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SEASONALITY AND SPATIAL PATTERNS OF SEAGRASS-ASSOCIATED AMPHIPODS OF THE INDIAN RIVER LAGOON, FLORIDA

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ABSTRACT

Amphipods of *Halodule wrightii* seagrass beds in the Indian River, Florida, showed variable seasonal patterns of abundance and diversity, but were generally more abundant in November–May than in June–October. These seasonal patterns of abundance and diversity are largely attributed to seasonality of fish and decapod predation, and are not attributable to seasonality of seagrass biomass. Spatially, amphipod densities were generally (1) lower near ocean inlets, and (2) lower at the southern versus northern sample locations within the Indian River. In both cases, these patterns are attributable to greater abundance of predators at sites where amphipod density was low. A total of only 15 species was collected from five sites over 4 years with overall mean density at these sites only 807 individuals per m^2.

Several recent studies have examined aspects of the regulation of species densities and the community structure of seagrass-associated macrobenthos in the Indian River lagoon, Florida (Young et al., 1976; Young and Young, 1977; 1978; Virnstein, 1978; Gore et al., 1980). Among the macrobenthos associated with seagrasses, amphipod crustaceans often contribute significantly to total macrofaunal abundance (Young et al., 1976; Young and Young, 1977; 1978). Amphipods in seagrass beds have been shown to be highly susceptible to predation (Nelson, 1979a; b; Young and Young, 1977; 1978). A gradient of predation pressure along the Indian River has been suggested by Young et al. (1976). The presence of such a gradient could have significant effect on the species densities and community structure of such highly preyed upon items as amphipods. Additionally, Young and Young (1977) have indicated that a gradient in the variability of environmental parameters exists along the length of the Indian River.

In view of these potentially important gradients, we have examined abundance data collected over a period of 4 years for the most abundant amphipod species and for the total amphipod assemblage at five study sites along the Indian River lagoon.

STUDY AREA

The Indian River is a shallow estuarine lagoon, bounded on the east by a series of barrier islands, located on the east-central coast of Florida. The Indian River has an average depth of 1.5 m (Young and Young, 1978) and varies in width from 0.4 to 8.9 km. Although six species of seagrass are found in the river, all sampling for the present study was carried out in areas characterized by pure stands of the seagrass *Halodule wrightii* Ascherson.

More extensive description of the Indian River including its physical, chemical, and biological characteristics, may be found in the publications of Young and Young (1977; 1978), Gilmore (1977) and in the Annual Reports of the Harbor Branch Consortium (RR 1, Box 196, Ft. Pierce, FL 33450). The five study sites proceeding from north to south were (1) Haulover Cove, (2) Banana River, (3) Sebastian Inlet, (4) Link Port, and (5) St. Lucie Inlet (Fig. 1).

METHODS

Sampling methods have been previously described by Young and Young (1978). Briefly, benthic samples consisted of intact cores of seagrass and sediment (15 cm × 15 cm to a depth of at least 15 cm) obtained with a post-hole type coring device. Cores were washed through a 1-mm mesh screen,

