THE ECOLOGY OF THE CARIDEAN DOMINATED SHRIMP COMMUNITY IN SEAGRASS BEDS OFF CEDAR KEY, FLORIDA

BY

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Thirteen species of penaeid and caridean shrimp were observed to coexist in the grassbeds off Cedar Key, Florida. This study was concerned with the structure of this shrimp community, with the degree of niche overlap among these species and with the mechanisms which allow overlap. The coexistence of *Hippolyte pleuracantha* (Stimpson) and *Tozeuma carolinense* Kingsley was given particular attention, as they are members of the same family and the two most numerous species.

The structure of the shrimp community was determined by monthly sampling of the shrimp species occupying the grassbeds and by determining their sizes, abundances, densities, percentages of ovigerous females and the lengths of the reproductive seasons. The organization of the shrimp community appeared to be regulated primarily by the physical environment and to a lesser degree by predation, although a variety of factors influence the organization.

The most numerous species, *Hippolyte pleuracantha*, appeared to be more tolerant of temperature extremes than *Tozeuma carolinense*, but the latter seemed to suffer less predation. The balance between the effects of predation and temperature extremes and the lesser effects of other biological and physical factors on the coexistence of these two species is discussed.

INTRODUCTION

Thirteen species of penaeid and caridean shrimp coexist at high densities in the grassbeds off Cedar Key, Florida. Most of the species appear to overlap in size, form, coloration and season of reproduction, suggesting that this system might provide an excellent opportunity to examine both the community structure and biological and physical factors permitting the coexistence of these thirteen species.

Few studies, excepting those by Hooks et al., 1976 and Heck, 1977 which deal with all invertebrates inhabiting seagrass beds, have examined the ecology of shrimp species inhabiting seagrass beds even though these shrimp may be locally dense and extremely important in the estuarine food chain. Earlier studies have, however, examined many of the shrimp species of the Gulf of Mexico from other perspectives including: 1) taxonomy (Burkenroad, 1939; Calman, 1906; Gurney, 1936; Holthius, 1947, 1951, 1952; Verrill, 1922); 2) such physiological adjustments as osmoregulation (Dobkin and Manning, 1964), cryptic coloration (Brown, 1934, 1935a, 1935b, 1939; Gamble and Keeble, 1900) and larval development (Bryce, 1961; Broad 1956, 1957; Dobkin, 1968); and 3) species' distributions (Chace, 1972; Hulings, 1961; Lyons et al., 1969; Rouse, 1970; Tabb and Manning, 1961; Wass, 1955; Williams, 1965).

The structure of the shrimp community at Cedar Key was determined by: (1) identifying the species of shrimp occupying the grassbeds; (2) determining the relative size range, abundance and density of each species throughout the year; (3) comparing the percentage of ovigerous females and the length of the reproductive season for each species; and (4) examining differences occurring in the shrimp community from one station to another as the dominant grass species changed.

The roles of three biological interactions (predation, competition and parasitism) and the effects of two physical factors (habitat structure and temperature) were examined in relation to their effects on the shrimp community. The examination of all relationships between the thirteen species was not feasible, but the coexistence of *Hippolyte pleuracantha* (Stimpson) and *Tozeuma carolinense* Kingsley is given particular attention, as they are members of the same family and are, by far, the two most numerous species. Differences in their responses to external forces are examined and related to their abilities to coexist.

Finally, the various biological interactions and physical factors are compared as to their relative apparent impacts on the structure of the shrimp community.

STUDY AREA

The study area was located in seagrass beds surrounding the Cedar Keys which are located approximately 90 miles north-northwest of Tampa on the Florida Gulf coast (see Figure 1). The dominant marine grasses of the area are *Thalassia testudinum* (turtle grass), *Syringodium filiforme* (manatee grass), and *Halodule beaudetti* (shoal grass). Red algae (which appear to be important in the habitat of several shrimp species) commonly found in the grass beds of this region include *Digenia simplex*, *Gracilaria verrucosa*, *G. folifera*, and *Laurencia portei* (Hooks et al., 1976).

Tides and wind conditions contribute to mixing of these inshore waters. Two tidal cycles generally occur daily in the Gulf of Mexico, although occasionally there may be only one (National Oceanic and Atmospheric Administration, 1977-1978a). The mean annual tidal range at Cedar Key is about 2.5 ft (0.8 m), with a spring range of 3.3 ft (1 m) (Reid, 1954). Because the water is shallow, winds also are important in circulation and they may counteract tidal rhythm (Reid, 1954).

The Cedar Keys lie approximately midway between the mouth of the Waccasassa River, 12 miles to the east, and the Suwannee River Delta system, 15 miles to the north-northwest. As a result of variations in precipitation influencing local freshwater runoff and river discharges, salinity fluctuated widely. The monthly mean salinity values which occurred during the present study are shown in Figure 2.

Monthly mean salinity values ranged from 23.3 to $29.1^{o}/oo$ during the study (February 1977 to January 1978) and generally range between 20

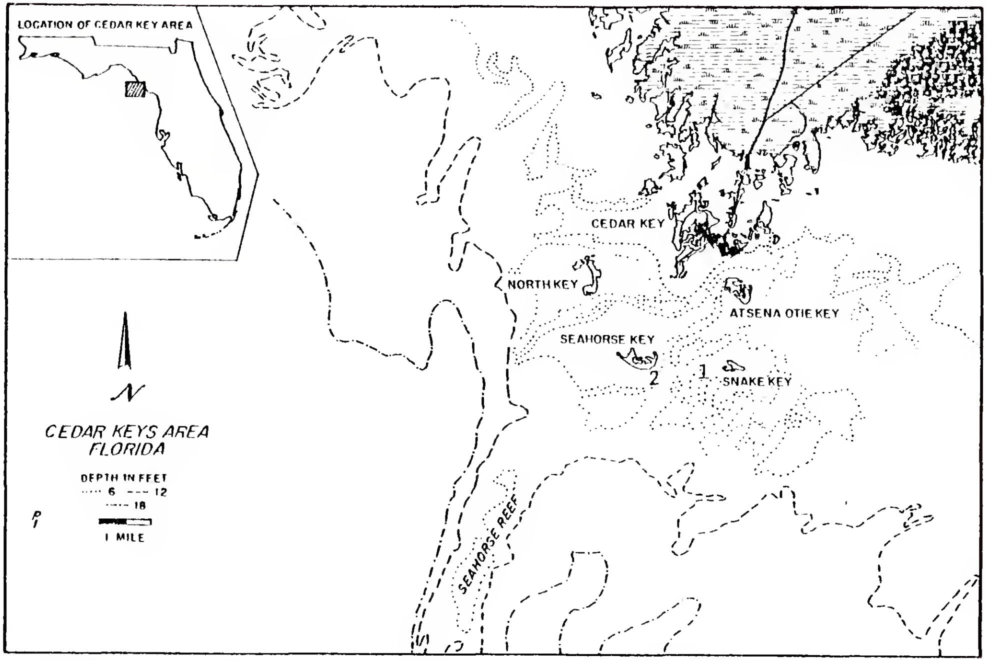

Figure 1. Study area with the locations of Stations 1 and 2 indicated.

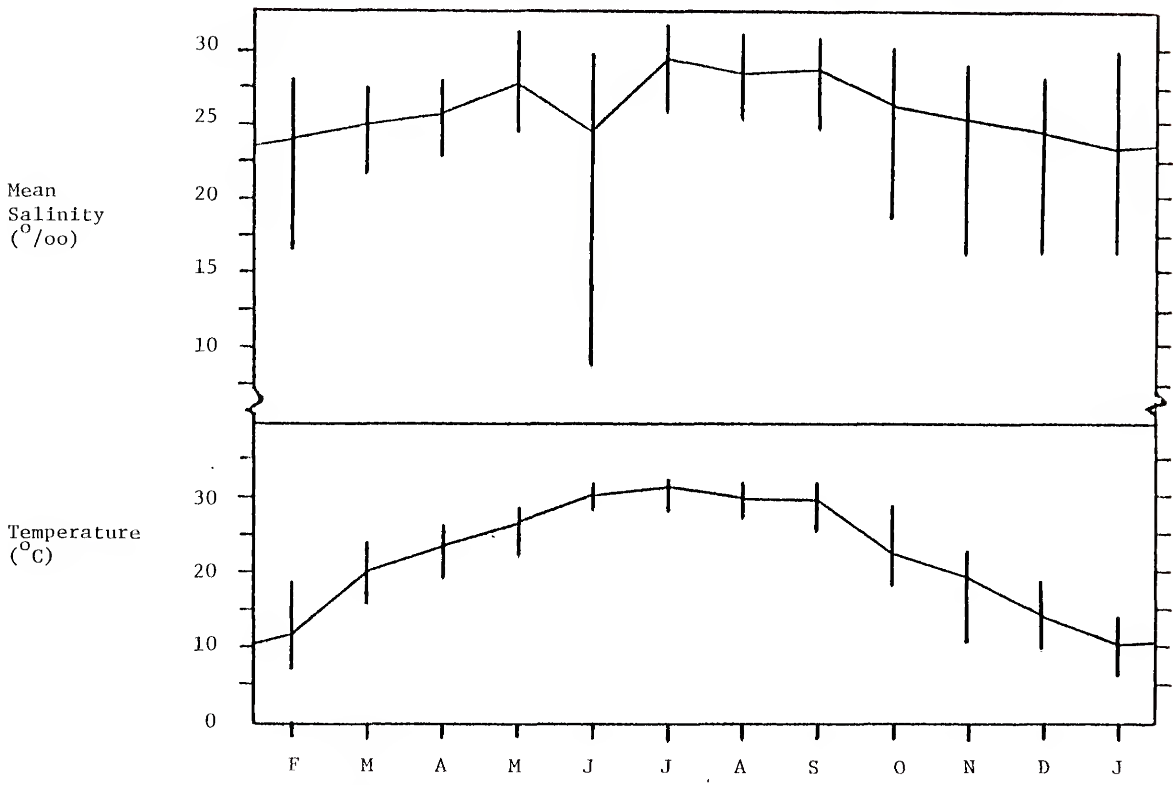

Figure 2. Monthly mean temperature and salinity values off Cedar Key from February 1977 to January 1978. The monthly ranges are indicated by vertical lines. (Data were taken by the National Oceanic and Atmospheric Administration.)

and $30^{o}/oo$ (Reid, 1954; Eng, 1968). Salinity conditions have been reported to be remarkably stable over long periods of time (Ingle and Dawson, 1953) but salinity values below $10^{o}/oo$ or up to $35^{o}/oo$ may occur occasionally and persist for a short time.

The water temperature and salinity values shown in Figure 2 were recorded off the pier at Cedar Key. Greater temperature and salinity ranges were observed in this study during sampling in shallow areas.

Two sampling stations were located 2.5 miles off Cedar Key (see Figure 1). Station 1, a few hundred meters east of Snake Key, was characterized by moderate to deep grass flats. Water depth ranged from one to three meters at low tide. *Thalassia testudinum* was the dominant grass at shallower depths (approximately 1-2 meters), while *Syringodium filiforme* was more common at increasing depths (2-3 meters). Station 2, about 100 to 300 meters off the south beach of Seahorse Key, was a shallower, more protected area. Water depth was generally from 0.3 to 1 meter at low tide and parts of the flats were exposed during extremely low winter tides. The grass density appeared lower than at Station 1 and the grass species occurring at different depths were reversed as compared to Station 1. That is, at Station 2, *S. filiforme* was more conspicuous in the protected shallows which had soft bottoms, while *T. testudinum* occurred at greater depths.

METHODS

Shrimp Community Structure

Three replicate dredges were taken monthly at Station 1 from February 1977 to January 1978 to determine the relative abundances of shrimp species throughout the year and to compare the percentage of ovigerous females and the length of the reproductive season for each species. Samples were taken diurnally within 3 hours of predicted low tide (National Oceanic and Atmospheric Administration, 1977-1978b). Each sample consisted of the catch from a tow of an A-frame scallop dredge pulled behind a 14-foot skiff powered by an outboard motor. The dredge opening, approximately 1 by 1.3 m, was fitted with a fiberglass screen bag of 1.7 mm mesh. The length of time the dredge was towed varied during the year as the shrimp density fluctuated. In the winter longer tows, up to five minutes, were necessary to obtain a sufficiently large sample (at least 50 individuals), while in the summer tows as short as 30 seconds were satisfactory.

To ascertain changes in shrimp density over seasons, three replicate quantitative samples were taken quarterly at Station 1 during the same time interval. These samples were taken using a cubic wooden frame, 0.91 m per side, covered with fiberglass screen of 1.7 mm mesh. The box was lowered from the boat at low tide so that the water depth did not exceed the height of the box. Shrimp were removed from the box with a long-handled dip net fitted with the same fiberglass screen. When ten consecutive sweeps of the net through the box produced no shrimp it was assumed that all shrimp had been removed.

