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NOCTURNAL AND TIDAL VERTICAL MIGRATIONS OF "BENTHIC" CRUSTACEANS IN AN ESTUARINE SYSTEM WITH DIURNAL TIDES

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ABSTRACT: Two field studies involving periodic sampling of the surface waters of the upper reaches of the Fowl River estuary in southwestern Alabama were completed to describe temporal changes in the densities of selected species of crustaceans larger than 505 μm. Regardless of tidal phase, triplicate 5-min surface tows collected very few crustaceans during the day, while nighttime zooplankton samples showed much higher densities of the amphipods *Gammarus tigrinus, Corophium lacustre, Grandidierella bonnieroides*, the isopod *Munna reynoldsi*, the cumacean *Almyracuma proximoculi* and the mysids *Taphromysis* spp. These results strongly indicate nocturnal vertical migration by crustaceans that are traditionally considered benthic. In addition, these species showed significantly higher densities near the water surface during nocturnal flood tides than during nocturnal ebb tides, indicating tidal vertical migration. These crustaceans are reported to inhabit low-salinity areas, and a transect along the length of this estuary showed relatively higher densities of these crustaceans in the lower-salinity waters upstream than in the higher-salinity waters downstream. While the adaptive value of vertical migration for an otherwise benthic organism is not clear, the nocturnal and tidal timing of such a migration appears to provide these oligohaline-mesohaline crustaceans with a behavioral mechanism that generally retains them in the upper reaches of the estuary with minimal exposure to visual predation in the water column.
[Keywords: *diurnal migration; crustaceans; tidal migration*]

Unlike deep lakes and offshore, oceanic environments, estuaries and coastal regions are shallow. This spatial closeness between the water surface and the physical bottom gives a swimming organism an opportunity to move quickly between the benthos and the entire overlying water column. Despite increasing evidence of vertical shuttling on short time scales (hours) (*e.g.* Fage, 1933; Watkin, 1941; Jansson and Kallander, 1968; Hughes, 1969; Anger and Valentin, 1976; Alldredge and King, 1980; Hiroki, 1980; Wooldridge and Erasmus, 1980; Dauer *et al.*, 1982; Macquart-Moulin, 1984, 1985; Hicks, 1986; Van Duyn-Henderson and Lasenby, 1986), shallow-water species have traditionally been classified as either pelagic or benthic.

For oligohaline-mesohaline organisms found in the lower-salinity, upper reaches of estuaries, vertical movement into and out of the water column must be precisely timed to avoid horizontal transport into higher-salinity waters downstream. Such vertical movement must also be precisely timed to minimize exposure to visual predation by fish in the water column.

The purposes of this research were (1) to test the traditional assumption that certain amphipods (*Gammarus tigrinus*

Sexton, *Corophium lacustre* Vanhoffen, *Grandidierella bonnieroides* Stephensen), an isopod (*Munna reynoldsi* Frankenberg and Menzies), a cumacean (*Almyracuma proximoculi* Jones and Burbanck) and a group of mysids (*Taphromysis* spp.) are always benthic; and (2) to relate the timing of vertical ascents of different developmental stages of these species into the water column with day/night and tidal phases in an estuary characterized by having diurnal tides.

MATERIAL AND METHODS

Two field studies were completed to determine temporal changes in the densities of the named species near the water surface of the Fowl River estuary, Mobile County, southwestern Alabama, USA (Fig. 1). The Fowl River estuary is characterized by diurnal tides, unlike the semidiurnal tides found along the east coast of the United States. The first field study (May 14-15, 1987) was designed to measure short-interval (1 - 4.5 h) changes in zooplankton surface density during daytime ebb, daytime flood, nighttime ebb and nighttime flood tides at station 1 in the upper reaches of the estuary. Each zooplankton sample was collected by towing a plankton net (505-μm mesh, rectangular mouth 105 cm wide, 55 cm high) for five minutes. The rectangular frame forming the mouth of the net was fitted with floats to keep the net near the water surface during towing. Towing speed was approximately constant for all samples; a flowmeter suspended in the mouth of the net was used to estimate the volume of water filtered. Each sample was preserved in the field by adding 10% formalin. All samples were later processed, without subsampling, for species identification and abundance. Field measurements were also made of water temperature, salinity and tidal height.

Data collected during a sampling station that occurred within 20 min of slack tide were not included in the statistical analyses, because there were not enough slack tide samples to warrant statistical consideration. To minimize sampling variance resulting from sudden crepuscular shifts in the vertical distributions of populations, no sampling was done within 1 h of sunrise or sunset.

The data for each species were grouped with respect to day/night phase, ebb/flood tidal phase and developmental stage (here defined to include gender of adults). Pooling across any of these categories for statistical analysis of independent, main effects was done only after testing for and finding no significant interaction. Pooling was sometimes not possible for several reasons: (1) significant interactions, (2) a variance of zero that rendered parametric tests for interactions ineffective, (3) unequal and disproportional cell sizes from which we chose not to delete data to obtain equal cell sizes and (4) daytime data that were too sparse to warrant statistical testing for a tidal effect on surface density.

Before any parametric test was used, the data set involved was tested for homoscedasticity using Bartlett's test (Sokal and Rohlf, 1981). Transformations were done only when necessary (Underwood, 1981). The parametric tests included the Model I, one-way analysis of variance (1-ANOVA), and the Model I, two-way analysis of variance with unequal but proportional subclass sizes (2-ANOVA) (Sokal and Rohlf, 1981). The nonparametric Mann-Whitney U test (Sokal and Rohlf, 1981) was used when parametric testing could not be done. Nonsignificance was determined at $P>0.05$.

