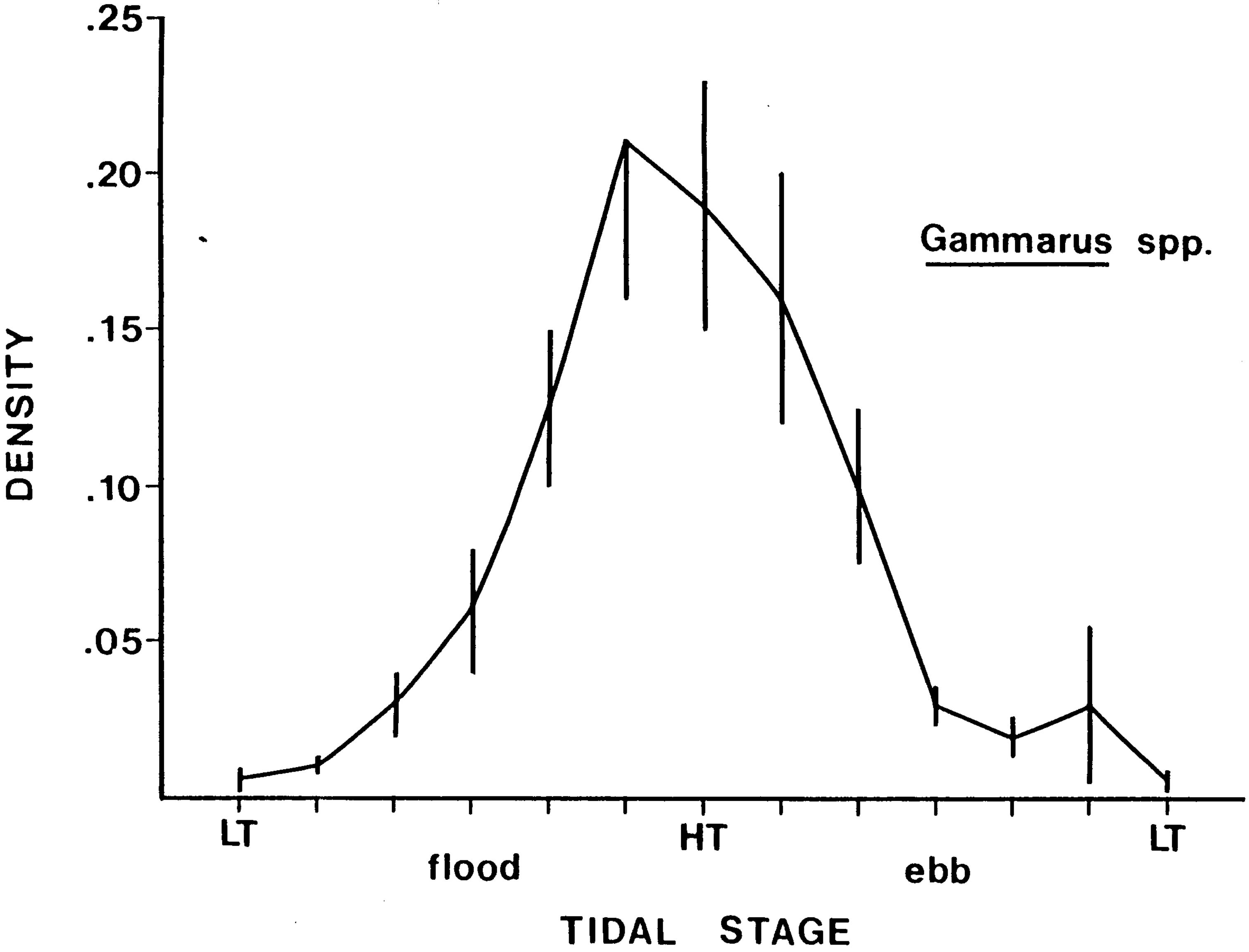

Mysidopsis bigelowi
DENSITY
5
4
3
2
1
LT
flood
HT
ebb
LT
TIDAL STAGE

Figure 5. Peak swimming activity of *Gammarus* spp. near high tide from both surface and bottom nocturnal plankton tows. See explanation of Fig. 2.