Both qualitative and quantitative samples were preserved in 10% formaldehyde and returned to the laboratory where the shrimp were sorted by species and counted. Most species identifications were made using keys by Williams (1965) and Chace (1972).

Since sexing shrimp by examination of external genitalia is not reliable for small and immature individuals and would be too time consuming for the number of shrimp taken, the occurrence of ovigerous females of nonpenaeid shrimp was recorded as a measure of the length of the reproductive season in each species. Penaeid shrimp were not sexed since their eggs are not carried by females, but are shed directly into the water and it is primarily the juveniles of these species which inhabit estuaries.

The sizes of ovigerous females of *Hippolyte pleuracantha* and *Tozeuma carolinense* were compared in different seasons by random sampling of individuals to determine if later breeding reflected females producing second clutches (in which case late breeding females would be expected to be larger than earlier breeding females) or if late breeders were recently matured females (these females should be small). The number of eggs carried by these ovigerous females was also counted to determine if female size and the number of eggs carried were correlated. The number of eggs carried was also of interest since fewer eggs might be carried by females producing a second clutch due to reproductive fatigue.

The size range for each species was determined by visually selecting several of the largest and smallest individuals of each species in each sample for measurement. An ocular micrometer was then used to determine the range of total length (the tip of the rostrum to the tip of the telson) of each species. In a few cases, carapace length (the posterior margin of the carapace to the hind margin of the orbit) also was measured for comparison with previous studies.

To allow size and distributional comparisons between data obtained during this study and those acquired from other studies done in southeastern estuaries, the numbers, months of reproduction and size ranges of the species are reported in the Appendix. However, it should be kept in mind that previous studies frequently sampled other habitats in addition to grassbeds; that sampling methods and equipment were different from that used in this study (in this study smaller individuals were collected in most species as a result of using a net with a very small mesh size); and that environmental conditions may have been quite different, even in adjacent areas. In cases where it is known, the ecology of a species is also presented in the Appendix and important distinguishing characteristics may be given to aid in separation of two closely related species.

Intersite comparisons of species diversity and dominance were made between Stations 1 and 2 by three replicate tows at each station in May and in October to examine differences between the grass bed environments. In addition, possible changes in species composition with increasing depth were examined by tows at both stations since it had been noted that at Station 1 dense *Thalassia testudinum* beds dominated the shallower depths, while *Syringodium filiforme* density increased in samples from deeper areas. At Station 2 the distribution of these two grass species with depth was reversed, that is, *T. testudinum* occurred at a greater depth than did *S. filiforme*.

At Station 1 tows were made at depths of 0.6, 0.9, and 1.2 m during August and at 0.8 and 1.4 m in November. (These depths were chosen to include samples from both grassbed environments). In order to sample both habitats at Station 2, samples were taken in October at depths of 1.2, 1.4, and 1.5 m.

Regulation of Community Structure

Predation: Predator Exclusion

Predation was postulated to be an important factor regulating shrimp community structure. Therefore, two caging experiments, in which predators were excluded, were conducted at Station 2 to determine what effect the absence of predators would have on the shrimp community. Station 2 was selected for the experiment since it was more protected from currents and closer to the research laboratory than was Station 1.

The cages used in the experiment consisted of cubic wooden frames, 0.9 m per side, covered with fiberglass screen. Tops, which were also covered with screen, were fitted on the boxes and secured by wire passed through screw eye fastners. Since the cages were covered at high tides, foam weather-stripping was used to prevent gaps between the tops and sides. The legs of the boxes were extended by half a meter and steel flashing was nailed around the bases. In order to secure the cages and to prevent organisms from burrowing into or out of the cages, the legs and flashing were driven into the ground until the wooden frame rested on the bottom. The outsides of the cages were brushed weekly with a soft brush to prevent buildup of detritus and fouling organisms on the screen.

On July 20, 1977, 3 cages were set out at low tide in about 0.5 m of water, 100 m offshore and the cages were emptied using a long-handled dip net. Nineteen days later, on August 8, 1977, the contents of two of the cages were collected. The third cage was not sampled because the screening was torn. Samples of the shrimp density in adjacent areas outside the cages were taken at the same time to serve as controls. On August 12, 1977 the experiment was repeated in deeper water (approximately 1 meter at low tide) approximately 200 to 300 meters offshore. The contents of one cage were removed 7 days later (August 19) and a control sample was taken. The remaining two cages were damaged and therefore could not be sampled.

Several short experiments were conducted in the laboratory using _Hippolyte pleuracantha_ and _Tozeuma carolinense_ to examine the effects of biological interactions and physical factors on these species. The shrimp were maintained in aerated 1 gallon aquaria which had a bottom area of 54.9 cm^2. To prevent the shrimp from jumping out of the water, fiberglass screening supported by cork sections was floated on the water surface.

Predation: Fish Preference

In the first experiment fish collected in the grass beds were added to aquaria containing both species of shrimp to determine if a feeding preference existed and to compare methods of predator avoidance by the shrimp. _Thalassia testudinum_ blades were present in the aquaria and were supported by a sand substrate. Ten individuals of each shrimp species were introduced one hour prior to the introduction of a single fish. Several of the most common fish species occurring in the grass-beds were used, i.e., _Urophycis floridanus_, _Lagodon rhomboides_, _Monacanthus hispidus_, _Centropristes melanus_, _Symphusus plagiusa_, _Astroscopus y-graecum_, _Paralichthys albigutta_, and _Sygnathus floridae_.

Competition:

The second laboratory experiment was concerned with interspecific and intraspecific interactions. Ten _Hippolyte pleuracantha_ were placed in one tank, 10 Tozeuma carolinense in a second tank, 5 individuals of each species in a third tank, and 10 of each species in a fourth tank. (These densities of shrimp were chosen since they exceeded observed shrimp densities.) The tanks were maintained for 36 hours, during which time three periods of 3-hour examinations were made for evidence of overt interspecific or intraspecific interactions. The experiment was repeated both in the presence of 5 blades of Thalassia testudinum and after commercial fish food flakes had been provided as food.

As a possible indication of the degree of interspecific competition, the size ranges of the various species collected in the qualitative samples were compared to determine the degree of overlap between species, particularily those within the same family. A high degree of overlap in size ranges might suggest that competition between species is not keen. Also to examine the degree of size overlap among adults, fifteen to twenty-one ovigerous females of the five most numerous caridean species were randomly selected for measurement. An analysis of variance was performed, followed by LDS (least significant difference) to determine which pairs of species were significantly different in size.

Parasitism:

In order to determine the extent of isopod parasitism on the different species, shrimp collected during qualitative sampling were examined for parasites. Total counts of parasites were made from all species except Hippolyte pleuracantha. For H. pleuracantha, total counts were made only on monthly samples containing less than 100 males. In larger samples, the number of parasites occurring on 100 randomly selected males was noted.

Physical Factors:

To determine the relationship between grass density and shrimp density, the number of grass blades per each quantitative sampling area was calculated by averaging counts made by two individuals.

For use in the final two laboratory experiments, a long, narrow aquarium was built which allowed a gradient of physical factors over a hortizontal distance. The tank was 1.8 m long, 25.4 cm high, and 20.3 cm wide.

A third series of experiments was conducted to determine if either shrimp species preferred a particular grass species. A sand substrate was used to anchor the grass, 2 blades of each species in each of six equal sections of the aquarium. Three grasses (Thalassia testudinum, Syringodium filiforme, and an artificial hairgrass, Eleocharis acicularis, made by Living World) were placed randomly on two sections each. Equal numbers of shrimp were introduced over each section and their positions noted one hour later. The experiment was done individually for each species.

Previous investigators (Drost-Hansen and Thorhaug, 1974) had shown a species of Hippolyte had a greater tolerance for high temperature than did Tozeuma carolinense. Therefore a comparison of differences in temperature preference between the two dominant shrimp species was examined in a fourth series of experiments. The aquarium was positioned next to a sink so that hot tap water ran through tubing into copper coils suspended in the water at one end of the tank. At the opposite end of the tank, two copper coils were arranged so that water from the cold tap passed through one coil suspended in an ice-brine bath and then through the second coil which was immersed in the aquarium. Sand was used as a substrate and its depth varied from 1.25 cm at the cool end of the tank to 7.5 cm at the warm end. The slight incline insured a constant vertical temperature, but had no effect on the distribution of shrimp within the tank as determined in a pretest. Eight thermometers were taped inside the tank, one at each end and the other six spaced equally along the length of the tank. A fairly stable temperature gradient from 25 to 34^{o}C was established. The shrimp were acclimated to room temperature (22-23^{o}C) overnight before being introduced into the experimental tank. Equal numbers of shrimp were added over each of the six sections. The experiment was conducted in the presence of *Thalassia testudinum* and repeated several times. After one hour, positions of the shrimp and the temperature nearest that position were noted.

Since all of the shrimp occupying the seagrass beds off Cedar Key are found in other areas of higher and lower salinities, salinity was not examined as a factor regulating the shrimp community.

RESULTS

Shrimp Community Structure

Component Species and Dominance Relationships:

A total of 58,984 individuals from 13 shrimp species were taken in monthly dredges at Station 1 during the year (see Table 1). The majority (94%) of the shrimp were carideans belonging to the family Hippolytidae. The most abundant species was *Hippolyte pleuracantha*, with 49,155 individuals comprising over 83% of the samples. More than 1000 individuals were taken over the year in three other species, *Tozeuma carolinense*, *Periclimenes longicaudatus*, and *Latreutes fucorum*. Two other species, *Trachypeneus constrictus* and *Thor dobkini*, were common, with more than 100 individuals of each species collected. Seven species were taken rarely: *Sicyonia laevigata*, *Ambidexter symmetricus*, *Processa bermudensis*, *Periclimenes americanus*, *Palaemon floridanus*, *Alpheus normanni*, and *Latreutes parvulus*. In the Appendix these species are described, their size ranges given, and comparisons are made with data collected in previous studies.

On the average, about 65% of the 13 species could be collected during any given month; less than 50% in April or May, but more than 90% in June and November. Dredges of less than five minutes yielded as many as 5500 shrimp in August and in September when grassbeds were most dense, but as few as 50 to 100 in April when *Thalassia testudinum* blades had been shed following a cold snap.

The dominance rank for each species, which is based on the percentage of the total number of individuals contributed by each species,

Table 1. Monthly shrimp abundances by species taken in three pooled, replicate dredges each month from February 1977 to January 1978. Blanks indicate the absence of a species. In the final columns the total number of each species collected is given, the species are ranked from 1 to 13 in order of numerical dominance during the year and the percent of the total number occupied by each species in indicated. The last rows list the monthly total numbers of shrimp and the Simpson Index for each month.

Species	Month												Species Total	Rank	Percent
	F	M	A	M	J	J	A	S	O	N	D	J			
Trachypeneus constrictus		1		17	17	170	81	22	6	31	5	1	351	6	0.60
Sicyonia laevigata	1	1			7		2	1		16	3	6	37	8	0.06
Periclimenes longicaudatus	27	46	34	165	315	14	564	686	316	685	48	12	2912	3	4.94
Periclimenes americanus									2			2	4	11.5	0.01
Palaemon floridanus	1				1		16	1		1	6	1	27	9	0.05
Alpheus normanni					1		1			4	8		14	10	0.02
Thor dobkini	3	5	3		59	4	36	44	6	69	122	31	382	5	0.65
Latreutes fucorum	4	1		99	78	22	450	550	98	318	330	194	2144	4	3.63
Latreutes parvulus		4			9	7	4	6	1	20	1		52	7	0.09
Hippolyte pleuracantha	727	567	8	1767	3056	7501	10,705	7941	2540	3774	7298	3275	49,155	1	83.34
Tozeuma carolinense	75	179	139	165	116	17	1056	773	803	353	188	38	3899	2	6.61
Ambidexter symmetricus					1			1		1			3	13	0.01
Processa bermudensis					2					2			4	11.5	0.01
Monthly Total	838	804	184	2203	3662	7735	12,912	10,025	3778	5274	8009	3560	58,984	-	100.00
Simpson Index	.762	.550	.607	.649	.705	.941	.697	.641	.514	.537	.831	.850	-	-	-

is also indicated in Table 1. Hippolyte pleuracantha is ranked number 1 since it is the most common species, while Ambidexter symmetricus, the rarest species, is ranked number 13.