The second field study (October 8-9, 1987) was designed to estimate zooplankton surface densities during nighttime ebb and nighttime flood tides at four locations in the Fowl River estuary (Fig. 1), to determine if the oligohaline-

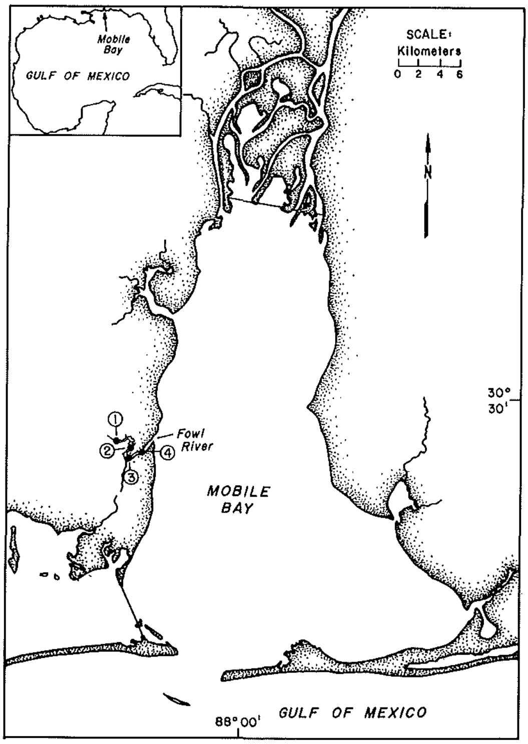

Figure 1. Locations of field sampling stations in the Fowl River estuary, Mobile County, southwestern Alabama, USA, during the first field study (May 14-15, 1987, station 1) and the second field study (October 8-9, 1987, stations 1-4).

mesohaline zooplankton species found in the upper reaches of the estuary during the first field study were found in higher-salinity waters downstream during different tidal phases. This study involved the same equipment and sampling procedure as described for the first field study. To avoid misinterpretation of results due to a possible seasonal difference in zooplankton species composition between May and October, this study included as one of its locations the site sampled during the first field study.

RESULTS

During the first field study, depth in the sampling region ranged from 3.5 to 5.5 m. Surface water temperature ranged from 20.5 to 23.5°C with little change over depth or time. Unlike temperature, salinity showed strong vertical heterogeneity: surface measurements ranged from 0 to $3^0/_{00}$, near-bottom measurements from 8 to $15^0/_{00}$ and surface-bottom differences from 7 to $13^0/_{00}$. The tides were characterized as diurnally tropical with an amplitude of 66 cm.

Juveniles, immatures and adults of the amphipod *Gammarus tigrinus* were collected. Independently of tidal phase and developmental stage, *G. tigrinus* appeared in surface waters at signifi-

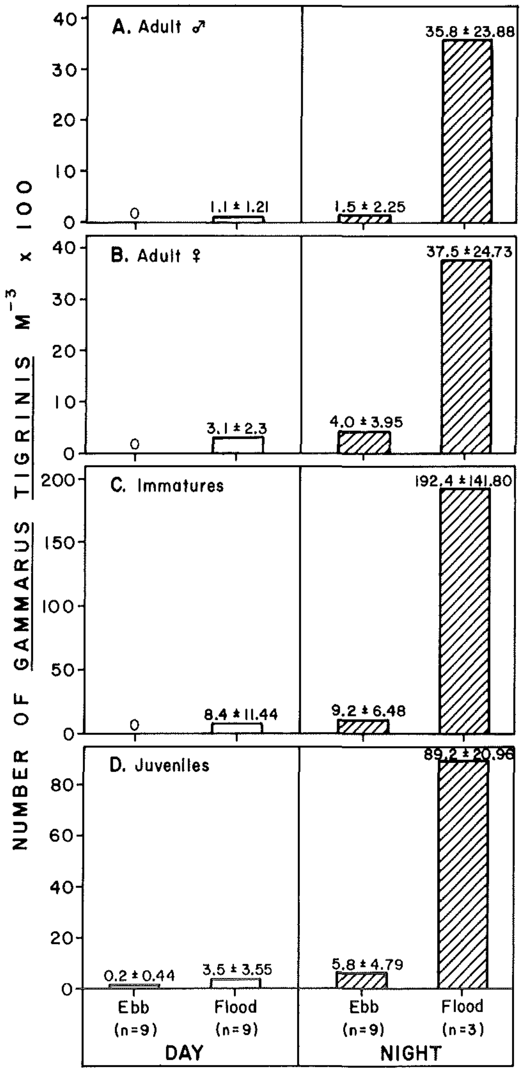

Figure 2. Near-surface densities (mean ± standard deviation) of (A) adult male, (B) adult female, (C) immature and (D) juvenile *Gammarus tigrinus* during different tidal and day/night phases at station 1 in the Fowl River estuary, Alabama, May 14-15, 1987. n: sample size.

Table 1. Results of statistical analyses testing for day/night and tidal effects on near-surface densities of six crustacean species at station 1 (Fig. 1) in the Fowl River estuary, Alabama, May 14-15, 1987. 1-ANOVA: Model I, 1-way analysis of variance; 2-ANOVA: Model I, 2-way analysis of variance with unequal but proportional subclass sizes; M-W: Mann-Whitney U-test (with or without tied variates across sample groups); t_s: t statistic; F_s: F statistic; U_s: Mann-Whitney statistic; df: degrees of freedom; ns: not significant ($P>0.05$); *: Log (x + 1) transformation.