Gammarus spp.
DENSITY
.25
.20
.15
.10
.05
LT
flood
HT
ebb
LT
TIDAL STAGE

Leptocheirus plumulosus was collected exclusively on flood tides (Fig. 2) indicating upstream transport. Conversely, *Parahesione luteola* and *Eteone heteropoda* (not illustrated) were collected primarily on ebb tides (Fig. 3) indicating downstream transport. *Mysidopsis bigelowi* showed peaks in swimming activity on both flood (large peak) and ebb (small peak) tides (Fig. 4) indicating transport on both tidal stages. Swimming activity of *Gammarus* spp., *Melita nitida* (not illustrated), and *Stenothoe minuta* (not illustrated) were correlated with the time of high tide (Fig. 5). The migratory pattern of *M. nitida* differed slightly from the patterns of *Gammarus* spp. and *S. minuta*. The high tide swimming activity of *M. nitida* was depressed.

Lunar Phase

Most demersal zooplankton showed significantly greater or lesser densities on one or more lunar phase (Table 5). For example, *Cyathura polita*, *Cyclaspis varians*, *Macoma* sp., *Mysidopsis bigelowi*, and *Palaemonetes pugio* were significantly more numerous during the new moon phase while *Corophium lacustre* and *Parahesione luteola* were significantly less abundant during the full moon phase (see Table 5). Three species (*Gitanopsis* sp., *Leptocheirus plumulosus*, and *Paracaprella tenuis*) showed no significant difference in density during the lunar cycle. Two species were not collected during a particular lunar phase (i.e. *Eteone heteropoda* during the third quarter phase and *P. pugio* during the first quarter phase).

Moonlight

Many migrating macrobenthos were significantly more abundant during periods when there was no moonlight regardless of cloud cover (Table 6). Only *Gammarus* spp. and *Nereis succinea* were significantly more numerous

Table 5. Differences between lunar phase and the mean density (individuals/100 m^3) of those species occurring in at least 5% of the samples. Means with a different script are significantly different ($P<0.05$) using Duncan's multiple range test.

Species	Lunar Phase			
	New Moon	First Quarter	Full Moon	Third Quarter
Eteone heteropoda#	0.03a	0.49b	0.14a	0a
Nereis succinea atokes	0.28b	0.07a	0.19ab	0.18ab
Nereis succinea epitokes	0.15a	0.05a	0.11a	0.31b
Parahesione luteola$	9.21b	6.80b	1.01a	6.67b
Macoma sp.	0.28b	0.04a	0.07a	0.04a
Mysidopsis bigelowi+	259b	125a	87.6a	84.1a
Neomysis americana	199b	217b	75.5a	115a
Cyclaspis varians	3.81c	1.34ab	1.06a	2.20b
Cyathura polita	0.24b	0.01a	0.04a	0.06a
Edotea triloba	4.32b	1.30a	1.49a	3.23b
Corophium lacustre+	9.38b	7.47b	4.12a	8.18b
Gammarus spp.	8.26b	3.26a	8.80b	11.0b
Gitanopsis sp.	0.03a	0.07a	0.04a	0.07a
Leptocheirus plumulosus@	51.9a	9.86a	46.6a	8.49a
Melita nitida	3.18b	0.52a	1.78a	3.84b
Paracaprella tenuis+	0.97a	0.35a	0.30a	0.82a
Stenothoe minuta	0.62b	0.31ab	0.21a	0.59b
Ogyrides alphaerostris	0.12a	0.05a	0.04a	0.27b
Palaemonetes pugio&	0.43b	0a	0.05a	0.15a

# only ebb tide abundances were considered in the analysis
$ only bottom and ebb tide abundances were used
+ only bottom abundances were used
@ only bottom and flood tide abundances were used
& only surface abundances were used

Table 6. Differences between the mean density (individuals/1000 m^3) of those species occurring in at least 5% of the samples and the presence or absence of moonlight relative to cloud cover. * = significantly different ($P<0.05$), ** = ($P<0.01$), *** = ($P<0.001$). See Table 5 for explanation of footnotes.