One species (Hippolyte pleuracantha) dominated the community, but a relatively high degree of diversity was observed during some seasons. The Simpson Index (C), which is a measure of the dominance concentration, was determined for each month using the following equation,

$$C = \sum_{i=1}^{s} p_i^2,$$

where s is the number of species in a sample and p_i, the relative importance values of the species (as proportions of the total number of shrimp) (Simpson, 1949). A community dominated by one species has an Index value of one, while the Index value decreases as more equitability exists. The Simpson Index indicated that the shrimp community had most equitability in numbers among species in the spring and in the fall (see Table 1). In March through May, C ranged from 0.550 to 0.649 and in September through November, from 0.514 to 0.641. In winter (December through February, C = 0.762 to 0.850) and in summer (June through August, C = 0.697 to 0.941) more dominance by H. pleuracantha was observed.

Seasonal Shrimp Density and Diversity:

An additional 1642 individuals, collected during quantitative sampling, were used to determine seasonal shrimp density and diversity. The quantitative changes which occurred in the populations over the seasons can be seen in Table 2. Numbers of shrimp collected in replicate samples from a column of water with a base of 0.84 m^2 are shown in the table and the average density (per m^2) for each month given.

Table 2. Shrimp density as determined from quantitative sampling from February 1977 to January 1978. Numbers of shrimp collected in replicate samples of 0.84 m^2 are shown and the average density per m^2 for each month given. Blanks indicate an absence of individuals. The Simpson Index of dominance concentration is also given for each month. Ovigerous females are shown in the upper half of the boxes.

Species	2-6-77	4-17-77	6-30-77	11-1-77	1-7-78
Trachypeneus constrictus			14 24	2	1 1
Sicyonia laevigata				2 1	
Periclimenes longicaudatus			1 3 7	35 8 12	
Ambidexter symmetricus				1	
Processa bermudensis			1		
Periclimenes americanus				1 1	
Palaemon floridanus				1	
Alpheus normanni			1	1	

continued

Table 2 continued.

Species	Date and Replicate Samples 2-6-77			4-17-77				6-30-77		11-1-77			1-7-78		
Thor dobkini		1						1 2	4	11	2	3	1		
Latreutes fucorum								1 1	3	18	2	6			
Latreutes parvulus								1							
Hippolyte pleuracantha	4 13	1 20	8			1 4	2	97 274	113 336	17 206	4 76	12 193	21	1 30	11
Tozeuma carolinense								2 4	3 6	2	1	2			
Sample Totals	19	22	8	0	0	5	2	401	498	294	93	234	23	32	11
Monthly average		16.3			1.8			449.5			207			22	
Average/m^2		19.6			2.2			541.6			249.4			26.5	
Simpson Index		.96			1.0			.83			.68			.91	

The shrimp density observed in this study fluctuated widely throughout the year, but may have reached greater densities than those reported in more tropical waters. The quantitative samples taken during this study showed that shrimp densities reached 541.6/m^2 during the summer.

Increased species richness was observed in the spring and in the fall in the quantitative samples, as it was in the monthly samples. The Simpson Index fluctuated in the same manner over seasons in both qualitative and quantitative samples, although it was consistently higher in the latter samples since fewer rare species were collected in the smaller sample sizes.

Reproduction:

All of the carideans for which sufficient numbers were collected exhibited a similar pattern of fecundity. The maximum percentage of ovigerous females (from 24 to 88% of each species) was collected in April through June (Table 3). A secondary peak of fecundity occurred in September or October for most species. The percentage of ovigerous females for the most numerous species averaged between 10 and 20% over the entire year. In the Appendix the lengths of the ovigerous period of each species collected in this study are compared with earlier studies.

Although the time of maximum reproduction was similar, a difference in the length of the period over which ovigerous individuals occurred was seen among species. Only *Hippolyte pleuracantha* females were ovigerous year-round. *Periclimenes longicaudatus* and *Tozeuma carolinense* were reproductively active from April through November and *Latreutes fucorum*, from May through January. Fewer ovigerous females and a shorter reproductive season were observed in the remaining four rarer species.

Table 3. Monthly abundances of ovigerous females in three pooled replicate dredges from February 1977 to January 1978. The number of ovigerous females is shown in the upper half of each box and the proportion of ovigerous individuals in the species is indicated in parentheses in the lower half of each box. Blanks indicate the absence of ovigerous females. In the final columns, the total number of ovigerous females of each species is indicated and the average percent of ovigerous females in the species is given.

Species	Month F	M	A	M	J	J	A	S	O	N	D	J	Total	Average Percent
Periclimenes longicaudatus			13 (38)	35 (21)	89 (28)	1 (7)	28 (5)	117 (17)	31 (10)	2 (.3)			316	11
Palaemon floridanus							5 (31)						5	19
Thor dobkini					14 (24)		3 (8)	3 (7)					20	5
Latreutes fucorum				9 (9)	30 (38)		47 (10)	122 (22)	11 (11)	14 (4)	11 (3)	10 (5)	254	12
Latreutes parvulus					3 (33)			2 (33)		2 (10)			8	15
Hippolyte pleuracantha	130 (18)	247 (44)	7 (88)	485 (28)	1318 (43)	1091 (15)	809 (8)	538 (7)	328 (13)	244 (6)	196 (3)	297 (9)	5690	12
Tozeuma carolinense			61 (44)	93 (56)	49 (42)	1 (6)	97 (9)	215 (28)	71 (9)	1 (.3)			588	15
Processa bermudensis					1 (50)								1	25

The critical conditions (probably a rise in water temperature) necessary to stimulate spawning apparently occurred by April for the most numerous species, although not until May for *Latreutes fucorum*.

The mean length of randomly selected ovigerous females was calculated for *Hippolyte pleuracantha* and for *Tozuema carolinense* to determine if the secondary reproductive peak observed in late summer represented a second clutch produced by females. The mean length was significantly different within species in the months measured (see Table 4 for the means and respective t values). For both species the mean length was shortest in October, suggesting that most of these ovigerous females are recently mature at this time, rather than being older females producing a second clutch.

The largest ovigerous females were found in June for both species. These individuals were probably hatched the previous fall or winter (in the case of *Hippolyte pleuracantha*). It is possible that some females may have been producing a second clutch in June (or in February in *H. pleuracantha*).

The mean number of eggs carried by females was also significantly different within species for June compared to October (see Table 4). Females of both species carried more eggs in June, when the mean female size was largest. Since ovigerous *Hippolyte pleuracantha* were present in February, the number of eggs carried by females at this time was also compared to the number carried by females in June and October. There were significantly more eggs carried in February as compared to October, but no significant difference was observed between the number of eggs carried in June versus February.

Table 4. The mean length of ovigerous females, the mean number of eggs carried, and the correlation between the two factors for *Hippolyte pleuracantha* and *Tozeuma carolinense* during different seasons. The number of randomly selected individuals measured each month (n) is indicated. Ranges are indicated in parentheses below mean values.

	Hippolyte pleuracantha			*Tozeuma carolinense*	
	June	October	February	June	October
n	20	20	10	10	10
Mean size (mm)[1]	13.4 (11.7-14.7)	12.0 (10.6-13.9)	15.6 (13.1-18.6)	44.3 (36.5-49.4)	34.4 (32.2-36.5)
Mean number of eggs[2]	111.2 (50-148)	75.8 (54-130)	108.9 (72-168)	403.2 (145-670)	84.6 (66-120)
Correlation between female size and number of eggs carried	0.412*	0.755***	0.644**	0.872***	0.513 NS

NS = non significant
* = $p<0.01$
** = $p<0.05$
*** = $p<0.01$

[1]The mean length within species was significantly different in the months measured [*H. pleuracantha*: June compared to October (t_{38} = 5.03***), June compared to February (t_{28} = 5.62***) and October compared to February (t_{28} = 4.98***); *T. carolinense*: June compared to October (T_{18} = 7.66***)].

[2]The mean number of eggs carried by *H. pleuracantha* was significantly different for June compared to October (t_{38} = 4.37***) and for October compared to February (t_{28} = 3.20***), but not for June compared to February (t_{28} = 0.08 NS). The mean number of eggs carried by *T. carolinense* was significantly different for June compared to October (t_{18} = 5.59***).

The relationship between the length of the female and the number of eggs carried is also shown in Table 4. For *Hippolyte pleuracantha*, the number of eggs carried by females was significantly correlated with female length for all three months examined. The strongest correlation was observed in October. For *Tozeuma carolinense*, the correlation between female size and the number of eggs carried was not significant in October, but highly significant in June.

Intersite Comparisons:

The dominant grass species varied between Stations 1 and 2. Station 1 had dense beds of *Thalassia testudinum*, while Station 2 had thinner grassbeds containing mainly *Syringodium filiforme*. [Strawn (1961) also observed greater proportions of *S. filiforme* at Cedar Key in more protected areas which had soft bottoms.] Station 2 was a more open grassbed since the blades of *S. filiforme* are terete as compared to the wider, flat blades of *T. testudinum* and the blades at Station 2 were less dense. Because of the difference in the distributions of the dominant grass species, the shrimp communities at the two sites were compared and the changes in the community with increasing depth were examined at both stations.

A comparison of the proportion of each shrimp species observed at the two stations on two separate occasions (May and October) showed greater dominance at Station 1 and more species equitability at Station 2 (see Table 5). The high levels of the Simpson Index at Station 1 resulted from dominance by *Hippolyte pleuracantha*, which comprised 84% of the community in May and 82% in October. At Station 2 this species accounted for only 69% and 48% of the community in these months. *Tozuema carolinense*, the second most abundant species at both stations

Table 5. Comparison of dominance concentration as measured by the Simpson Index between Stations 1 and 2 in May and in October and the percentage similarity between the two communities for the same dates.

MEASURE	DATE 5-4-77	10-2-77
Simpson Index		
Station 1	0.71	0.70
Station 2	0.51	0.38
Percent Similarity		
Stations 1 and 2	0.86	0.64

showed the opposite trend. A greater percentage of these individuals was observed at Station 2 (12 and 37% versus 6 and 9% at Station 1). All of the other species declined in abundance from Station 1 to 2, except Latreutes fucorum which comprised nearly the same percentage at both stations in both months (46% in May and 23% in October).

The percentage of similarity (PS) between the two stations was determined for the two months and is also shown in Table 5. The calculation is based on the sum of the differences in proportions of each species occupying the two stations and is given by the following equation:

$$PS = 2 \Sigma \min (n_a \text{ or } n_b)/N_a + N_b).$$

In this equation, min is the minimum value, n_a and n_b are the proportions of a given species at Stations 1 and 2, and N_a and N_b are the totaled proportions of all species comprising both stations (Whittaker, 1975). Using this measure, the two stations were more similar in May (86%) than in October (64%).

Comparisons of community composition at increasing depth indicated that shallow communities showed more dominance at both stations (see Table 6). Although three depths were examined, only two different types of grass beds were observed. Some grassbeds were composed entirely of Thalassia testudinum and others had this species mixed with Syringodium filiforme. At both stations, the medium and deep samples were very similar, but different from the shallow samples. The shallow sample at Station 1 was taken in grassbeds of primarily T. testudinum, while the other two samples were taken from a mixed grassbed. At Station 2 the opposite was true, with the deeper samples being taken from primarily T. testudinum.

At Station 1, Hippolyte pleuracantha dominated the shallower waters where Thalassia testudinum was thickest and the proportion of this

Table 6. Shrimp community dominance values related to water depth at Station 1 in August and in November and at Station 2 in October. The depths are indicated by S, M, and D which refer to shallow, medium, and deep, respectively.

	DATE		
	Station 1		Station 2
DEPTH	8-5-77	11-6-77	10-2-77
S	0.87	0.56	0.47
M	0.62	-	0.41
D	0.70	0.40	0.38

shrimp species decreased with increasing depth (see Table 7). At Station 2 the proportion of *H. pleuracantha* increased with depth as the density of the grass bed and the amount of *T. testudinum* increased. *Tozuema carolinense* dominated in the shallow beds at Station 2.

The percentage similarity between the depths can be seen in Table 8. The species composition is similar at all depths sampled at Station 1. However, at Station 2, proportions of shrimp species in the shallowest sample, which was in an area of primarily *Syringodium filiforme*, differed from the two deeper samples in grassbeds containing more *Thalassia testudinum*.

Comparisons of the two stations showed that Station 1 had a higher Simpson Index as a result of dominance by *Hippolyte pleuracantha* in the grassbeds composed almost entirely of *Thalassia testudinum*. More species equitability was observed at Station 2 and at both stations with increasing depth.

Regulation of Community Structure

Two major factors regulating community structure were examined--biological interactions and the physical conditions of the environment. Three biological interactions were studied: competition, predation, and parasitism. The effects of these interactions will be described first. Then, the effect of the physical environment will be examined as to its role in providing habitat heterogeneity and in influencing the presence of species through their tolerances to extremes or to fluctuations in physical conditions.