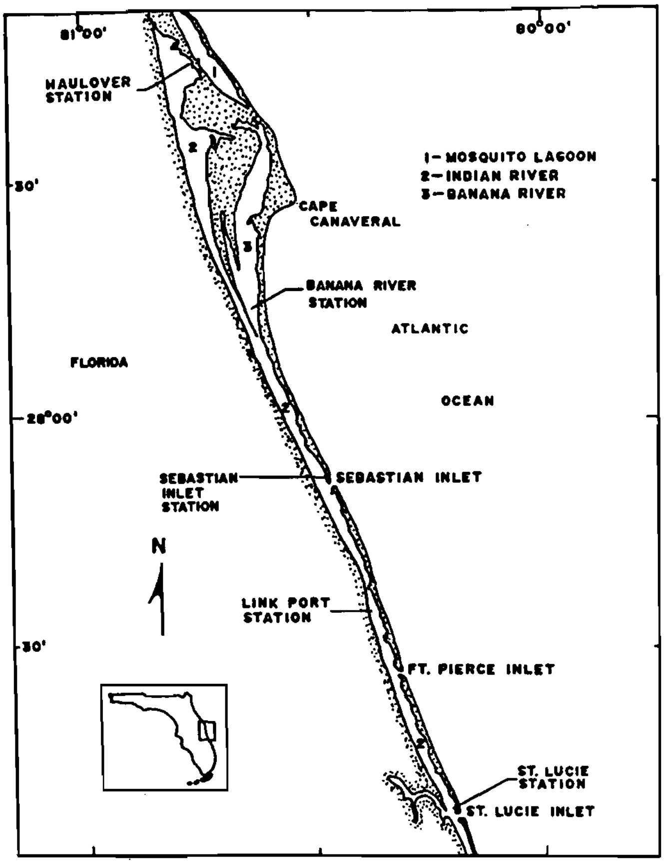


Figure 1. Chart of the Indian River, Florida, region showing the location of the Haulover, Banana River, Sebastian, Link Port, and St. Lucie study sites.

narcotized, stained, fixed in formalin-seawater and preserved in 70% ethyl alcohol. All sorting and identification of amphipods were carried out under a dissecting microscope. Measurements of water temperature, salinity, and water depth were made on each sampling date.

Initially, a sample at all sites consisted of five cores per sampling date, but this number was subsequently reduced to four (Young and Young, 1978). Total number of sampling dates and intervals between samples varied from site to site. Sampling at the Banana River and Sebastian study sites was carried out over the period June 1974 to July 1975 at approximately monthly intervals (11 and 9 monthly samples, respectively). Sampling at the Haulover and St. Lucie study sites was begun in August and September 1974, respectively, and was carried out at approximately monthly intervals until December 1975. Subsequently, the sampling interval was increased to bimonthly. Although sampling at the Haulover and St. Lucie sites is presently continuing, the present paper treats data only through February 1978 (25 monthly samples at each site). Sampling at Link Port was begun in September 1974 and has continued at monthly or bimonthly intervals to the present time. Data through April 1978 will be reported here (35 monthly samples).

For each core, number of individuals and number of species were recorded and the Shannon-Weaver diversity index (H') and evenness (J') were calculated using natural logarithms (Pielou, 1969).

Mean values of density, number of species, H' diversity, and evenness were compared for the periods June–October and November–May at all five study sites with *t*-tests. Additionally, mean values of density were compared for the individual amphipod species between the two seasonal periods for all five study sites.

In order to compare the relative variability of temperature, salinity, and water depth at the various study sites, a composite variability index was computed which could range from 0 to 100. Potential variability was considered to be from the minimum to the maximum value recorded at any of the sites

Table 1. Range of variation in temperature, salinity, and water depth, and the composite index of variability for the Indian River study sites

Parameter	Haulover	Banana River	Sebastian	Link Port	St. Lucie
Surface water temperature, °C	11–34	15–35	14–29.5	11.5–32	17.5–31.5
Salinity, ‰	20–46	18–40.5	25–36	20–38	28–36
Water depth, cm	22–100	12–100	24–130	30–60	34–65
Variability index	84.9	79.4	64.6	58.4	37.7

for a particular parameter (e.g. 11–35°C). The actual range of variation at a site was divided by this maximum variation. This fraction of maximal variation for each of the three environmental variables was then scaled by multiplying times 33 (i.e. ⅓ of 100) and added together to give the composite variability index.

RESULTS

The range in values of temperature, salinity, and water depth at the five sites over the period of study are given in Table 1. The composite index for these three parameters clearly indicates a gradient of decreasing environmental variability proceeding from the most northern (Haulover) to the most southern (St. Lucie) sample site (Table 1).

A total of 6,414 amphipods comprising 15 species was collected (Table 2). Eight species comprised over 99% of total amphipod abundance. Amphipoda of the suborder Gammaridea were represented by 13 species constituting 99.9% of total abundance. The remaining two species were of the suborder Caprellidea and were represented by only seven specimens in the 433 cores taken.