Species	Clear		Partly Cloudy		Cloudy	
	No Moon	Moonlit	No Moon	Moonlit	No Moon	Moonlit
Eteone heteropoda#	0.81	2.58	0	0.52	0.66	0.75
Nereis succinea atokes	0.63	2.31***	4.93**	0.38	1.58	0
Nereis succinea epitokes	2.59	1.84	0	0.25	0.54	0
Parahesione luteola$	140**	23.9	49.1	27.7	21.7	17.2
Macoma sp.	0.93	0.76	3.97*	0.21	0.90	0
Mysidopsis bigelowi+	1680*	1000	3520*	527	1280**	346
Neomysis americana	1610**	868	2520*	1140	2470***	411
Cyclaspis varians	24.8**	12.6	49.5***	9.09	22.4***	3.07
Cyathura polita	1.43*	0.04	3.79	0.40	0.59	0
Edotea triloba	36.1**	16.7	56.8***	12.4	16.5***	3.44
Corophium lacustre+	82.2*	60.5	110*	24.0	61.1	42.0
Gammarus spp.	49.6	115***	103**	25.0	54.6**	7.39
Gitanopsis sp.	0.70	0.38	1.28	0	0	0
Leptocheirus plumulosus@	182	433	922	14.9	86.8	97.6
Melita nitida	28.1	27.7	26.2*	6.54	9.78	2.73
Paracaprella tenuis+	6.82	3.06	18.2*	1.72	4.07	3.23
Stenothoe minuta	5.07	3.95	5.61	1.59	3.61**	0
Ogyrides alphaerostris	1.36	1.25	1.04	0.65	0.32	0
Palaemonetes pugio&	2.62	0.95	4.46	0	0.38	0

during cloudless, moonlit hours. Six taxa (*Eteone heteropoda*, *Gitanopsis* sp., *Leptocheirus plumulosus*, *Nereis succinea* heteronereids, *Ogyrides alphaerostris*, and *Palaemonetes pugio*) showed no significant difference in density.

Water Mass Properties

Some descriptive statistics of the measured environmental variables are presented in Table 7. There were numerous significant correlations between the environmental variables and the abundance of commonly collected species (Table 8). Four species were positively correlated with current velocity indicating greater abundances on flood and/or ebb tides. Four species were negatively correlated with current velocity indicating greater abundances during slack tides. Of the seven species with abundances significantly correlated with tidal height, five were positive indicating greater abundances at high tides. Five of seven species were positively correlated with tidal range indicating greater abundances on spring tides. Most species were positively correlated with water temperature and/or salinity. Only *Gitanopsis* sp. was not significantly correlated to any of the variables.

As predicted, most species that showed easily identifiable migratory Spatterns (Figs. 2-5) were significantly correlated to current velocity or tidal height. For example, flood and/or ebb tide dominants (*Leptocheirus plumulosus*, *Mysidopsis bigelowi*, and *Parahesione luteola*) were positively correlated with current speed. Species that showed peaks in swimming acitivity near the time of high tide (*Gammarus* spp., *Melita nitida*, and *Stenothoe minuta*) were positively correlated with tidal height. Only *Eteone heteropoda* was not significantly correlated to current velocity as would be expected.

Table 7. Some descriptive statistics of the measured environmental variables.