Biological Interactions: Predation

Predator exclusion. To examine the effect of reduced predation on the shrimp community structure, two caging experiments were performed in

Table 7. Comparisons of the proportions of *H. pleuracantha* and *T.* collected with increasing depth at Station 1 in August and November and at Station 2 in October. The depths are indicated by *S*, *M*, and *D*, referring to shallow, medium, and deep, respectively and the depths in meters are given below the letter.

	DATE							
	Station 1					Station 2		
	8-5-77			11-6-77		10-2-77		
	S	M	D	S	D	S	M	D
SPECIES	0.6	0.9	1.2	0.8	1.4	1.2	1.4	1.5
H. pleuracantha	0.93	0.77	0.83	0.73	0.57	0.24	0.48	0.51
T. carolinense	0.05	0.15	0.02	0.06	0.10	0.64	0.42	0.33

Table 8. Percentage similarity between communities at different depths for Station 1 in August and in November and for Station 2 in October. The depths are indicated by S, M, and D, referring to shallow, medium, and deep, respectively.

DEPTH COMPARISONS	DATE Station 1 8-5-77	Station 1 11-6-77	Station 2 10-2-77
S-M	0.84	-	0.76
M-D	0.86	-	0.90
S-D	0.87	0.82	0.66

the field. The results of the experiments can be seen in Table 9. Exclusion of predators resulted in increased shrimp density in both experiments. On August 8th, after cages had been in place 19 days, the average shrimp density in two cages significantly increased ($t_1 = 6.35$, $p < 0.1$) from an average of $341/m^2$ to $7346/m^2$, or over 21 times the control. (The difference in density between the two replicate cages may reflect a large variance in density from one site to another or may have resulted from a partial lack of contact of Cage 1 with the bottom.) Considering only Cage 2, shrimp density increased 27 times over the control. The shrimp density also increased in one cage after 8 days of caging on August 19th. An increase of 3.8 times the control was observed, from 200 shrimp/m^2 to $754/m^2$. Since the replicate cages of the 8 day experiment were damaged, the large variance obtained during the August 8th experiments was used and this almost fourfold increase was not significant ($t_1 = 0.502$, NS). In both caging experiments, the Simpson Index increased as a result of increased proportions of _Hippolyte pleuracantha_. No significant difference was noted between the mean size of shrimp in the experimental cages versus the controls.

Fish preference: Predation was expected to be of primary importance in determining the community structure since shrimp were found to be a major component in the diet of numerous fish species present at Cedar Key (Reid, 1954). However, the species of shrimp eaten by fish were not identified in that study. In order to determine if fish predators selected a particular species of shrimp or if they fed on the most numerous species, several fish species were collected from the grassbeds and examined for feeding behavior in the presence of 10 individuals of each of the two most numerous shrimp species, _Hippolyte_

Table 9. The effect of predator exclusion by caging on the shrimp community for 19 days and 8 days in July and August 1977. Numbers of shrimp taken in replicate cages (C1 and C2) are compared to quantitative control samples (Q1 and Q2) taken in an adjacent uncaged area. The Simpson Index of dominance concentration is also given for the caged and control samples for both dates.

SPECIES	19 days Q1	19 days Q2	19 days C1	19 days C2	8 days Q1	8 days C1
Trachypeneus constrictus	10	11	11	21	7	4
Sicyonia laevigata					1	7
Periclimenes longicaudatus	1	2	12	33	8	14
Ambidexter symmetricus						7
Periclimenes americanus			1			
Palaemon floridanus	1		22	38	2	
Alpheus normanni	1	2	11	8		12
Thor dobkini	1			14	3	18
Latreutes fucorum				1	32	20
Latreutes parvulus				1		
Hippolyte pleuracantha	318	218	4474	7519	114	541
Tozeuma carolinense		1	6	22	5	3
Total	332	234	4537	7657	166	626
Simpson Index	.918	.870	.972	.964	.514	.750
Mean Shrimp density/m^2	341		7346		200	754

pleuracantha and Tozeuma carolinense. The fish species tested were ones which were most common in the grassbeds and which were known to consume shrimp (Reid, 1954).

Although both of the shrimp species were eaten by most of the species of fish tested, several of the most common fish species appeared to prefer *Hippolyte pleuracantha* (see Table 10). The fish generally consumed *H. pleuracantha* first and switched to *Tozeuma carolinense* only after *H. pleuracantha* was no longer present. Two fish were particularly voracious, an 80 mm *Urophycis floridanus* (Gulf Hake) and a 40 mm *Lagodon rhomboides* (Pinfish). Both fish immediately attacked and consumed *H. pleuracantha*, but appeared to have more difficulty recognizing and handling *T. carolinense*.

Other fish species had to be kept as long as 12 hours with the shrimp before the latter were consumed. Both a 75 mm *Monacanthus hispidus* (Planehead Filefish) and a 100 mm *Centropristes melanus* (Black Sea Bass) also consumed both species of shrimp. A 75 mm *Symphurus plagiusa* (Blackcheek Tonguefish) and a 44 mm *Astroscopus y-graecum* (Southern Stargazer) consumed only *H. pleuracantha*. Neither a 75 mm *Paralichthys albigutta* (Gulf Flounder) nor an 110 mm *Sygnathus floridae* (Florida Pipefish) consumed either species of shrimp, although both fish species are known to consume shrimp occasionally (Reid, 1954).

In these experiments, *H. pleuracantha* and *T. carolinense* were observed to have different methods of avoidance of fish predators. *H. pleuracantha* darted rapidly from place to place in the presence of fish. The shrimp were able to avoid capture at first, but the fish rapidly learned to catch them. *T. carolinense* appeared more difficult for fish to recognize. This shrimp did not move as rapidly and jumped only after

Table 10. Preference of common fish species for *Hippolyte pleuracantha* as compared to *Tozeuma carolinense*. Ten individuals of each shrimp species were introduced into an aquarium one hour prior to the introduction of a single fish. The shrimp species selected first for consumption by the fish and the time elapsed before consumption were noted. (I = immediately consumed; S = secondarily consumed, after all individuals of *H. pleuracantha* had been been consumed; D = delayed consumption--12 hours later; N = not consumed).

Fish species	*H. pleuracantha*	*T. carolinense*
Urophycis floridanus	I	S
Lagodon rhomboides	I	S
Monacanthus hispidus	D	D
Centropristes melanus	D	D
Symphurus plaguisa	D	N
Astroscopus y-graecum	D	N
Paralichthys albigutta	N	N
Syngnathus floridae	N	N

being accidently bumped. However, once the fish developed a search image and learned how to eat this species, T. carolinense individuals were chased and consumed rapidly. The smaller fish, particularly, appeared to have difficulty handling the large size and long rostrum of T. carolinense.

Biological Interactions: Competition

No direct evidence of competition for either space or food was observed within or between the two most numerous species (Hippolyte pleuracantha and Tozeuma carolinense) during 3 hour periods of direct observations in the laboratory. Aggression appeared to be lacking as individuals of both species were observed to cling passively to grass blades, to the sides of aquaria, or to each other.

Some indirect evidence of competition for habitat was suggested by the distributions of the two dominant shrimp species. Samples from grassbeds containing the two major grass species (Thalassia testudinum and Syringodium filiforme) showed that some segregation by habitat was occurring between the two most numerous shrimp species. H. pleuracantha was more numerous in beds of T. testudinum while T. carolinense was more common in S. filiforme, although both shrimp species were collected in association with both grass species (see Table 7). Less segregation by grass species was observed in the other shrimp species. However, the habitat segregation may also be related to the different densities of red algae associated with the different grass species and the effect of algal density on predators and mobility of the shrimp (see the discussion).

Since the degree of overlap in the size of the various species may influence the level of competition between them, the shrimp species are listed in Table 11 by family. The size range of individuals collected

Table 11. Sizes of species collected at Cedar Key. The size range of each species is given by family and the frequency of occurrence of each species in the monthly trawls is indicated. Abundant = more than 1000 individuals per year; Common = more than 100 individual per year; Rare = less than 100 individuals per year. The mean sizes of ovigerous females of the five most numerous caridean species are also given.

FAMILY	SPECIES	SIZE RANGE (mm)	FREQUENCY OF OCCURRENCE	MEAN SIZE OVIGEROUS FEMALES (mm)
Penaeidae	*Trachypeneus constrictus*	6.5 - 61.0	common	
	Sicyonia laevigata	4.2 - 35.1	rare	
Palaemonidae	*Periclimenes longicaudatus*	5.4 - 24.4	abundant	19.0
	Periclimenes americanus	5.2 - 10.4	rare	
	Palaemon floridanus	8.1 - 41.9	rare	
Alpheidae	*Alpheus normanni*	5.9 - 24.2	rare	
Hippolytidae	*Thor dobkini*	3.9 - 15.9	common	12.5
	Latreutes fucorum	5.4 - 18.0	abundant	15.5
	Latreutes parvulus	7.3 - 11.5	rare	
	Hippolyte pleuracantha	3.6 - 18.4	abundant	13.3
	Tozeuma carolinense	9.6 - 53.8	abundant	39.4
Processidae	*Ambidexter symmetricus*	4.0 - 09.7	rare	
	Processa bermudensis	12.3 - 21.2	rare	

is given and the frequency of occurrence of each species is indicated. The data show an extensive overlap in size ranges occurs, particularly within and between the two most numerous families. Measurements of a random selection of ovigerous females were made in the five most numerous caridean species. The analysis of variance of the mean sizes and the subsequent use of LSD (least significant difference) indicated that mean sizes were significantly different for all species except Hippolyte pleuracantha and Thor dobkini ($F_{4,86} = 226.75$, $p < 0.0001$).

Biological Interactions: Parasitism

Table 12 illustrates the amount of parasitism by bopyrid isopods observed. Isopod parasites were most common on Hippolyte pleuracantha, occurring on an average of 3% of the individuals. A single parasite was found on Thor dobkini in two different months and one was also observed on Periclimenes longicaudatus. Parasites were not observed on other species. No ovigerous individuals of any species were parasitized.

Physical Influences: Habitat Structure

Grassbed density. The significant correlation ($r_3 = 0.923$, $p < 0.05$) between grass blade density and shrimp density can be seen in Table 13. During the winter, when temperature and salinity were low at Cedar Key, the grass beds were brown and less dense. An average of approximately 85 blades/m^2 was observed during quantitative sampling. Shrimp densities at this time were low and the samples were dominated by Hippolyte pleuracantha (see Table 2). Only two other species, Thor dobkini and Trachypenaeus constrictus were observed at this time in the shallows, although more species were present in the winter monthly dredges which were longer and included shrimp from slightly deeper water (see Table 1).

Table 12. Percent of non-ovigerous individuals parasitized by isopods. Percentages for *Hippolyte pleuracantha* were determined from examination of 100 randomly selected non-ovigerous individuals. All individuals of other species were examined for parasites. Blanks indicate an no parasites observed. Species not listed lacked parasites.

Shrimp Species	Month F	M	A	M	J	J	A	S	O	N	D	J
Hippolyte pleuracantha	2.0	4.0		4.0	9.0	4.0		4.0	1.0	5.0	1.0	2.0
Periclimenes longicaudatus							0.2					
Thor dobkini								2.4				0.8

Table 13. Relationship between the density of grass blades and the mean shrimp density during the four seasons ($r_3 = 0.923$, $p < 0.05$). The number of grass blades was determined by averaging the blades counted by 2 individuals during replicate quantitative sampling.

Date	Grass blades/m^2	Shrimp/m^2
2-6-77	85	16.3
4-17-77	35	1.8
6-30-77	2125	449.5
11-1-77	1856	207.0

In early April, most of the *Thalassia testudinum* blades had been shed, resulting in a density of grass blades of only 35/m^2. The only shrimp species collected in the shallows at this time was *Hippolyte pleuracantha* and its density was reduced drastically. Deeper beds of *Syringodium filiforme* were not damaged as much by the low temperatures.

The beds were most dense during the midsummer, reaching approximately 2125 blades/m^2. At this time salinity and temperature also reached their highest values (see Figure 2). Many shrimp species were present, although juvenile *Hippolyte pleuracantha* dominated the community.

The grassbeds remained dense into the fall (1856 blades/m^2), although many of the blades became brown. Even though total shrimp density declined at this time, species diversity increased (see Table 2).

No quantitative studies were performed on the seasonal variation in red algae density. However, *Hippolyte pleuracantha* appeared to be more numerous and *Tozuema carolinense* numbers seemed to decline in samples which had many clumps of red algae.

Habitat preference. Since the two most numerous shrimp species off Cedar Key appeared to be associated with different grass bed habitats, a set of experiments was designed to determine if these two species would select different habitats. First, both shrimp species were tested for habitat preference among four different substrates, each of which supported two blades of *Thalassia testudinum*. Randomized block analyses were performed since it had been noted that both species of shrimp in the absence of grass preferred the ends of the aquarium which provided more glass surface to cling to. In the presence of grass, neither position in the tank (edges versus middle) (F_1 = 0.82, NS for *Hippolyte pleuracantha*; F_1 = 4.54, NS for *Tozeuma carolinense*) or any substrate type (F_3 = 0.67, NS for *H. pleuracantha*; F_3 = 3.45, NS for *T. carolinense*) was preferred by either species (see Table 14). In almost all cases, individuals were observed clinging to the blades, rather than to the substrate or glass.