Species	Test	Method	Result; statistic	df
Gammarus tigrinus	Day/night effect (pooled over stage, tidal phase)	M-W (tied variates)	Night>Day; $t_s = 6.091$ ($P<0.001$)	
	Tidal effect (pooled over stage, day/night phase)	M-W (tied variates)	Flood>Ebb; $t_s = 4.215$ ($P<0.001$)	
Corophium lacustre	Day/night effect (pooled over stage, tidal phase)	M-W (tied variates)	Night>Day; $t_s = 8.382$ ($P<0.001$)	
	Tidal effect at night (pooled over stage)	2-ANOVA	*Flood>Ebb; $F_s = 30.135$ ($P<0.001$)	1,30
Grandidierella bonnieroides	Day/night effect during ebb tide	M-W (no tied variates)	Night>Day; $U_s = 81$ ($P<0.002$)	9,9
	Day/night effect during flood tide	M-W (no tied variates)	Night>Day; $U_s = 26$ ($P<0.02$)	9,3
	Tidal effect at night	1-ANOVA	Flood>Ebb; $F_s = 20.867$ ($P<0.005$)	1,10
Munna reynoldsi	Day/night effect during ebb tide	M-W (no tied variates)	Night>Day; $U_s = 81$ ($P<0.002$)	9,9
	Day/night effect during flood tide	1-ANOVA	*Night>Day; $F_s = 191.409$ ($P<0.001$)	1,10
	Tidal effect at night	1-ANOVA	Flood>Ebb: $F_s = 51.571$ ($P<0.001$)	1,10
Almyracuma proximoculi	Day/night effect (pooled over stage, tidal phase)	M-W (tied variates)	Night>Day; $t_s = 12.821$ ($P<0.001$)	
	Tidal effect at night: Adult male	1-ANOVA	Flood = Ebb; $F_s = 0.037$ ns	1,10
	Adult female	1-ANOVA	Flood = Ebb; $F_s = 0.251$ ns	1,10
	Juvenile	1-ANOVA	*Flood>Ebb; $F_s = 8.132$ ($P<0.025$)	1,10
Taphromysis spp.	Day/night effect (pooled over stage, tidal phase)	M-W (tied variates)	Night>Day; $t_s = 8.771$ ($P<0.001$)	
	Tidal effect at night (pooled over stage)	2-ANOVA	*Flood>Ebb; $F_s = 9.665$ ($P<0.005$)	1,30

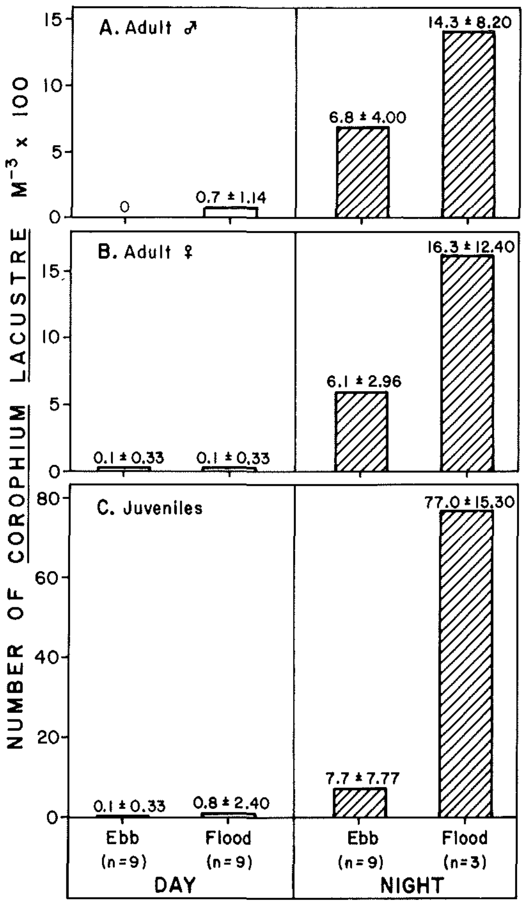

Figure 3. Near-surface densities (mean ± standard deviation) of (A) adult male, (B) adult female and (C) juvenile *Corophium lacustre* during different tidal and day/night phases at station 1 in the Fowl River estuary, Alabama, May 14-15, 1987. n: sample size.

cantly higher densities at night compared with daytime measurements, evidence of nocturnal vertical migration (Table 1, Fig. 2). There is evidence that this species also migrates with a tidal periodicity: significantly higher densities were found near the surface during flood than during ebb tide, regardless of day/night phase or developmental stage (Table 1, Fig. 2).

Juveniles and adults of the amphipod *Corophium lacustre* showed distributions similar to those for *Gammarus tigrinus*. There is evidence of nocturnal vertical migration and migration into surface waters during flood tide at night, regardless of developmental stage (Table 1,

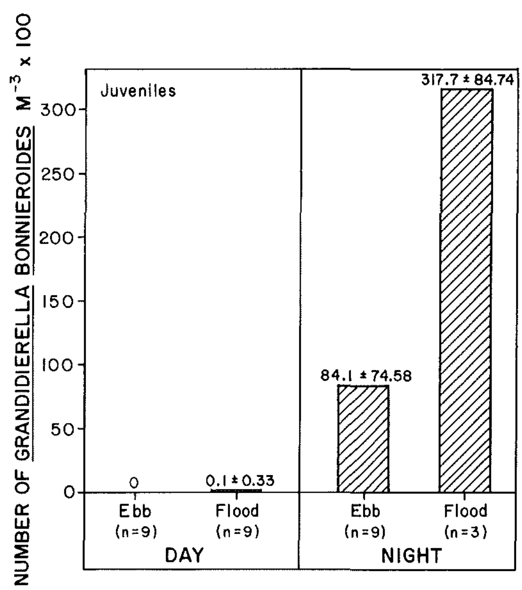

Figure 4. Near-surface densities (mean ± standard deviation) of juvenile *Grandidierella bonnieroides* during different tidal and day/night phases at station 1 in the Fowl River estuary, Alabama, May 14-15, 1987. n: sample size.