Variable	Mean	Standard Error	Range	Maximum	Minimum
surface current (cm/s)	9.5	0.6	32.9	32.9	0
bottom current (cm/s)	5.1	0.5	21.7	21.7	0
tidal height (m)	0.49	0.02	1.10	1.07	-0.03
tidal range (m)	0.79	0.01	0.55	1.04	0.49
temperature (°C)	23.7	0.1	5.2	26.6	21.4
salinity (o/oo)	19.6	0.1	5.5	23.5	18.0

Table 8. Spearman's correlation coefficients showing the relationship between measured environmental variables and the abundance of those species occurring in at least 5% of the samples. Vel = current velocity, Hth = tidal height, Ran = tidal range, Tem = water temperature, and Sal = water salinity. * = significantly different from zero (P<0.05), ** = (P<0.01), *** = (P<0.001). See Table 5 for explanation of footnotes.

Species	Environmental Variables				
	Vel	Hth	Ran	Tem	Sal
Eteone heteropoda#	.07	-.09	-.15*	-.21**	-.22**
Nereis succinea atokes	.03	.19***	.12*	.07	.03
Nereis succinea epitokes	.17**	.02	.01	.23***	.02
Parahesione luteola$	.34**	.07	.09	.32**	.47***
Macoma sp.	.06	.01	.21***	.09	.10
Mysidopsis bigelowi+	.30***	-.23**	.14	.28**	.17*
Neomysis americana	.008	-.004	-.17**	.23***	.24***
Cyclaspis varians	-.19**	.06	.002	.22***	.34***
Cyathura polita	-.03	-.16**	.08	.19***	.10
Edotea triloba	-.03	.008	.11*	.34***	.36***
Corophium lacustre+	-.02	-.12	-.08	.17*	.29***
Gammarus spp.	-.14*	.63***	-.04	.12*	.28***
Gitanopsis sp.	-.08	-.01	-.08	.008	.005
Leptocheirus plumulosus@	.49***	-.18	.11	.09	-.08
Melita nitida	-.15**	.41***	.08	.31***	.28***
Paracaprella tenuis+	-.07	-.02	.16*	.10	.06
Stenothoe minuta	-.18**	.29***	-.04	.11*	.26***
Ogyrides alphaerostris	.10	.05	.01	.15**	.07
Palaemonetes pugio&	-.04	.18*	.22**	.22**	.24**

Principal Component Analysis

The factor scores of the first three principal component axes of the untransformed and transformed environmental variables were not correlated with the abundance of commonly collected species. It was concluded that the eight environmental variables in combination have no effect upon the nocturnal migrations of macrobenthos. Principal components 1, 2, and 3 of the untransformed variables explained 27.0%, 22.0%, and 13.0%, respectively, of the variation in the environmental data. Principal components 1, 2, and 3 of the transformed variables explained 26.4%, 19.9%, and 17.9%, respectively, of the variation.

DISCUSSION

Factors Affecting Dispersal

The swimming activity of a number of marine and estuarine benthic invertebrates are known to be rhythmic with the tidal cycle (e.g. Dauer *et al.*, 1980; Dieleman, 1977, 1979; Isaac and Jarvis, 1973; Morgan, 1965). Laboratory experiments indicate that hydrostatic pressure changes associated with the tidal cycle may synchronize the endogenous tidal rhythms in these organisms. However, the mechanism by which marine invertebrates detect small changes in hydrostatic pressure is unknown (Morgan, 1984). These pressure sensitive organisms utilize tidal currents for transport during different seasons. For example, the annual migrations of the estuarine polychaete, *Scolecolepides viridis* and amphipods, *Gammarus chevreuxi* and *G. zaddachi* are necessary for successful downstream reproduction (i.e. fertilization and early development of these species requires higher salinities) and upstream recruitment (Dauer *et al.*, 1980; Dieleman, 1977, 1979). Similar nocturnal migratory patterns were identified in this study (see Figs. 2-5) and suggest that these migrating species may be able to perceive and respond to tidal pressure changes. Furthermore, the nightly peaks in swimming activity of *Gammarus* spp., *Melita nitida*, and *Stenothoe minuta* (see Fig. 5) of this study were identical to the nocturnal migratory patterns of *G. chevreuxi* and *G. zaddachi* described by Dieleman (1977, 1979). Possibly, these patterns represent a part of the species' annual migratory cycle.