Providing a choice of three grass types, including *Thalassia testudinum*, *Syringodium filiforme*, or green plastic grass, indicated no significant preference among the choices for either *Hippolyte pleuracantha* (F_2 = 1.42, NS for grass and F_3 = 0.13, NS for substrate) or *T. carolinense* (F_2 = 0.30, NS for grass and F_3 = 0.09, NS for substrate), although both species of natural grass were slightly preferred over the artificial grass (see Table 15).

Physical Influences: Temperature

At Cedar Key, proportions of *T. carolinense* individuals were highest in monthly samples in the spring and fall, but the proportions declined sharply in the summer and winter when extreme temperatures occurred in the shallows (Table 1). The density of *H. pleuracantha* decreased during winter, although the species was still numerous and the highest density occurred in the summer (Table 2). Since it appeared that *T. carolinense* might be more sensitive to temperature extremes than *H. pleuracantha*, a final set of experiments was performed to determine any differences in temperature preference between the two species. An aquarium with a temperature gradient was used and the results of seven experiments were pooled (see Table 16). A Chi-square analysis indicated a highly significant ($p < 0.005$) difference in preferred temperature for the two species. Forty-three percent of *H. pleuracantha* individuals

Table 14. Selection of *H. pleuracantha* and *T. carolinense* for different substrates, based on grain size (M = mud, S = sand, G = gravel, R = rock). Two blades of *T. testudinum* anchored in each substrate type. A randomized block design was used, with two positions in the aquarium and four treatments (grain size) for each shrimp species. The average number of shrimp taken in each position was calculated after adjustments were made for differences in the number of shrimp used in replicate tests. Analysis of variance indicated no significant preference for either the positions or the substrates for either shrimp species in the presence of grass (for *H. pleuracantha*, $F_1 = 0.82$ for position, NS and $F_3 = 0.67$ for substrates, NS; for *T. carolinense*, $F_1 = 4.54$, NS for position, $F_3 = 3.45$, NS for substrates).

	H. pleuracantha				*T. carolinense*		
	POSITION				POSITION		
SUBSTRATE	edge	middle	TOTAL	SUBSTRATE	edge	middle	TOTAL
mud	0	3.7	3.7	mud	3.8	4.0	7.8
sand	9.4	0	9.4	sand	7.3	3.8	11.1
gravel	4.6	6.0	16.6	gravel	4.3	3.8	8.1
rock	12.0	4.6	16.6	rock	7.5	4.7	12.2
TOTAL	26.0	14.3	40.3	TOTAL	22.9	16.3	39.2

Table 15. Selection by *H. pleuracantha* and *T. carolinense* for different types of grass, *T. testudinum*, *S. filiforme*, and artificial grass. A randomized block design was used, in which two blades of each grass type were placed in each substrate. The number of shrimp taken over each grass type and substrate is indicated. Analysis of variance showed that no significant preference existed for either grass type or substrate for *H. pleuracantha* (F_2 = 1.42 NS for grass type, F_3 = 0.13, NS for substrate) and for *T. carolinense* (F_2 = 0.30, NS for grass type and F_3 = 0.09, NS for substrate).

H. pleuracantha					*T. carolinense*				
	GRASS TYPE					GRASS TYPE			
SUBSTRATE	*T.*	*S.*	plastic	TOTAL	SUBSTRATE	*T.*	*S.*	plastic	TOTAL
mud	2	0	1	3	mud	2	1	2	5
sand	3	1	3	7	sand	1	2	1	4
gravel	3	0	0	3	gravel	2	3	1	6
rock	1	5	3	9	rock	3	4	2	9
TOTAL	9	6	7	22	TOTAL	8	10	6	24

Table 16. Temperature ranges selected by *H. pleuracantha* and *T. carolinense* in an aquarium with a temperature gradient. The number of individuals selecting each range during the seven replicate tests were pooled. The percentage of individuals in each temperature range is indicated in parantheses. A Chi-square analysis indicated a highly significant ($p < 0.005$) difference in preferred temperature for the two species.

	TEMPERATURE				
SPECIES	Below 26°	26-28°	28-30°	Above 30°	TOTAL
H. pleuracantha	24(23)	35(33)	11(10)	35(33)	105
T. carolinense	46(34)	45(33)	26(19)	18(13)	135

were observed above 28°C and 33 % above 30°C. Only 32 % of _T_. _carolinense_ were found above 28° C and 13% above 30°C.

DISCUSSION

Shrimp Community Structure

Component Species and Dominance Relationships:

Although shrimp diversity was observed to be high in grassbeds off Cedar Key, much greater diversity is seen in tropical grassbeds. The greatest diversity of shallow-water shrimp along the western Atlantic coast occurs near the larger West Indian islands where 170 shallow-water and fresh-water shrimp have been identified (Chace, 1972). The Smithsonian-Bredin Caribbean Expeditions in 1956, 1958 and 1959 resulted in the collection of 111 species of shallow-water marine species of penaeidean, caridean, and stenopodidean shrimps (Chace, 1972). At one station in English Harbour, Antigua Island, 31 species were taken in one afternoon and an additional 17 species were collected at other stations in that port.

Sampling along the Florida coast has resulted in less diversity. Tabb and Manning (1961) collected 31 shrimp species from many different habitats in Florida Bay. Wass (1955) collected 28 species in Alligator Harbor and Eng (1968) collected 20 species at Cedar Key. (One additional species was found at Cedar Key during this study.) Sampling only the shrimp species occurring in seagrass meadows, Heck (1977) collected 17 species off Panama, as compared to the 13 species collected during the present study at Cedar Key. Approximately half of the species identified by Heck also were observed at Cedar Key.

Since shrimp have pelagic larvae, they generally have wide distributions. The presence or absence of a particular species, therefore, is not limited by its dispersing ability, but is most dependent upon the size and availability of suitable habitats and proper climatic conditions. All but one of the species found in the grassbeds off Cedar Key also are found in the West Indies and in the Carolinian fauna (Williams, 1965; Chace, 1972), suggesting that most of the species collected off Cedar Key have very broad habitat requirements.

Although Chace (1972) postulated that there are no endemic marine natantian fauna in the West Indies due to the lack of natural barriers, one species collected at Cedar Key, *Palaemon floridanus*, is endemic to the west coast of Florida. The presence of an endemic species is not unexpected since the northern Gulf of Mexico has a temperate climate, but is isolated from the climatically similar Atlantic Ocean by a warm water barrier. These warmer waters which contain a shrimp fauna having a much greater affinity with the West Indies Fauna than with the Gulf of Mexico or with the Atlantic coast (Rouse, 1970) must limit the dispersal of *P. floridanus*.

Although the shrimp species collected at Cedar Key are the same as those collected in nearby similar habitats, the order of dominance in the shrimp community varies with location. *Hippolyte pleuracantha* was found to dominate the shrimp community at Cedar Key, but this species was not dominant in other studies. In the northeastern Gulf of Mexico in shallow waters off the mouths of the Econfina and Fenholloway Rivers, Hooks et al. (1976) reported that the four most numerous shrimp species were, in order: *Tozeuma carolinense*, *Palaemon floridanus*, *Hippolyte pleuracantha* and *Periclimenes longicaudatus*. Heck (1977) also reported that *T. carolinense* was the most numerous shrimp collected in grassbeds in the Caribbean off Panama. Several other shrimp species including

Alpheus floridanus, P. americanus, P. longicaudatus, Sicyonia laevigata, Thor floridanus and Latreutes fucorum were more numerous than the Hippolyte species (H. zostericola) he collected. Rouse (1970) reported that the dominant shrimp in grassbeds off south Florida were T. carolinense and P. longicaudatus. The apparent replacement of T. carolinense by H. pleuracantha as the most numerous shrimp species at Cedar Key may be related to a difference in the predominant vegetation which is discussed in a later section.

Seasonal Shrimp Density and Diversity:

The shrimp fauna of more tropical and subtropical grassbeds probably shows less seasonal variation in density and diversity than does the fauna of grassbeds off Cedar Key, although studies of seasonal variation of the shrimp community in more tropical grassbeds were not available for comparison. Some studies have pointed out that tropical communities also experience unpredictable disturbances which limit diversity (Moore, 1972; Sale, 1977; Connell, 1978). However, the frequency and intensity of disturbance generally increase from the equator to the poles. The fluctuations in density of shrimp in temperate grassbeds may be greater than those observed in the tropics as a result of the more prominent cycles of grass and algae, both of which (along with their associated epiphytes) provide the shrimp with food and shelter from predation. At Cedar Key, shrimp density and diversity, therefore, show seasonal oscillations corresponding to fluctuations in the habitat.

Reproduction:

All of the common species of shrimp exhibited a similar pattern of fecundity, with the maximum number of ovigerous females present in June and October. This synchronization of spawning may confer at least two advantages to the shrimp community. Concurrent release of young may serve to overwhelm predators and breeding may be restricted to times of optimal environmental conditions.

Since Hippolyte pleuracantha, the most numerous species (and probably the species experiencing the greatest predation), is the only species which reproduces throughout the year, environmental conditions rather than predation appeared to be more important in regulating shrimp reproduction. The adverse environmental conditions may have been due to temperature extremes or due to the loss of habitat and food which occurred when grass blade density decreased (these factors are discussed further in the section dealing with physical influences on shrimp populations).

There is some evidence to suggest that in warmer climates both Hippolyte pleuracantha and Tozeuma carolinense females are ovigerous for a greater part of the year and that they make up a greater percentage of the total number of each species. Ovigerous females of H. pleuracantha are present from April to October off Beaufort, N. C. (Williams, 1965), but are present all year at Cedar Key where they average 23.5% (range, 3 - 88%) of the individuals collected (see Table 3). Off south Florida, Rouse (1970) reported that approximately three-fourths of H. pleuracantha individuals collected were ovigerous females.

Throughout much of the range of Tozeuma carolinense females are ovigerous from May to October (April to November in this study), although in warmer climates females can be ovigerous in the winter months (Williams, 1965; Rouse, 1970; Heck, 1977). In this study ovigerous females averaged 16.2% over the year and 26.9% (range, 0.3

-56%) of the species in the months they were present (see Table 3). In south Florida, where females are ovigerous all year, 46% of _T. carolinense_ individuals were ovigerous females (Rouse, 1970). Heck (1977) also observed that the percentage of ovigerous females was greater than 60% of the population year-round along the west coast of Panama.

Year-round reproduction may not be advantageous for many shrimp species in a seasonally fluctuating environment. Fluctuating environments do not always favor a longer reproductive season if reproduction makes an ovigerous female more susceptible to environmental conditions or to predation (Schaffer, 1974). In a variable environment, a trade-off may exist between adult survival and reproductive effort, such that an adult which does not extend reproduction into winter may have a better chance of surviving to the next breeding season than would the young had the adult reproduced (Sterns, 1976; Goodman, 1979). This appears to be the case for most of the shrimp species at Cedar Key. Here most species postpone breeding during the colder months (see Table 3), although many _Hippolyte pleuracantha_ individuals do not. Ovigerous females and juveniles of this species may be better able to survive extreme winter (or summer) temperatures, as well as the shedding of the grass blades than can other species.

Examination of the mean lengths of ovigerous _Hippolyte pleuracantha_ and _Tozeuma carolinense_ in different months suggested that the second reproductive peak observed in the fall did not represent a second clutch produced by females. Ovigerous females were smallest at this time (see Table 4), indicating they had hatched earlier in the same year and were reproducing for the first time. The ovigerous females present in the first half of the year may have been producing a second clutch, although they most likely hatched the previous fall. The size of the females of both species was correlated to the number of eggs carried so that fewer eggs were carried by the smaller females present in the fall. Additional evidence for only a single clutch being produced by females was that no evidence of reproductive fatigue (larger females carrying fewer eggs in the second clutch) was observed.

Intersite Comparisons:

A comparison of two stations which were dominated by different species of grass yielded a difference in proportions of the various shrimp species present. *Thalassia testudinum* beds were dominated by *Hippolyte pleuracantha* while more species equitability existed in beds of *Syringodium filiforme*. *Tozeuma carolinense* individuals comprised a much greater percentage of the total number of shrimp in *S. filiforme* beds.