The number of species encountered at each station was relatively similar despite a more than three-fold increase in sampling effort at Link Port as compared with the Banana River and Sebastian sites. Total number of species sampled per site ranged from 8 at Haulover to 13 at Link Port (Table 2). If those species which are represented by fewer than seven individuals are excluded, total number of species among sites ranges from four at Sebastian to seven at Link Port.

Six species were found at all study sites—*Cymadusa compta, Grandidierella bonnieroides, Corophium ellisi, Ampelisca abdita, Corophium lacustre,* and *Ampithoe longimana* (Table 2). These species ranked first, second, fourth, fifth, seventh, and eighth, respectively, in total abundance. *Melita elongata* (ranked third) was found at all sites except Sebastian, while *Gammarus mucronatus* (ranked sixth) was found at three sites but was extremely patchy seasonally, with 70% of its abundance at the Banana River site occurring during 2 months and 93% of its abundance at Link Port occurring during a single month.

The amphipod species collected fall into three major microhabitat types: epifaunal tube builders, epifaunal free living forms, and infaunal species. Epifaunal tube builders comprised 85% of total abundance (Table 2) while epifaunal free living species comprised 11% and infaunal species (including the commensal *Colomastix* sp.) composed the remaining 4% (78%, 12%, and 10%, respectively, if the two *Corophium* species which may be functionally infaunal are included in this category).

Patterns of total amphipod abundance show considerable variation in their details among the five study sites within the Indian River system (Fig. 2). Months of peak abundance within a given year were rarely the same even for the most closely adjacent stations. However, certain tendencies may be noted at the three long-term stations. Peak abundances at Haulover were observed during Decem-

Table 2. Total abundances, overall numerical ranks, and microhabitat types for the amphipod species found at the Haulover, Banana River, Sebastian, Link Port, and St. Lucie sample sites. I—Infaunal, ET—Epifaunal tube building, EF—Epifaunal free living, C—Commensal

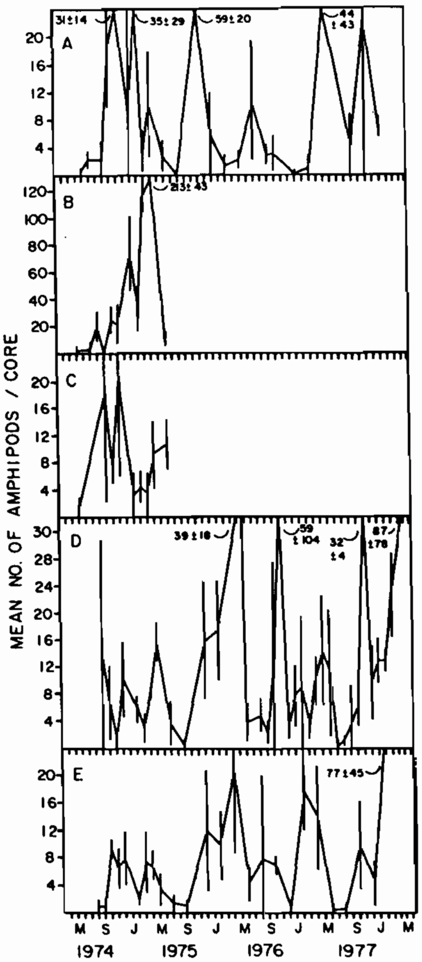
	Site							
Species	Haulover	Banana River	Sebastian	Link Port	St. Lucie	Total No.	Rank	Microhabitat
Cymadusa compta	553	215	227	1,134	573	2,702	1	ET
Grandidierella bonnieroides	205	1,461	10	122	329	2,127	2	ET
Melita elongata	80	4		199	174	457	3	EF
Corophium ellisi	288	10	2	4	3	307	4	ET(I)
Ampelisca abdita	11	170	15	42	13	251	5	I
Gammarus mucronatus	6	105		99		210	6	EF
Corophium lacustre	22	159	3	11	3	198	7	ET(I)
Ampithoe longimana	2	1	50	54	35	142	8	ET
Paracaprella tenuis		2	1	2	1	6	9	EF
Ampelisca vadorum			1	2	1	4	10.5	I
Melita appendiculata			1	3		4	10.5	EF
Colomastix sp.				2		2	12.5	C
Erichthonius sp.			2			2	12.5	ET
Caprella equilibra			1			1	14.5	EF
Lysianassa alba				1		1	14.5	I
Total no. of species	8	9	11	13	9	15		