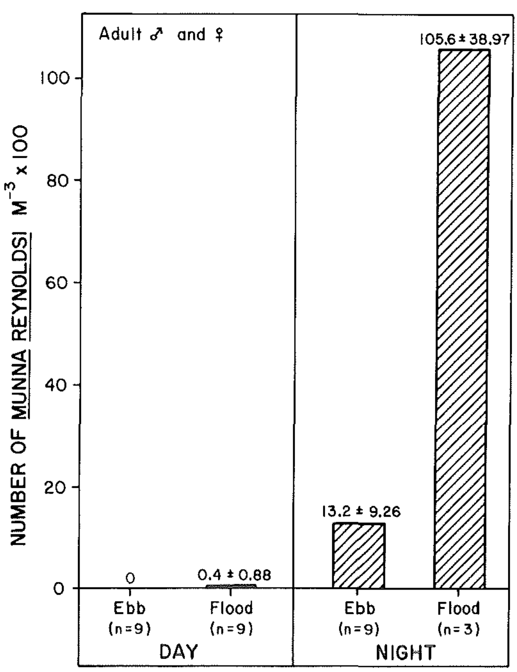

Figure 5. Near-surface densities (mean ± standard deviation) of adult *Munna reynoldsi* during different tidal and day/night phases at station 1 in the Fowl River estuary, Alabama, May 14-15, 1987. n: sample size.

Fig. 3).

Only juveniles of the amphipod *Gran-*

didierella bonnieroides were collected during the first field study. They were significantly more abundant in surface waters at night than during the day, regardless of tidal phase, and they were significantly more abundant during flood tide at night when compared with nocturnal ebb tide (Table 1, Fig. 4).

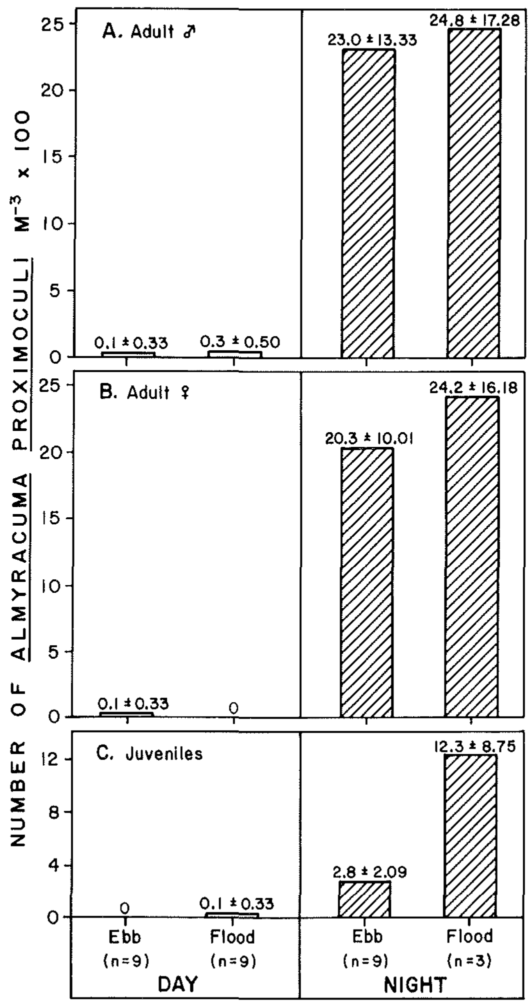

Figure 6. Near-surface densities (mean ± standard deviation) of (A) adult male, (B) adult female and (C) juvenile *Almyracuma proximoculi* during different tidal and day/night phases at station 1 in the Fowl River estuary, Alabama, May 14-15, 1987. n: sample size.

We found it difficult to separate adult males and females of the isopod *Munna reynoldsi* and chose to group them together. Results regarding day/night and tidal effects on surface densities of adult *M. reynoldsi* (Table 1, Fig. 5) were similar to those found for juvenile *Grandidierella bonnieroides*.

Juveniles and adults of the cumacean *Almyracuma proximoculi* were collected at significantly higher surface densities at night than during the day, regardless of tidal phase (Table 1, Fig. 6). Tidal migration was evident, however, only for the juveniles, with significantly higher densities near the water surface during nocturnal flood tide than during nocturnal ebb tide.