The predominant vegetation apparently influences not only shrimp density, but also influences the dominant shrimp species. Both Tabb et al. (1962) and Heck (1977) suggested that the lower shrimp densities they observed might be related to a reduction in red algae in the grass-beds of south Florida and off the Caribbean coast of Panama. The red algae provide shelter for shrimp, but herbivorous fish, which are more dominant in the tropics, consume the algae (Weinstein and Heck, 1979). Tabb et al. (1962) found that *Thalassia testudinum* beds with little red algae were dominated by *Periclimenes longicaudatus* and *Tozeuma carolinense*, while *Hippolyte pleuracantha* dominated and numbers of *Thor dobkini* and *Latreutes fucorum* increased when more red algae were present. This observation also appears to be supported by Rouse (1970).

His study found the dominant shrimp to be _T. carolinense_ and _P. longicaudatus_ in grassbeds off south Florida. Heck (1977) found that _T. carolinense_ also dominated the grassbed community off Panama.

The dominance of the shrimp community by _Hippolyte pleuracantha_ at Cedar Key may be related to abundant red algae in the grassbeds. In the present study no quantitative studies were performed on the seasonal variation in red algae density. However, _H. pleuracantha_ was more numerous while the proportion of _Tozeuma carolinense_ declined in samples which had many clumps of red algae. The red algae (primarily _Gracilaria sp._) were very dense in samples in which the density of _H. pleuracantha_ individuals was greatest (June through September, see Table 1). _T. carolinense_ proportions were lowest in June and July, although this may have also been a function of high temperatures occurring in the shallows.

The greater species equitability in beds of _Syringodium filiforme_ may have been due to the more open habitat which might allow greater predation. Beds of _Thalassia testudinum_ were shallower, denser and had more clumps of red algae. These habitats may also have been less optimal for fish predators, allowing large densities of _Hippolyte pleuracantha_ to occur.

Regulation of Community Structure

Biological Interactions: Predation

Predation appeared to be the most important biological factor regulating community structure. Results of the first caging experiments of predator exclusion indicated that shrimp density increased significantly in the absence of fish predators. In both caging experiments the Simpson Index of dominance concentration increased as a result of increased proportions of Hippolyte pleuracantha. Several previous studies have also shown that prey species increase in numbers when free of predators (Hutchinson, 1961; Paine, 1966; Castenholz, 1961; Haven, 1973; Dayton, 1971; Kitching and Ebling, 1967; and Paine and Vadas, 1969). The lack of predation in the cages would be expected to benefit H. pleuracantha most if this species experiences the greatest predation as is suggested by the experiments of fish preference.

These experiments of fish preference indicated that predation pressure was greater for Hippolyte pleuracantha than for Tozeuma carolinense. The species of fish examined in the lab experiments generally preferred H. pleuracantha, which appeared easier to recognize and to handle. In the grassbeds, larger fish might prefer the larger size of T. carolinense, although small fish of the sizes and species used in the experiments dominate the shallow grass beds and as fish become larger, their diets tend to become more varied (Reid, 1954). In the absence of prey selection by fish, predation would also be expected to be greatest on H. pleuracantha since it is the most numerous species. Emlen (1966) predicted that rare species should be even less common in the diet of predators and abundant species more common than they would be expected to be by their frequencies since rarity would prevent predators from forming a search image while abundance would allow this phenomenon to occur.

The form and behavior of shrimp also suggest that predation has an important influence on them. Shrimp maintained in aquaria in the laboratory obviously had excellent vision since they were observed to hide behind grass blades and to shift their position slightly to remain hidden whenever the position of the observer changed. They were also capable of rapid darting movements to escape if disturbed.

Most species of shrimp collected (including Hippolyte pleuracantha and Tozeuma carolinense) avoid detection by predators by matching their body color with the environment, either through their feeding habits or by regulation of body pigments (Hornell, 1897; Gamble and Keeble, 1900; Minkiewicz, 1908; Brown, 1934, 1935a, 1939; Voss, 1956; and Ewald, 1969). The two most numerous species, Hippolyte pleuracantha and Tozeuma carolinense, have evolved additional behavioral and morphological adaptations which may further reduce predation. H. pleuracantha individuals have feathery structures along their bodies which resemble hydroids and which help to camouflage them. This species was observed to dart rapidly from place to place when disturbed.

The predator avoidance strategy of Tozeuma carolinense was different. While clinging to grass or while swimming, the long axis of the body of T. carolinense is oriented in a vertical direction, with the head directed downward. Individuals drift slowly through the water, resembling a stick or a piece of grass and are not easily dislodged when clinging to vegetation. However, like H. pleuracantha, they also may dart rapidly backward from danger.

The unusually long rostrum and body of Tozeuma carolinense, although effective as camouflage and in making handling by fish more difficult, pose problems during development. Larval mortality may be increased due to difficulty in casting off the old exoskeleton (Bryce, 1961). However, Levins (1975) using loop analysis to examine community properties, showed that a prey population cannot be increased through an increase in feeding efficiency or through increased viability or fecundity, but could be increased by selection for effective predator avoidance, even if the strategy were accompanied by lower fecundity or by a reduced resistance to physical factors. Therefore, these adaptations of _T. carolinense_ for escaping predation may be important in allowing high densities of this species to occur in a fairly open habitat.

Biological Interactions: Competition

Competition was not observed to play a significant role in maintaining shrimp community structure. No direct evidence of competition was observed in the laboratory aquaria. In addition, the results of the caging experiments suggested that competition in nature was not keen. As shrimp numbers increased in the cages over time, interspecific competition should have also increased. However, no significant difference was observed in the number of species present in the cages versus the controls so that competitive exclusion did not occur. As indicated in an earlier section, the relative proportion of _Hippolyte pleuracantha_ in the cages did increase at the expense of the other species, but this may also be attributed to a lack of predation which would allow the most heavily preyed-upon species to increase most.

Examination of the degree of overlap in size among shrimp species suggested that rather than a competitive separation of sizes occurring, extensive size overlap was observed. Evidently being within a particular size range was of more importance for avoiding predation, for finding food, or for some other reason than was the avoidance or reduction of competition.

Comparisons of the mean sizes of ovigerous caridean females showed a significant difference in all but two species. However, the size separations between species were narrow in several cases so that even though the species were mathematically distinct, they may not have been ecologically distinct. The three least distinct species (*Hippolyte pleuracantha*, *Thor dobkini*, and *Latreutes fucorum*) generally coexist in shallow grassbeds containing abundant red algae while the two larger species (*Periclimenes longicaudatus* and *Tozeuma carolinense*) are often collected together in more open grassbeds (Tabb et al., 1962). This coexistence of the most similar species within the same habitats suggests that competition is not strongly felt.

Evidence for the existence of moderate levels of competition is the difference in size and shape and the habitat segregation of the two most numerous species. Being most numerous these two species might be expected to compete heavily without the separation in morphology. However, the habitat segregation may not only result from competitive pressure but may also be attributed to differences in the abundance of red algae in each habitat and to reduced predation in the denser *Thalassia testudinum* beds. It is very possible that diffuse competition [which MacArthur (1972) has defined as the impingement on a species to varying degrees by several other species] occurs within the shrimp community and is difficult to detect or measure.

Biological Interactions: Parasitism

Of all the factors considered in this study, parasitism appeared to play the least significant role in maintaining community structure. Only *Hippolyte pleuracantha* was regularly parasitized by isopods and the average percentage of individuals parasitized was only 3%. Parasitized individuals may have been subject to greater predation than non-parasitized individuals so that the extent of parasitism may have been underestimated. However, Anderson (1977) determined that parasitism of *Probopyrus pandalicola* on *Palaemonetes pugio* influenced the growth efficiency of the host but had no significant effect upon host vitality or activity. Also, assuming selection towards less damage done to hosts by parasites, the actual percentage of parasitized individuals is not expected to be much greater than the 3% observed.

Isopod parasites do affect the sex and sexual development of their host. Sexual reversal (parasitic castration) has been observed in many species (Schultz, 1969; Anderson, 1977). Even in species which do not undergo sex reversal, parasitized individuals may be sterile (Callan, 1940). However, the loss of reproductive ability by a few individuals is probably of little importance considering the high level of fecundity of non-parasitized individuals. The reproductive loss by parasitism would also be of little importance compared to losses experienced through predation.

Considering the varying influences of the three biological interactions it is not surprising that predation is the most important. In competition and parasitism both species involved usually benefit most by not severely interferring with another organism. However, the goals of predator and prey organisms are diametrically opposed to each other and effective predation is an essential element in the food chain. Therefore, moderate levels of predation are not likely to be selected against.

<u>Physical Influences: Habitat Structure</u>

Since the grassbeds provide cover and food for the shrimp it was not unexpected that seasonal shrimp density was directly related to grass blade density. Only one species, *Hippolyte pleuracantha*, was collected when the grass blades were shed and its density was significantly reduced at this time.

In this study and in others Hippolyte pleuracantha and Tozeuma carolinense have been found associated with specific grass species. Off Cedar Key H. pleuracantha was more abundant in beds of Thalassia testudinum, while T. carolinense was more numerous in Syringodium filiforme. Ewald (1969) observed a correlation between the abundance of T. carolinense and S. filiforme. Heck (1977) also noted that T. carolinense was most abundant at sites off the Panama coast in which S. filiforme was most abundant. He postulated that the shape of this species of shrimp might be less conspicuous to predators on round blades.

Examination of habitat preference by Hippolyte pleuracantha and Tozeuma carolinense indicated that the general grass form was selected by both species, but that the grain size of the substrate was unimportant. Similarly, Fricke and Hentschel (1971) showed that a palaemonid shrimp which is commensal with sea urchins preferentially approached patterns of long, thin, spine-line forms. Barry (1974) also found that the caridean shrimp, H. californiensis, which inhabits Zostera marina (eel grass), preferentially selected patterns of vertical stripes. Examination of the preference of specific grass species by Hippolyte pleuracantha and Tozeuma carolinense resulted in an unexpected finding. Although the long vertical form of grass was definitely selected, neither species of shrimp had a significant preference for grass species, even with a plastic, artificial grass included as a choice.

The distributional differences of the shrimp observed in the field may be related to the density of the grassbeds or to the presence of associated red algae. Both shrimp species were found in beds containing both species of grass. However, Thalassia testudinum beds were more dense than Syringodium filiforme beds and by being more dense trapped more clumps of red algae which may serve as protection for H. pleuracantha from fish predation. An increase in the amount of red algae was observed in trawls which had large numbers of shrimp. Therefore, a correlation between beds of T. testudinum and H. pleuracantha may be observed in the field.

Syringodium filiforme beds were more open and allowed better access for shrimp predators. Although Hippolyte pleuracantha may be a better competitor in the absence of predation, the size and behavior of Tozeuma carolinense make it the better competitor when predation pressure is high. The long form of its body matches the shape of S. filiforme well, but would be a hindrance in dense clumps of algae which are most associated with T. testudinum. Therefore, a correlation between T. carolinense and S. filiforme usually is observed in the field.

Physical Influences: Temperature

Temperature appeared to play an important role in influencing the seasonal distribution and reproduction of the shrimp species (see Tables 1, 2 and 3). All of the species were absent or declined in density during the winter. In addition, numbers of all species except Hippolyte pleuracantha also declined in the shallows during the warmest month. This seasonal variation in density suggested that temperature might influence the distribution of shrimp at Cedar Key.

One of the reported effects of temperature is on reproduction. Previous investigators have noted the sensitivity of reproduction to high temperature. Using mainly gravid Tozeuma carolinense in laboratory experiments, Drost-Hansen and Thorhaug (1974) observed less than 50%

survival between 29.0 and 32.3°C, but at least 80% survival below 29.0°C. They also observed a critical upper level of 32.8°C and a lower critical level of 10°C for an unidentified species of *Hippolyte*.

The larval development time is dependent upon temperature in many carideans and is flexible as to the number of molts and the length of the intermolt period (Bryce, 1961). Ewald (1969) showed an increase in mortality prior to metamorphosis of *Tozeuma carolinense* larvae at 25°C (33%) and at 15°C (78%) as compared with 20°C (25%). Most decapod larval deaths occur at times of molting rather than during intermolt periods (Broad, 1957; Rees, 1959). Lower temperatures may increase the number of molts or prevent metamorphosis. Bryce (1961) found that *T. carolinense* larvae molted as many as 24 times without metamorphosing at 22°C. The long rostrum also interferes with the shedding of the old exoskeleton and makes molting hazardous (Bryce, 1961). Therefore, at low temperature, *T. carolinense* may be subject to extremely high larval mortality.

A set of laboratory experiments indicated a significant difference in preferred temperature for *Hippolyte pleuracantha* and *Tozeuma carolinense*, with *H. pleuracantha* generally selecting higher temperatures than *T. carolinense* (see Table 17). The higher temperature preference of *H. pleuracantha* may allow the species to remain in shallow water during the warmest seasons when most other species are absent (see Table 3). Selection of a warmer temperature by *H. pleuracantha* may be advantageous since the preferred habitat of this species is shallow water where grassbeds are most dense and where red algae accumulate. Likewise, *T. carolinense* would be expected to prefer a cooler temperature, indicative of its preference for deeper, cooler and more sparse grassbeds.