Alldredge and King (1980) showed that several species of migrating amphipods and isopods and total demersal zooplankton were negatively affected by moonlight. They suggested that certain demersal zooplankton, especially larger species, avoid moonlit periods when predation from visually feeding predators (fish) in the water column may be increased. Smaller species did not avoid moonlight and may be small enough to escape predator detection. A similar pattern of moonlight avoidance was observed during this study (see Table 6). Moveover, the pattern was repeated during sampling periods when moonlight was obstructed by cloud cover and suggests that this behavior was endogenous. Ohlhorst (1982) uncovered no such relationship between nocturnal migrations of demersal zooplankton and lunar phase or moonlight.

Substrate disturbances due to tides, waves, storms, etc. may also cause nocturnal migrations of macrobenthos (Dauer et al., 1982; Dobbs and Vozarik, 1983; Grant, 1980). Disturbance related migrations can be active or passive. The nocturnal prevalence of passively migrating macrobenthos seems contradictory. In other words, passive migrants should be just as common during the day as at night. However, diurnal differences in the activity of macrobenthos may explain this discrepancy. For example, Grant (1980) suggested that two haustoriid amphipod species were more active in surface sediments at night. Increased nocturnal activity near the substrate surface in high energy benthic habitats exposes these organisms to a greater risk of displacement via tidal current erosion. If displacement is likely, it would be advantageous for haustoriids (as well as other macrobenthos) to be more active near the substrate surface at night when predation from visually feeding predators in the water column is minimized (Grant, 1980).

The effects of planktonic predators such as the scyphozoans and ctenophores collected during this study upon the nocturnal migrations of macrobenthos are unknown. Densities of scyphomedusae and ctenophores appeared to vary during the night (i.e. ctenophores were prevalent around the high tide hours and scyphozoans were generally abundant throughout the night except during the high tide hours), but they were not quantified. Dauer _et al_. (1982) suggested that the seasonal migrations of some demersal zooplankton may be affected by scyphomedusae and ctenophores. They reported that the majority of polychaetes (species with relatively poorer powers of swimming and more likely to be captured by predators) were least abundant during portions of the year when scyphozoans and ctenophores were abundant. In contrast, amphipods (species with good swimming abilities and better able to avoid predators) were abundant during the summer months when predatory jellyfish and comb jellies were present. During this study, several _Chrysaora quinquecirrha_ were collected which contained partly digested _Nereis succinea_ heteronereids within their gastric pouches.

Dispersal of Peracaridans

The prevalence of nocturnally migrating peracaridan crustaceans has been well documented. Peracaridans may be actively dispersing for a number of reasons. Firstly, peracaridans may enter the water column to feed. Predatory mysids probably migrate up in the water column to feed upon plankton and possibly, other demersal zooplankton (Alldredge and King, 1980). In an experimental study using radioactive isotopes to label prey species, Smith _et al_. (1979) showed that some estuarine and coral reef demersal zooplankton (including amphipods and cumaceans) fed upon zooplankton. The experimental and observational study of Stepien and Brusca (1985) showed that adult kelp bed fishes were attacked and killed by nocturnal swarms of biting isopods and ostracods. They also reported the irregular presence of a lysianassid amphipod during the isopod attacks. However, the amphipods did not attack the fish, but appeared to feed on mucus and scales dislodged from the attacked fish.