ber 1974, 1975, and 1977; while sharp peaks in abundance at Link Port were repeated in May 1975 and 1976, April 1978, and November 1976 and 1977 (Fig. 2). At the St. Lucie station, sharp peaks in abundance were observed in February 1977 and 1978 and in April of 1976 (Fig. 2). Minimum abundances in 1975 and 1977 at Haulover and in 1975 and 1976 at Link Port were observed in September.

Maximum amphipod abundances generally occurred during cool water months and minimum abundance during warm water months. The warm period June through October as compared with November through May for the entire sampling period at Link Port, Banana River, and St. Lucie had significantly lower amphipod densities (Table 3). The mean density of amphipods in the June–October period at Haulover was not significantly lower than for the November–May period when all species are considered (Table 3). However, if *Corophium ellisi,* which has an unusual and highly variable seasonal abundance pattern, is excluded from the analysis, then the June–October period is found to have significantly lower densities of all other amphipod species ($P < 0.025$)—the same pattern as found for the other three stations. Only at the Sebastian station is this pattern of lower June–October amphipod density unclear, possibly due to few samples being available from the June–October period as compared with the other sites. Maximum densities ranged from 910 to 9,470 amphipods per m^2 at the Sebastian and Banana River sites, respectively.

Mean number of amphipod species per core (Fig. 3) showed generally similar patterns to that of amphipod density at the five study sites. There were significantly fewer species per core present during the months June–October as compared with November–May (Table 3) for all sites except the Sebastian site.

Both Shannon-Weaver diversity (H′) and the evenness component of diversity (J′) displayed patterns highly similar to those found for density and number of species. Values of both indices were significantly lower during the period June–October than for the period November–May (Table 3). Once again this seasonal pattern is unclear at the Sebastian site.



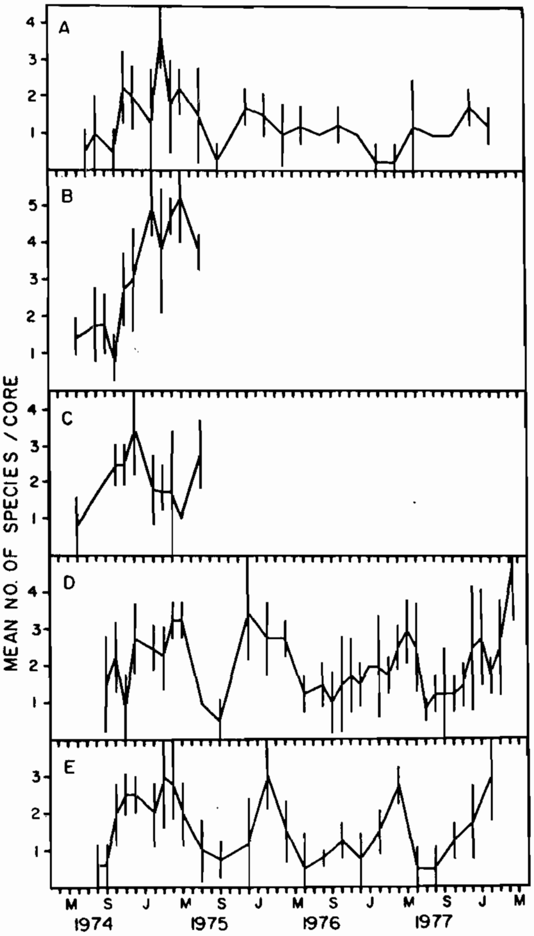


Figure 2. (Left) Mean number of amphipods per 1/44 m^2 core (±1 standard deviation) at the five study sites: A, Haulover; B, Banana River; C, Sebastian; D, Link Port; E, St. Lucie.