Taphromysis spp. refers to a group of mysids with close morphological similarities to both *Taphromysis louisianae* Banner and *Taphromysis bowmani* Bacescu. Juveniles and adults were collected during the first field study. Significantly higher surface densities

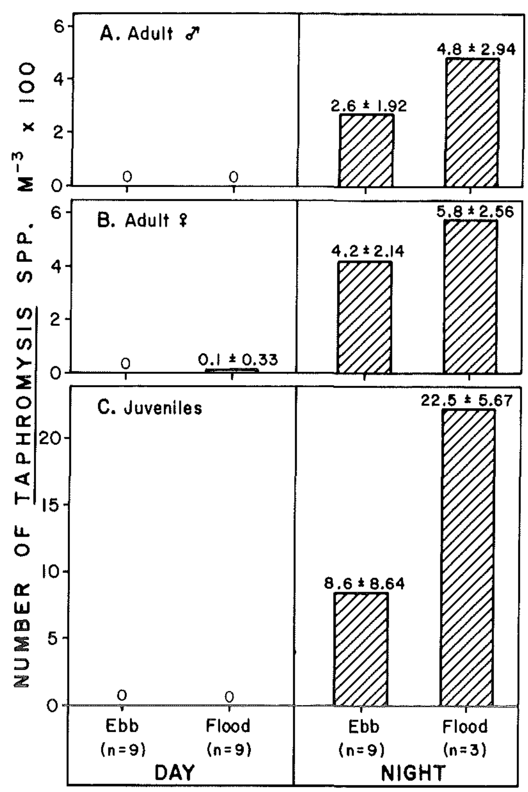

Figure 7. Near-surface densities (mean ± standard deviation) of (A) adult male, (B) adult female and (C) juvenile *Taphromysis* spp. during different tidal and day/night phases at station 1 in the Fowl River estuary, Alabama, May 14-15, 1987. n: sample size.

Table 2. Surface and bottom salinities ($^0/_{00}$) and near-surface densities (No. of animals $m^{-3} \times 100$, mean ± standard deviation) of six crustacean species during different nocturnal tidal phases at four stations (Fig. 1) in the Fowl River estuary, Alabama, October 8-9, 1987; n = 3 except station 3 ebb tide (n = 2).

	Station 1		Station 2		Station 3		Station 4	
	Ebb	Flood	Ebb	Flood	Ebb	Flood	Ebb	Flood
Salinity (surface, bottom)	2,15	2,15	5,15	4,12	8,15	8,14	10,15	14,14
Surface Density								
Gammarus tigrinus (Adults and juveniles)	0	0	0	0.8 ± 0.69	0	1.2 ± 2.08	0	0
Corophium lacustre (Adults and juveniles)	0.4 ± 0.69	2.4 ± 2.08	0	1.2 ± 1.20	0	0	0	0
Grandidierella bonnieroides (Adults, immatures, juveniles)	0.8 ± 0.69	25.0 ± 11.57	2.3 ± 2.02	27.4 ± 4.65	1.8 ± 0.78	4.7 ± 1.15	0	0
Munna reynoldsi (Adults)	0	1.9 ± 0.64	3.1 ± 4.37	15 ± 19.2	13.9 ± 19.59	50 ± 71.1	0	0
Almyracuma proximoculi Adults and juveniles)	1.6 ± 2.77	11.6 ± 7.57	1.2 ± 0	1.6 ± 1.83	0	0.8 ± 0.69	0	0
Taphromysis spp. (Adults and juveniles)	0.8 ± 0.77	0.8 ± 1.33	0.4 ± 0.69	0.8 ± 1.33	0	0.8 ± 0.69	0	0

were found at night than during daylight hours, regardless of tidal phase or developmental stage (Table 1, Fig. 7). Nighttime densities were significantly higher during flood tide than during ebb tide, regardless of developmental stage (Table 1, Fig. 7).

During the second field study, water temperature ranged from 20 to 22°C with little change vertically, horizontally or temporally. Salinity showed strong vertical heterogeneity at all four stations during ebb tide and at stations 1-3 during flood tide (Table 2). Measurements taken near the end of the flood tide phase showed that surface waters at stations 1-3 did not exceed $8^0/_{00}$, while surface salinities were higher at station 4 (Table 2).

The abundances of the six crustacean species during the second field study are shown in Table 2. None of these species was found at station 4. Station 3 was the downstream limit for the amphipods *Gammarus tigrinus* and *Grandidierella bonnieroides*, the isopod *Munna reynoldsi*, the cumacean *Almyracuma proximoculi* and the mysid *Taphromysis* spp. Station 2 was the downstream limit for the amphipod *Corophium lacustre*. Although abundances were generally too low to warrant statistical treatment, in almost every case zooplankton surface density was higher during nocturnal flood tide than during nocturnal ebb tide.

DISCUSSION

Each of the six species has generally been described as oligohaline-mesohaline and closely associated with the estuarine bottom (*Gammarus tigrinus*: Sexton and Cooper, 1939; Bousfield, 1958; Sutcliffe, 1968; Boesch and Diaz, 1974; Dorgelo, 1974; Gilles, 1975; Dorgelo, 1976; Van Maren, 1978; Reish and Barnard, 1979; Pinkster and Platvoet, 1983; Simpson *et al.*, 1985; *Corophium lacustre*: Bousfield, 1973; Boesch and Diaz, 1974; Van Maren, 1978; Steen, 1981; Heard, 1982; *Grandidierella bonnieroides*: Livingston *et al.*, 1976, 1977; Sheridan, 1979; McLane, 1980; Steen, 1981; Heard, 1982; Sheridan and Livingston, 1983; *Munna reynoldsi*: Frankenberg and Menzies, 1966; Schultz, 1969; Callahan *et al.*, 1977; Livingston *et al.*, 1977; Heard, 1982; *Almyracuma proximoculi*: Jones and Burbanck, 1959; Boesch and Diaz, 1974; Steen, 1981; Duncan, 1984; Simpson *et al.*, 1985; Modlin and Dardeau, 1987; *Taphromysis* spp.: Compton and Price, 1979; Hamaker and Matthews, 1979; Steen, 1981; Head, 1982). An examination of benthic grab samples collected at station 1 during the first field study corroborated these reports of benthic, oligohaline-mesohaline habits.