CONCLUSION

The shrimp community at Cedar Key consists of 13 species of penaeid and caridean shrimp. The community is dominated by one species, Hippolyte pleuracantha, although members of two families of carideans are abundant. Shrimp density also is high, especially during the summer, when it was found to reach 541.6 individuals/m^2.

This community is like most complex communities in that organization is maintained through the action of a variety of factors. Several biological interactions and physical factors were examined for their effects on the shrimp community, and particularly on the two most numerous species. Although the factors interact and it is difficult to separate the effects of one from another, some factors appeared to be more important than others in maintaining the observed organization (see Figure 3).

The most important factor appeared to be the effect of physical factors on the shrimp community. Perhaps the most significant physical effect was the indirect influence of temperature on the habitat. Temperature was moderate for most of the year allowing dense grassbeds to become established. These beds provided shrimp with food and protection. However, winter low temperatures caused grass blades to be shed and shrimp density and diversity fell drastically. The lack of a suitable habitat when the grass blades were shed in March appeared to be more detrimental to Tozeuma carolinense than to Hippolyte pleuracantha (see Table 2) and is so indicated in Figure 3. The species and density of grass also was observed to influence the numbers and dominance

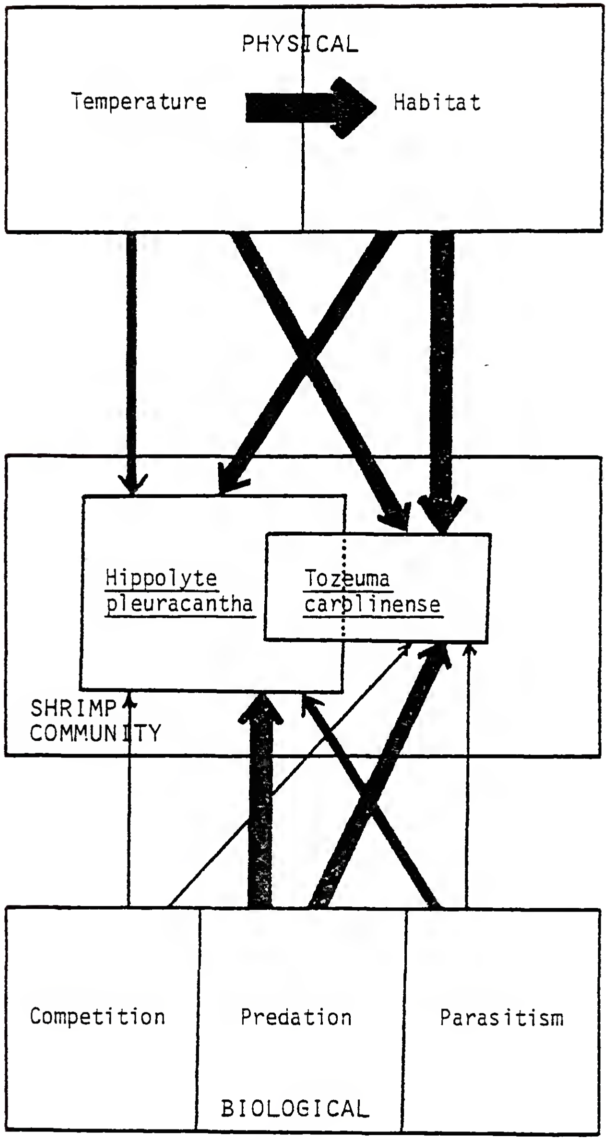

Figure 3. The relative effects of physical and biological factors on the two dominant members of the shrimp community. The thickness of the arrows indicates the relative importance of the factors on the shrimp.

relationships of the shrimp. *H. pleuracantha* was most numerous in dense beds of *Thalassia testudinum* which trapped clumps of red algae, while *T. carolinense* was more common in more open beds of *Syringodium filiforme*.

Temperature also appeared to have a direct influence on the shrimp. Extremes of temperature seemed to have the greatest influence on shrimp distribution and reproduction, although synergistic effects of temperature and salinity also may have been important. Several species were absent from the grassbeds during the coldest months and only one species (*Hippolyte pleuracantha*) had ovigerous females present during the winter. The diversity and density of shrimp also declined in the shallows during the warmest month, but less for *H. pleuracantha* than for other species. Therefore, temperature is shown to influence *Tozeuma carolinense* more than *H. pleuracantha* in Figure 3.

Predation appeared to be the most important biological regulator of the organization of the shrimp community. Predation was expected to be important since it was known that shrimp were a primary portion of the diet of many fish in the area (Reid, 1954) and that all of the shrimp species present had morphological and/or behavioral mechanisms of providing crypsis. Predator exclusion by caging also showed predation levels were high since shrimp density increased inside the cages as much as 27 times in 19 days in the absence of predation. Predation pressure also appeared to be greatest on the most dominant shrimp species (see Figure 3), resulting in much of the observed shrimp diversity.

Comparing the two dominant shrimp species, *Hippolyte pleuracantha* appeared to be more tolerant of temperature extremes, but the second most numerous species, *Tozeuma carolinense*, seemed to suffer less predation. This balance between the effects of predation and temperature extremes may be important in the coexistence of these two species.

High levels of predation and a harsh and fluctuating environment appeared to prevent high levels of competition, so that competition is not shown as a major factor influencing the shrimp community or the two dominant species in Figure 3. The amount of competition which did occur was difficult to assess, but indirect evidence that it had some influence on structure was seen. Interspecific competition may have resulted in some resource partitioning in the two most numerous species and in the less common shrimp families as evidenced by size differences between species. However, the two most dominant families appeared to tolerate high densities of individuals which apparently overlapped on resources. In these species, high densities might be expected to increase intraspecific competition. The generalist nature of many species may be explained by the high intraspecific competition which would act to increase the variety of resources used by these species.

Parasitism probably had little effect on the shrimp populations since very few individuals were parasitized. However, it is likely that parasitized individuals were unable to reproduce and these individuals also may have been more susceptible to predation.

In summary, the organization of the shrimp community, although influenced by many factors, appears to be regulated primarily by the physical environment and to a lesser degree by predation. This finding is not unexpected due to the location of the grassbeds. Although the frequent fluctuations which occurred in temperature and salinity and the temperature extremes encountered are indicative of a temperate estuary, the fluctuations are not severe and the temperature extremes are of short duration. The climate off Cedar Key is intermediate between subtropical south Florida and more temperate areas to the north.

The relatively mild climate off Cedar Key results in a fairly dense and diverse shrimp community. Compared with more subtropical or tropical environments, this shrimp community shows less diversity, but an increased density. Since competition and predation might be expected to be greater in milder climates, shrimp density probably is not as great as that found off Cedar Key during optimal conditions. However, density would not be expected to fluctuate as much seasonally in more tropical grassbeds. Although diversity is greater in the tropics, a moderately high level of shrimp diversity is seen at Cedar Key. The diversity of Cedar Key may be maintained not only by high predation pressure, but also by habitat heterogeneity and the high dispersal ability of shrimp.

APPENDIX

Order DECAPODA

Suborder Natantia

Section Penaeidae

Family Penaeidae

Trachypeneus constrictus (Stimpson)

T. constrictus is known as the roughneck shrimp and is translucent with bluish blotches. Individuals are found at depths of up to 30 fathoms (Williams, 1965). Spawning occurs offshore (Eldred et al., 1965; Williams, 1965). When present in estuaries, the species prefers sand, mud, and shell substrates (Burkenroad, 1939; Hildebrand, 1955; Williams, 1965).

This species was the most common penaeid occurring in the samples (351 individuals collected during the year). The species was present every month except February and April and was most abundant in July and August. Greater numbers generally were observed in months having higher mean salinity values. *T. constrictus* also is fairly common in the Tampa Bay area, although it is more numerous in shallow offshore waters (Eldred et al., 1965). Few individuals have been taken at Alligator Harbor, at Crystal River, or in the southwestern Florida estuaries where salinity is frequently low (Wass, 1955; Tabb and Manning, 1961; Lyons et al., 1969; Rouse, 1970). However, the species was common in trawls within St. Andrews Bay, Florida and in inshore samples on the northeast coast of Florida near Jacksonville (Joyce, 1965; Brusher and Ogren, 1976). The hydrological conditions of these two areas are unusual compared to surrounding areas. St. Andrews Bay has a low freshwater inflow, resulting in waters more similar in salinity to waters in the Gulf of Mexico. Near the mouth of the St. Johns River in northwestern Florida, many salt and brackish water organisms have been reported to penetrate the almost fresh waters, presumably due to high calcium ion concentrations present (Joyce, 1965). Therefore, it seems likely that the distribution of this species may be at least partially regulated by salinity tolerance.

Individuals ranged in size from 6.5 to 61 mm in the present study. Larger individuals were observed from August to November. Williams (1965) reported that individuals reach lengths of 92 mm, although individuals observed in littoral areas of the Gulf of Mexico are not this large. Previous reports of maximum lengths in this area are: 43 mm at Cedar Key (Eng, 1968); 30 mm in Florida Bay (Tabb and Manning, 1961); 75 mm in Tampa Bay (Eldred et al., 1975); and 66 mm in Alligator Harbor (Wass, 1955).

Sicyonia laevigata Stimpson

Called hardbacks or coral shrimp, *S. laevigata* individuals are yellowish with bluish or greenish areas. This species prefers depths of 6 to 40 fathoms and spawns offshore in winter (Williams, 1965; Williams, 1974). Inshore, shell or mud bottoms are preferred (Wass, 1955; Eng, 1968). However, *S. laevigata* also was collected over grassbeds at Crystal River (Lyons et al., 1969).

Only 37 individuals were collected over the year in this study, almost half (16) of these in November. Individuals ranged from 4.2 to

35.1 mm in length. Williams (1965) reported males reached 50 mm, although maturity might be reached by females at 18 mm. One female of 35 mm in length was reported from Tampa Bay (Eldred et al., 1965).

Both species of penaeids (*Trachypeneus constrictus* and *Sicyonia laevigata*) appear to use the Cedar Key estuary as a nursery since only small individuals were collected in the shallow grassbeds. These juveniles are most numerous during seasons when salinity and temperature are high and food probably is most abundant.

Section Caridea

Family Palaemonidae

Periclimenes longicaudatus (Stimpson)

This species was the most numerous palaemonid observed (2912 individuals) and the third most abundant of all species taken. Although the two more numerous species (*Hippolyte pleuracantha* and *Tozeuma carolinense*) regulate their body color to match the vegetation by turning various shades of green and brown, *P. longicaudatus* is camouflaged by its almost perfect transparency. The species often is found in association with *H. pleuracantha* and *T. carolinense* in grassbeds, but also may be observed on algae, *Sargassum*, soft corals, or on sponge (Schmitt, 1924; Williams, 1965; Eng, 1968; Chace, 1972). It occurs in shallow water up to six fathoms in depth (Williams, 1965).

One individual that was taken in this study in August had a bopyrid isopod in its gill cavity. Rouse (1970) also collected parasitized individuals of this species and identified the isopod as *Bopyrina urocardis*.

P. longicaudatus is common inshore along the Gulf of Mexico when salinity is not too low. It was the eighth most numerous invertebrate and fifth most numerous caridean in grassbeds in Apalachee Bay, Florida (Hooks et al., 1976). Ovigerous females were observed off Panama City (Holthius, 1951) and previously off Cedar Key (Eng, 1968). No ovigerous females were observed at Crystal River, where salinity ranged from 16 to 30 $^{o}/oo$, although the species was common there. In southwest Florida few ovigerous females were observed, although the species was common (Rouse, 1970). The species was collected there at salinities as low as 15 $^{o}/oo$, but was more numerous between 24 and 43 $^{o}/oo$. The species was uncommon at Alligator Harbor (Wass, 1955). Thus, it appears that the distribution of the species, and especially that of ovigerous females, is limited by low salinity values in many areas of Florida.

Water temperature also appeared to be important in determining the presence of P. longicaudatus. The species was present in this study every month and was abundant from May to November. However, the numbers of individuals declined during the cold winter months and also in July when the shallow waters may have become too warm. Reproduction, in particular, appeared to decline under temperature stress. Ovigerous females (316) were present only from April to November, when they averaged 11% of the species. The highest proportion of ovigerous females was observed from April to June when they comprised from 21 to 38% of the species. During the warmer and colder months, few, if any, ovigerous females were observed. It also is possible that the distribution of the species was regulated by a synergistic effect of temperature and salinity since during temperature stress, osmoregulatory abilities may decline (Zein-Eldrin, 1963).