Figure 3. (Right) Mean number of species per core (±1 standard deviation) of amphipods at the five study sites: A, Haulover; B, Banana River; C, Sebastian; D, Link Port; E, St. Lucie.

DISCUSSION

The gradient in variability of environmental factors observed among the five sites in the Indian River corresponds to the north-south pattern previously described by Young and Young (1977) for the Haulover, Link Port, and St. Lucie sites. The order of variability (Haulover > Banana River > Sebastian > Link Port > St. Lucie) is the same as for the location of the stations proceeding from north to south. However, there is little evidence that the amphipod assemblage is responding directly to this gradient. Values of mean number of species per core, for example (Fig. 3), were relatively similar along the gradient. This pattern agrees with Young and Young's (1978) statement that high diversity for the entire macrofauna can occur at both extremes of the environmental gradient.

In contrast, the abundance of amphipods showed a tendency towards a north-south pattern. Mean abundance of amphipods collected at Haulover and Banana

Table 3. Values of t calculated for comparisons designed to test whether parameter values for the months November through May are significantly greater than for the period June through October. All tests are one-tailed. *—$P < .05$, **—$P < .025$, ***—$P < .005$, ns—not significant

Parameter	Study Site				
	Haulover	Banana River	Sebastian	Link Port	St. Lucie
Density of amphipods	1.1ns	2.2**	.39ns	2.2**	1.8**
Number of species	2.1**	3.3**	.05ns	4.3***	5.1***
H′ diversity	2.5**	2.4**	.23ns	3.9***	4.9***
J′ (evenness)	2.9**	2.1**	.24ns	4.2***	4.5***

River (1,021/m^2) was twice as great as at the Sebastian, Link Port, and St. Lucie stations combined (480/m^2). We propose, however, that this pattern is more directly related to a second gradient from north to south within the Indian River which is related to predation pressure rather than being due to a direct response to environmental variability. Such a gradient was suggested by Young et al. (1976) who reported total macrobenthos densities of 14,236/m^2 at Haulover, 6,644/m^2 at Link Port, and 3,994/m^2 at St. Lucie. This density gradient was partially attributed by Young et al. (1976), based on the results of experimental predator exclusion studies, to a concurrent increase in the number of species and densities of decapod predators in the same north-to-south direction.

An additional aspect of the distributional pattern of these amphipods relates to the proximity of the sampling stations to the ocean inlets. Mean density was lowest at the Sebastian Inlet and St. Lucie Inlet stations. Available data indicate that biomass and abundance of the pinfish, *Lagodon rhomboides* (L.), which has been shown to be an important predator on amphipods in seagrass beds (Adams, 1976; Carr and Adams, 1973; Nelson, 1979a; b; Stoner, 1980), are greater near the Sebastian and St. Lucie Inlets than at the Link Port station. Mean biomass of *L. rhomboides* from January to August 1975 was 0.07 g/m^2 wet weight at Link Port, 0.20 g/m^2 at Sebastian, and 0.69 g/m^2 at St. Lucie Inlet (Jones et al., 1975). It is, therefore, possible that greater abundance of pinfish at the inlet stations was responsible for the lower amphipod densities at these stations. Although less is known of their feeding ecology, mojarras and gobies are also abundant carnivores and may also play a role in determining amphipod distribution and abundance.

With respect to the distribution of individual species in the Indian River, the greater total abundance of *Ampithoe longimana* at the southern three sites (Table 2, $P < 0.005$) may be largely a function of the tendency of this species to be found in higher salinities (down to 22‰, Bousfield, 1973). The greater abundance of *Melita elongata* at the two southern sites ($P < 0.01$) may also reflect an environmental preference; however, little information on the ecology of this species is yet available. Conversely, the distribution of *Cymadusa compta*, a species tolerant of low salinities (to 5‰, Bousfield, 1973), shows no marked pattern within the Indian River system.