Nocturnal vertical migration has been reported for *Gammarus tigrinus* >1 mm (Williams and Bynum, 1972), adult and juvenile *Corophium lacustre* (Williams and Bynum, 1972; Steen, 1981; Dauer *et al.*, 1982), juvenile *Grandidierella bonnieroides* (Steen, 1981), juvenile *Munna reynoldsi* (Steen, 1981) and adult and juvenile *Almyracuma proximoculi* (Steen, 1981; Heard, 1982). In general, our field results corroborate these reports of nocturnal vertical migration and extend them to include specific ontogenetic stages of *G. tigrinus* (juveniles, immatures, adult males and females), adult *M. reynoldsi* and adult male, adult female and juvenile *Taphromysis* spp.

In sharp contrast to the field reports of nocturnal vertical migrations, there is little published information regarding tidal vertical migrations of these estuarine crustaceans. Dauer *et al.* (1982), in a study of macrobenthos in the Lafayette River, Virginia, mentioned that "*Corophium lacustre* was slightly more common at the surface of flood tides." The other five species were not found during that study. The results of our research in the Fowl River estuary strongly indicate that all collected stages of the six described species are tidal vertical migrators except the adult *Almyracuma proximoculi*. The tidal migrators were significantly more abundant in the water column during nocturnal flood tides than during nocturnal ebb tides.

The results of the second field study show that all of these species are found only in the upper reaches of the Fowl River estuary. The nocturnal tidal phases of this study were opposite those of the first field study with respect to time of day, yet the same tidal trends in surface densities of these crustaceans were found. This finding indicates that the tidal migrations found in the first field study were truly associated with the tides, not the specific time of day or night. Tidal rhythms in surface density at a given station could not be explained by horizontal oscillation of surface populations over a tidal cycle, because downstream distribution was not extended during ebb tide. The first field study's finding that for all species this tidal rhythm was pronounced at night but often not found during the day indicates that the tidal changes in surface density of these crustaceans did not result from physical disturbance and passive suspension by tidal currents. Taken together, these field studies provide evidence that the observed day/night and tidal patterns in surface density are the behavioral result of nocturnal and tidal vertical migrations that shuttle these animals between the bottom and the overlying waters in a precisely timed manner.

The adaptive value of these vertical migrations is not the immediate rescue of a physiologically stressed organism: such stress would not be expected to occur only during nocturnal flood tides.

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Other possible advantages of leaving the bottom include avoidance of benthic predation (*e.g.* Jansson and Kallander, 1968; Fincham, 1970; Williams and Bynum, 1972; Gibson, 1973; Robertson and Howard, 1978; Alldredge and King, 1980; Ambrose, 1984), enhanced reproductive contact (*e.g.* Foxon, 1936; Mills, 1967; Fincham, 1970; Williams and Bynum, 1972; Robertson and Howard, 1978), an alternative feeding strategy (*e.g.* Alldredge and King, 1980; Grant, 1980) and dispersal (*e.g.* Foxon, 1936; Watkin, 1941; Jansson and Kallander, 1968; Hughes, 1969; Robertson and Howard, 1978; Alldredge and King, 1980; Weinstein *et al.*, 1980; Hughes, 1988). While these factors may influence the selection of nocturnal vertical migration, they do not by themselves explain the tidal timing of nocturnal movements by these crustaceans: no tidal migration is required to meet these adaptive goals.

A possible advantage of tidal migration is dispersal **and** retention of otherwise localized, benthic populations within the oligohaline-mesohaline region of the estuary. For dispersal to be confined to the upper reaches of the estuary where these species are found, movement off the bottom must be precisely timed. The tidal timing of vertical migration allows for such estuarine retention. The nocturnal timing of migration minimizes exposure to visual predation in the water column. These two cyclic behaviors may work together in the upper reaches of estuaries to enhance the survival of otherwise benthic crustaceans by (1) increasing dispersal within the oligohaline-mesohaline estuarine region, (2) retaining these crustaceans within a physiologically and biologically adequate environment and (3) accomplishing these goals with minimal exposure to visual predation in the water column.

There is increasing evidence that benthic and pelagic systems in shallow environments share biological components not only through variable physical vectors that induce mixing or allow sinking (*e.g.* Palmer, 1984) but also through the more predictable, cyclic behavior of diel vertical migration (see Introduction). This research demonstrates the general presence of tidal vertical migration of macrobenthos, a poorly documented behavior that, when coupled with diel migration, may help explain the retention of oligohaline-mesohaline organisms in the upper reaches of estuaries. Such benthic-pelagic coupling may characterize most shallow-water environments. Evidence of this interaction emphasizes the need to examine such systems from an integrated perspective instead of considering benthic and pelagic ecosystems as separate entities.

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LITERATURE CITED

Alldredge, A.L., and J.M. King. 1980. Effects of moonlight on the vertical migration patterns of demersal zooplankton. *J. Exp. Mar. Biol. Ecol.* 44:133-156.

Ambrose, W.G., Jr. 1984. Increased emigration of the amphipod *Rhepoxynius* *abronius* (Barnard) and the polychaete *Nephtys caeca* (Fabricius) in the presence of invertebrate predators. *J. Exp. Mar. Biol. Ecol.* 80:67-75.