Secondly, many tubiculous peracaridans enter the water column to reproduce or search for mates (Borowsky, 1983). He described two types of reproductive behavior: (1) synchronous swimming or swarming (known only to occur in two amphipods, *Ampelisca abdita* and *A. vadorum*) and (2) asynchronous swimming. During swarming events, both sexes enter the water column simultaneously to reproduce. Such events appear to be initiated by certain environmental factors (e.g. moonlight and lunar periodicity). Many polychaetes are known to exhibit this type of reproductive behavior (Schroeder and Hermans, 1975). Nevertheless, the factors cueing swarming, for both peracaridans and polychaetes, are poorly understood. During asynchronous swimming, only one sex (usually sexually mature males) leaves its tube to search for a mate. There is no single pulse of reproductive activity and swimming is not initiated by some external factor.

Thirdly, peracaridans may enter the water column to molt. Anger and Valentin (1976) observed the cumacean *Diastylis rathkei* to swim in the water only during ecdysis. They suggested that this is a behavioral response to avoid nocturnal benthic predators during a vulnerable portion of the organism's life cycle. Finally, emigration may be an important component of Peracarida ecology (Dauer *et al.*, 1982; Grant, 1980). Since all peracaridans have direct development, local populations can escalate. Thus, emigration may function to lessen density dependent interactions.

General Comments

The nightly swimming activity of macrobenthos was highly variable (i.e. note the magnitudes of the standard errors of the mean in Figs. 2-5). Ohlhorst (1982) observed such variation in nocturnal activity of Jamaican coral reef demersal zooplankton. She suggested that nocturnal migratory patterns may not be duplicated when many nights are examined. Although the magnitude of peak swimming activity varied nightly, the nocturnal migratory patterns of some species identified during this study (Figs. 2-5) were repeated.

Alldredge and King (1980) suggested that most demersal zooplankton swim near the bottom, rarely venturing far into the water column. Several studies using plankton nets (e.g. Dauer _et al._, 1980, 1982; Dean, 1978a, 1978b; Graham and Creaser, 1978; Robertson and Howard, 1978; Williams and Bynum, 1972; Williams and Porter, 1971; Williams, 1972a, 1972b; this study) have collected a multitude of migrating macrobenthos in surface waters. Additionally, this study and the study by Dauer _et al_. (1982) detected few significant ($P<0.05$) differences in vertical distribution of the major taxa collected. Thus, contrary to Alldredge and King's (1980) conclusion, many migrating macrobenthic invertebrates are capable of swimming considerable distances (at least several meters) up into the water column. Based on the vertical distribution results of this study (see Table 4), it was not possible to make any generalizations about the swimming abilities (poor vs. good) of migrating macrobenthos.

The occurrence of juvenile *Libinia dubia* (a total of 33 individuals) in nocturnal plankton tows was surprising. However, reports of this species association with scyphozoans have been documented (see Williams, 1984, p. 317). Thus, it is dubious that the spider crabs were actively dispersing since the scyphozoans, *Chrysaora quinquecirrha* and *Aurelia aurita*, were abundant throughout the study. No specimens of *L. dubia* were observed "riding" scyphomedusae.

CONCLUSIONS

As other studies have documented, peracaridan crustaceans were the most common group of dispersing macrobenthos. Although differences in vertical distribution were detected, the results did not indicate that "poor" or "good swimmers" were stratified in the water column. The present study showed that certain environmental variables (e.g. tidal periodicity and moonlight) appear to influence dispersal behavior of some demersal zooplankton. The contradictive results (PCA vs. univariate statistics and nocturnal migratory patterns) are perplexing. Possibly, statistics appropriate for these data do not exist. Because the nocturnal movements of demersal zooplankton are well known, many macrobenthic invertebrates are no longer considered sedentary (non-swimming) organisms. The importance of dispersal by macrobenthos is the potential to rapidly recolonize disturbed benthic habitats (Bell and Devlin, 1983; Dauer, 1984; Dauer and Simon, 1976; Dobbs and Vozarik, 1983; see Santos and Simon, 1980, for contrasting conclusion).

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