Four species—*Grandidierella bonnieroides*, *Ampelisca abdita*, *Corophium lacustre*, and *Corophium ellisi*—have maximum total abundances at one of the two northern study sites (Table 2), either Haulover or Banana River. The first three of these species had significantly greater total abundances at the Banana River site as compared to the means of the other four sites ($P < 0.05$, $P < 0.01$, $P < 0.01$, respectively), while *C. ellisi* had a significantly greater total abundance at the Haulover site ($P < 0.01$). These patterns may be a result of the reduced predation pressure at the northern terminus of the Indian River which may be partly a result of the more disturbed nature of this area. The largest inputs of sewage discharge into the Indian River system are located in the Haulover-Banana River area (Gibson, 1975). Grizzle (1979) reported very high densities of *Grandidierella bonnieroides, Ampelisca abdita,* and *Corophium ellisi* (in individual samples on the order of 8,000 to 30,000 per m^2) from Sykes Creek, a lagoon located between the Indian River and Banana River, which receives large quantities of treated sewage. Young and Young (1978) demonstrated that increased densities of *Grandidierella bonnieroides* occurred after the application of processed sewage sludge to seagrass areas at the Link Port site if predators were excluded as well. Grizzle (1979) also reported that numerous fish kills took place in Sykes Creek, providing a mechanism for reducing predator density in this area. Increased nutrient input apparently results in increased growth of seagrasses and their epiphytes (Orth, 1977; Young and Young, 1978), which has the dual effect for amphipods of increasing food supply and perhaps more importantly providing better refuge from fish predators (Nagle, 1968; Stoner, 1979). These factors may therefore be responsible for the elevated amphipod densities observed at the Banana River site.

The observed patterns of decreased abundance, number of species, H′ diversity, and evenness for the amphipod assemblage during the months June through October as compared with the remainder of the year may be largely related to seasonal variations in predator density within the Indian River. The similar patterns observed for the abundance of the majority of the amphipod species considered individually may also be explained by this factor. At the Link Port site, maximum abundance of decapod crustaceans was during the summer months (Gore et al., 1980). Nelson (1979a) has demonstrated that a variety of crabs and shrimps are capable of capturing and consuming amphipods, and that several species are highly proficient amphipod predators. Similarly, seasonal densities of *Lagodon rhomboides,* an omnivore which can feed heavily on amphipods, are greatest during the spring and summer months at a variety of sites within the Indian River (Jones et al., 1975). This pattern of pinfish abundance corresponds to that previously described from a variety of other areas (Caldwell, 1957; Cameron, 1969; Hoss, 1974; Adams, 1976).

It is unlikely that seasonal variation in food supply is significant in generating the observed seasonal pattern in amphipod abundance and diversity. Highest seagrass biomass in the Indian River *Halodule* beds is reached during the summer months (Eiseman et al., 1974), the period when amphipod densities are lowest. A similar relationship of low amphipod abundance, high seagrass biomass, and high predator abundance during the summer months has been found for the amphipods of an eelgrass (*Zostera marina*) system near Beaufort, N.C. (Nelson, 1979a; b). In contrast, a positive correlation of the biomass of the seagrass *Thalassia testudinum* and amphipod abundance, with highest densities of each occurring during the summer months, has been reported by Zimmerman (1978) from Puerto Rico. In contrast to the temperate Beaufort and subtropical Indian River regions, the pinfish is absent from the tropical Puerto Rican system (Caldwell, 1957).

The pattern which emerges for the amphipods associated with *Halodule* beds in the Indian River is of an assemblage of relatively limited diversity and abundance. Predation pressure by the diverse and abundant fish and decapod faunas is known to be a significant regulator of the seagrass macrobenthos of the Indian River in general (Young and Young, 1977; 1978; Young et al., 1976; Virnstein, 1978). The seasonal characteristics of the amphipod populations and their predators indicate that predation may also play a central role in the organization of the amphipod component of the Indian River seagrass community.

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