Anger, K. and C. Valentin. 1976. In situ studies on the diurnal activity pattern of *Diastylis rathkei* (Cumacea, Crustacea) and its importance for the "hyperbenthos." Helgol. Wiss. Meeresunters. 28:138-144.

Boesch, D.F., and R.J. Diaz. 1974. New records of peracarid crustaceans from oligohaline waters of the Chesapeake Bay. *Chesapeake Sci.* 15:56-59.

Bousfield, E.L. 1958. Freshwater amphipod crustaceans of glaciated North America. *Can. Field-Nat.* 72:55-113.

Bousfield, E.L. 1973. Shallow Water Gammaridean Amphipoda of New England. Cornell University Press, Ithaca, New York. 312 p.

Callahan, B.J., S.T. Clark, and P.B. Robertson. 1977. Occurrence of the brackish water asellote isopod *Munna (Uromunna) reynoldsi* in Texas. *Gulf Res. Rep.* 6:77-78.

Compton, C.E., Jr., and W.W. Price. 1979. Range extension to Texas for *Taphromysis bowmani* Bacescu (Crustacea: Mysidacea) with notes on its ecology and generic distribution. *Contrib. Mar. Sci.* 22:121-125.

Dauer, D.M., R.M. Ewing, J.W. Sourbeer, W.T. Harlan, and T.L. Stokes, Jr. 1982. Nocturnal movements of the macrobenthos of the Lafayette River, Virginia. *Int. Rev. Gesamten Hydrobiol.* 67: 761-775.

Dorgelo, J. 1974. Comparative ecophysiology of gammarids (Crustacea: Amphipoda) from marine, brackish and freshwater habitats exposed to the influence of salinity-temperature combinations. I. Effect on survival. *Hydrobiol. Bull.* 8:90-108.

Dorgelo, J. 1976. Comparative ecophysiology of gammarids (Crustacea: Amphipoda) from marine, brackish and freshwater habitats exposed to the influence of salinity-temperature combinations. II. Preference experiments. *Verh. Int. Ver. Limnol.* 19:3007-3013.

Duncan, T.K. 1984. Life history of *Almyracuma proximoculi* Jones and Burbanck, 1959 (Crustacea: Cumacea) from intertidal fresh-water springs on Cape Cod, Massachusetts. *J. Crustacean Biol.* 4:356-374.

Fage, L. 1933. Migrations verticales periodiques des animaux benthiques littoraux. *J. Cons. Int. Explor. Mer* 85: 60-69.

Fincham, A.A. 1970. Rhythmic behaviour of the intertidal amphipod *Bathyporeia pelagica*. *J. Mar. Biol. Assoc. U.K.* 50: 1057-1068.

Foxon, G.E.H. 1936. Notes on the natural history of certain sand-dwelling Cumacea. *Ann. Mag. Nat. Hist.* 17:377-393.

Frankenberg, D. and R.J. Menzies. 1966. A new species of asellote marine isopod, *Munna (Uromunna) reynoldsi* (Crustacea: Isopoda). *Bull. Mar. Sci.* 16:200-208.

Gibson, R.N. 1973. The intertidal movements and distribution of young fish on a sandy beach with special reference to the plaice (*Pleuronectes platessa* L.). *J. Exp. Mar. Biol. Ecol.* 12:79-102.

Gilles, R. 1975. Mechanisms of ion and osmoregulation, p. 259-347. *In* O. Kinne (ed.), Marine Ecology, II. Physiological Mechanisms, Part 1. John Wiley & Sons, New York.

Grant, J. 1980. A flume study of drift in marine infaunal amphipods (Haustoriidae). *Mar. Biol.* 56:79-84.

Hamaker, T.L., and E. Matthews. 1979. First Florida record of *Taphromysis louisianae* (Crustacea: Mysidacea). *Northeast Gulf Sci.* 3:112-113.

Heard, R.W. 1982. Guide to Common Tidal Marsh Invertebrates of the Northeastern Gulf of Mexico. Mississippi-Alabama Sea Grant Consortium MASGP-79-004, Reinbold Lithographing & Printing Co.,

DOI: 10.18785/negs.1102.01

Booneville, Mississippi. 82 p.

Hicks, G.R.F. 1986. Distribution and behaviour of meiofaunal copepods inside and outside seagrass beds. *Mar. Ecol. Prog. Ser.* 31:159-170.

Hiroki, M. 1980. Relation between the two diel phenomena shown by freshwater gammarids - drift and vertical migration. *Crustaceana Suppl.* (Leiden) 6:182-193.

Hughes, D.A. 1969. On the mechanisms underlying tide-associated movements of *Penaeus duorarum* Burkenroad. *FAO Fish. Rep.* 57:867-874.

Hughes, R.G. 1988. Dispersal by benthic invertebrates: the *in situ* swimming behavior of the amphipod *Corophium volutator. J. Mar. Biol. Assoc. U.K.* 68: 565-579.

Jansson, B.-O., and C. Kallander. 1968. On the diurnal activity of some littoral peracarid crustaceans in the Baltic Sea. *J. Exp. Mar. Biol. Ecol.* 2:24-36.

Jones, N.S., and W.D. Burbanck. 1959. *Almyracuma proximoculi* gen. et sp. nov. (Crustacea, Cumacea) from brackish water of Cape Cod, Massachusetts. *Biol. Bull.* 116:115-124.

Livingston, R.J., G.J. Kobylinski, F.G. Lewis, III, and P.F. Sheridan. 1976. Long-term fluctuations of epibenthic fish and invertebrate populations in Apalachicola Bay, Florida. *Fish. Bull.* 74:311-321.

Livingston, R.J., P.F. Sheridan, B.G. McLane, F.G. Lewis, III, and G.J. Kobylinski. 1977. The biota of the Apalachicola Bay system: functional relationships, p. 75-100. *In* R.J. Livingston and E.A. Joyce, Jr. (eds.), Proceedings of the Conference on the Apalachicola Drainage System. Florida Department of Natural Resources, Marine Resources Laboratory Publication 26.

Macquart-Moulin, C. 1984. La phase pelagique nocturne et les comportements migratoires des amphipodes benthiques (Mediterranée nord-occidentale). *Téthys* 11:171-196.

Macquart-Moulin, C. 1985. Le controle des phases pélagiques nocturnes chez les crustacés péracarides benthiques. *Téthys* 11:275-287.

McLane, B.G. 1980. An investigation of the infauna of East Bay-Apalachicola Bay. M.S. Thesis, Florida State University, Tallahassee, Florida.

Mills, E.L. 1967. The biology of an ampeliscid amphipod crustacean sibling species pair. *J. Fish. Res. Board Can.* 24:305-355.

Modline, R.F., and M. Dardeau. 1987. Seasonal and spatial distribution of crustaceans in the Mobile Bay estuarine system, Alabama. *Estuaries* 10:291-297.

Palmer, M.A. 1984. Invertebrate drift: behavioral experiments with intertidal meiobenthos. *Mar. Behav. Physiol.* 10: 235-253.

Pinkster, S., and D. Platvoet. 1983. Further observations on the distribution and biology of two alien amphipods, *Gammarus tigrinus* Sexton, 1939, and *Crangonyx pseudogracilis* Bousfield, 1958, in the Netherlands (Crustacea, Amphipoda). *Bull. Zool. Mus. Amst.* 9: 153-164.

Price, W.W. 1982. Key to the shallow water Mysidacea of the Texas coast with notes on their ecology. *Hydrobiologia* 93:9-21.

Reish, D.J., and J.L. Barnard, 1979. Amphipods (Arthropoda: Crustacea: Amphipoda), p. 345-370. *In* C.W. Hart, Jr. and S.L.H. Fuller (eds.), Pollution Ecology of Estuarine Invertebrates. Academic Press, New York.

Robertson, A.I., and R.K. Howard. 1978. Diel trophic interactions between vertically-migrating zooplankton and their fish predators in an eelgrass community. *Mar. Biol.* 48:207-213.

Schultz, G.A. 1969. How to Know the Marine Isopod Crustaceans. William C. Brown Co., Dubuque, Iowa. 359. p.

Sexton, E.W., and L.H.N. Cooper. 1939.

On a new species of *Gammarus (G. tigrinus)* from Droitwich district. *J. Mar. Biol. Assoc. U.K.* 23:543-552.

Sheridan, P.F. 1979. Three new species of *Melita* (Crustacea: Amphipoda), with notes on the amphipod fauna of the Apalachicola estuary of northwest Florida. *Northeast Gulf Sci.* 3:60-73.

Sheridan, P.F., and R.J. Livingston. 1983. Abundance and seasonality of infauna and epifauna inhabiting a *Halodule wrightii* meadow in Apalachicola Bay, Florida. *Estuaries* 6:407-419.

Simpson, K.W., J.P. Fagnani, D.M. DeNicola, and R.W. Bode. 1985. Widespread distribution of some estuarine crustaceans *(Cyathura polita, Chiridotea almyra, Almyracuma proximoculi)* in the limnetic zone of the lower Hudson River, New York. *Estuaries* 8:373-380.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry, 2nd ed. W.H. Freeman and Company, New York. 859 p.

Steen, J.P., Jr. 1981. Spatial and temporal distribution of zooplankton in a low salinity Mississippi bayou system. Ph.D. Dissertation, Department of Biology, University of Mississippi, Jackson, Mississippi. 183 p.

Sutcliffe, D.W. 1968. Sodium regulation and adaptation to fresh water in gammarid crustaceans. *J. Exp. Biol.* 48: 359-380.

Underwood, A.J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol. Annu. Rev.* 19:513-605.

Van Duyn-Henderson, J.A., and D.C. Lasenby. 1986. Zinc and cadmium transport by the vertically migrating opossum shrimp, *Mysis relicta. Can. J. Fish. Aquat. Sci.* 43:1726-1732.

Van Maren, M.J. 1978. Distribution and ecology of *Gammarus tigrinus* Sexton, 1939 and some other amphipod Crustacea near Beaufort (North Carolina, U.S.A.). *Bijdr. Dierkd.* 48:45-56.

Watkin, E.E. 1941. Observations on the night tidal migrant Crustacea of Kames Bay. *J. Mar. Biol. Assoc. U.K.* 25:81-96.

Weinstein, M.P., S.L. Weiss, R.G. Hodson, and L.R. Gerry. 1980. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. *Fish. Bull.* 78: 419-435.

Williams, A.B, and K.H. Bynum. 1972. A ten-year study of meroplankton in North Carolina estuaries: amphipods. *Chesapeake Sci.* 13:175-192.

Wooldridge, T., and T. Erasmus. 1980. Utilization of tidal currents by estuarine zooplankton. *Estuarine Coastal Mar. Sci.* 11:107-114.

DOI: 10.18785/negs.1102.01