Slightly larger individuals were collected in this study as compared with previous studies. Ovigerous females ranged from 12 to

24.4 mm in length and males as small as 5.4 mm were observed in these samples. Holthius (1951) reported that males reach 17 mm and that ovigerous females vary from 15 to 22 mm near Panama City and Cape San Blas, Florida.

Periclimenes americanus (Kingsley)

P. americanus is grayish with three oblique brown lateral lines and a pair of dorsal lines on the carapace. Each abdominal segment also is crossed with brown lines (Verrill, 1922). The species has been found in water up to 40 fathoms in depth (Williams, 1965), although it is most often observed in one to three feet of water (Chace, 1972). The species has been observed along Florida's west coast, associated with sand, rock, or shell bottoms or with Sargassum (Holthius, 1951; Wass, 1955; Lyons et al., 1969).

Off Cedar Key, P. americanus individuals were rare. Only four individuals were taken, two in January and two in October. Eng (1968) did not collect any individuals of this species previously off Cedar Key, although he sampled many habitats. However, Hooks et al. (1976) found this species to be common in grass beds in Apalachee Bay, Florida, where salinity frequently dropped below 20 $^{o}/oo$. Perhaps the species is rare at Cedar Key because it is a better competitor at lower salinity values than are generally encountered at Cedar Key.

The four individuals collected in this study ranged from 5.2 to 10.4 mm in length and no ovigerous females were observed. Holthius (1951) observed males up to 22 mm in length and ovigerous females varying from 13 to 20 mm. The species is ovigerous year-round in southern Florida (Rouse, 1970).

Perhaps due to the few individuals collected, no parasitized individuals were observed in the present study. A few individuals collected during the Smithsonian-Bredin Caribbean Expeditions (Chace, 1972) had abdominal bopyrid parasites. One of these parasitized individuals was an ovigerous female.

Palaemon floridanus Chace

P. floridanus was the only species taken that is endemic to the west coast of Florida. Red pigmentation occurs in five longitudinal lines on the anterior carapace of this species. This coloration may be cryptic since Hooks et al. (1976) observed large numbers of the species associated with large clumps of the red alga Digenia simplex. The species also has been collected in submerged vegetation or near piers, pilings, and bridges (Tabb and Manning, 1962; Eng, 1968).

In the present study, twenty-seven individuals were collected from June to February, but only in August and in December was more than one individual observed. Previously, Eng (1968) found that this species was common at Cedar Key in his samples from many habitats. The species also was collected at Crystal River between 18 and 30 $^{o}/oo$ (Lyons et al., 1969) and in southwestern Florida between 31 and 52 $^{o}/oo$ (Rouse, 1970). Therefore, the distribution of P. floridanus appears to be restricted to areas of relatively high salinity and abundant red algae.

Due to the rarity of the species in the grassbeds at Station 1, few ovigerous females were observed. In August, five ovigerous females were taken, ranging in size from 27.1 to 41.9 mm. Males as small as 8.1 mm were observed. Eng (1968) reported that ovigerous females ranged from 27 to 46 mm. Wass (1955) described one ovigerous female 45 mm in length taken at Alligator Harbor. Holthius (1952) observed ovigerous females of 31 to 35 mm in length, but reported that they may reach 50 mm.

Ovigerous females have previously been observed from March to August off the Florida coast (Wass, 1955; Tabb and Manning, 1962; Eng, 1968; Lyons et al., 1969, Rouse, 1970).

Family Alpheidae

Alpheus normanni Kingsley

A. normanni is a very common snapping shrimp on the west coast of Florida (Wass, 1955; Hulings, 1961; Tabb and Manning, 1962; Eng, 1968; Lyons et al., 1969; Rouse, 1970). It burrows in sand and is most often taken over shell, sand, or rock bottoms or in association with tunicates (Wass, 1955; Williams, 1965; Eng, 1968). However, Eng previously reported observations of *A. normanni* over grassbeds off Cedar Key. The species also was collected in grassbeds at Apalachee Bay (Hooks et al., 1976).

In the present study, *A. normanni* was rarely collected in the grassbeds. Fourteen individuals were collected between June and December, most of these in November and December. Individuals ranged in size from 5.9 to 24.2 mm and no ovigerous females were observed.

The few individuals and the lack of ovigerous females in the present study suggest that *A. normanni* is not a permanent resident of the grass beds at Cedar Key. The few individuals taken may have been collected as the trawls crossed patches of sand or shell bottom. Eng (1968), sampling more habitats off Cedar Key, collected ovigerous females in September and in June, ranging in size from 18 to 21 mm. Rouse (1970) collected ovigerous females only during the winter in salinities ranging from 24 to 43 $^{o}/oo$.

Family Hippolytidae

Thor _dobkini_ Chace

_T_. _dobkini_ (previously _T_. _floridanus_) is a short, stocky shrimp which closely resembles _H_. _pleuracantha_ in color and size. The species has been collected in association with sponge, algae, soft coaral, and tunicates (Broad, 1957; Williams, 1965; Eng, 1968); in grassbeds (Hooks et al., 1976); and over rocky substrates or on _Sargassum_ (Wass, 1955). It occurs in shallow water to 14 m in depth (Chace, 1972).

_T_. _dobkini_ is the only species collected at Cedar Key which has been reported to require no animal component in its diet. Although the food items which are consumed in the field are unknown, Broad (1957) successfully reared all the larval stages in the laboratory on an exclusively algal diet.

Previously this species was included within _T_. _floridanus_. Rouse (1970) reported the possibility that _T_. _floridanus_ included two species, based on a difference in egg size. The larger egg size (1.01 mm) was carried by females in Florida Bay where salinity was as low as 9 $^{o}/oo$. Females in the Gulf of Mexico, in water above 15 $^{o}/oo$, carried smaller eggs (0.6 mm). However, the two forms have also been collected side by side (Dobkin, 1968).

Dobkin (1968) showed that the two forms were distinct species. The larval development of the form with the larger eggs (now _T_. _floridanus_) was abbreviated, with metamorphosis occurring 48 hours and two molts after hatching. The second form (now _T_. _dobkini_) required more time to reach metamorphosis and had at least six larval stages (Lebour, 1940; Broad, 1957). _T_. _dobkini_ is believed to be a protandrous hermaphrodite, but no sexually intermediate forms have been observed (Chace, 1972).

Thor dobkini individuals can be distinguished from T. floridanus by the presence of a spine on the distal half of the flexor margin of the merus of the first pereiopod (Chace, 1972). Because it would be very time-consuming, not all of the individuals taken in the present study were examined for the presence or absence of this spine. Therefore, it is possible that some non-ovigerous T. floridanus individuals were taken.

T. dobkini was a common shrimp in grassbeds off Cedar Key, with 382 individuals collected during the year. The species was present every month except May and ovigerous females were collected in June, August, and September. Ovigerous females have previously been observed in other areas from January to September (Wass, 1955; Tabb and Manning, 1962; Williams, 1965; Lyons et al., 1969).

In the present study, egg size varied between 0.4 and 0.5 mm. Ovigerous females taken at Crystal River between 20 and 31 $^{o}/oo$ also had smaller eggs (0.44 to 0.56 mm, mean 0.49). Males as small as 3.9 mm and ovigerous females between 4 and 15.9 mm were collected off Cedar Key in this study. Wass (1955) collected ovigerous females between 11 and 13.2 mm in length and Eng (1968) collected one ovigerous female 16 mm long.

In the present study, bopyrid isopods were occasionally observed in the gill cavity of individuals. One female of this species taken in the West Indies had a branchial bopyrid parasite (Chace, 1972) which was probably Bopyrinella antillensis (Schultz, 1969). Other species of isopods have been identified on Thor, including Boyprina thorii (Schultz, 1969) and Probopyrus latreuticola (Rouse, 1970).

Latreutes fucorum (Fabricius)

L. fucorum can be recognized by its distinctive rostrum which is very thin, but long and deep. Shrimp coloration can vary from nearly transparent, to mottled and striped browns, to green, depending upon the type and condition of the vegetation the shrimp is associated with. The color may vary both as a result of genetic differences and as a response to local situations (Brown, 1939). Four kinds of pigments are present (white, red, yellow, and blue), similar to the pigments found in *Hippolyte*. The preferred habitat for the species is *Sargassum*, seaweeds, or *Thalassia testudinum* (Wass, 1955; Williams, 1965; Eng, 1968; Lyons et al., 1969; Rouse, 1970).

No isopod parasites were observed in the gill cavities of *L. fucorum* in these samples, although *Bopyrus latreuiicola* was reported in the gill cavity of this shrimp near Port Aransas, Texas (Pearse, 1952) and on a single females collected in the West Indies (Chace, 1972).

In the present study this species was abundant, with 2144 individuals taken. Most individuals were observed between May and January when ovigerous females also were present, although the species was most numerous in the fall and rare in early spring. Ovigerous females have been collected between March and November in nearby regions (Tabb and Manning, 1962; Williams, 1965; Lyons et al., 1969; Rouse, 1970).

Ovigerous females collected were between 11.7 and 18 mm in length. Males were as small as 5.4 mm. Williams (1965) reported that the species varied in size between 12 and 20 mm. In previous sampling off Cedar Key a size range of 10 to 18 mm for ovigerous females was observed (Eng, 1968). Wass (1955) collected ovigerous females from 12.2 to 18.5 mm in length.

Latreutes parvulus (Stimpson)

L. parvulus is a short, stocky shrimp with a thin, almost circular rostrum. The species is found assoicated with sponge, shell, hydroids, and Sargassum (Wass, 1955; Williams, 1965; Lyons et al., 1969; Rouse, 1970) and occurs to a depth of 44 m (Chace, 1972).

L. parvulus was uncommon in the present study. Fifty-two individuals, most taken between June and November, were observed. This species apparently is uncommon throughout its range (Tabb and Manning, 1962; Williams, 1965; Lyons et al., 1969).

Ovigerous females were present in June, September, and November, when they averaged 25% of the species. However, ovigerous females were present year-round in southwest Florida where they represented 60% of the population (Rouse, 1970).

In this study, size ranged from 7.3 mm for males and from 9.1 to 11.5 mm for ovigerous females. Williams (1965) reported a size range of 7 to 12 mm for L. parvulus. Wass (1955) observed ovigerous females from 8 to 12.8 mm in length.

Hippolyte pleuracantha (Stimpson)

H. pleuracantha individuals varied in color from nearly colorless to mottled brown and red to bright green, depending upon the type and color of vegetation predominating when they were collected. Their color is a result of concentration and/or dispersion of four pigments (white, red, yellow, and blue). The species has been reported to be very abundant in submerged vegetation (Wass, 1955; Tabb and Manning, 1962; Lyons et al., 1969; Hooks et al., 1976). The species also has been found associated with Sargassum and on rock jetties (Gurney, 1936; Williams, 1965).

Presently H. zostericola and H. pleuracantha (Stimpson) are recognized as distinct species of Hippolyte, although the two have been confused over the years. H. zostericola usually is distinguished from H. pleuracantha {or H. pleuracanthus (Chace, 1972)} by the length and proportions of the rostrum. In H. zostericola the rostrum is long, overreaching the antennular peduncle and often nearly reaching the tip of the antennal scale. The rostrum in H. pleuracantha is much shorter, with the tip just reaching to the end of the antennular peduncle.

Chace (1972) questioned the distinctions between the two species of Hippolyte. He reported that Hippolyte females from Woods Hole had long rostrums which overreached the antennular peduncle, but that the rostrum of females collected between Connecticut and North Carolina was much shorter, being no longer than the antennular peduncle, as is typical of H. pleuracantha. Along the east coast of Florida, the rostrum once again overreaches the antennular peduncle. In the northern and eastern Gulf of Mexico, the rostrum reaches its greatest length. Therefore, it appears that the rostrum length varies with geographical location and it may not be a good taxonomic characteristic for distinguishing between these two species. However, Chace (personal communication, 1979) now believes the two species will be shown to be distinct.

Although the species present on the western coast of Florida has a long rostrum, most previous reports of Hippolyte from this area refer to H. pleuracantha (Wass, 1955; Tabb and Manning, 1962; Eng, 1968; Rouse, 1970). These individuals lack a prominent distal spine on the basal article of the antennular peduncle which is supposed to be lacking in H. pleuracantha, but which H. zostericola is supposed to have (Williams, 1965). However, Chace (1972) determined that the species with the spine was a third species, *H. curacaoensis*. *H. pleuracantha* (ovigerous females 12 to 18 mm in length) also has been reported to be larger than *H. zostericola* (ovigerous females 10 to 12 mm) (Williams, 1965). The species taken in this study had a long rostrum, no prominent spine, and ovigerous females reached the larger body size. This species is referred to as *H. pleuracantha* throughout this paper.

Bopyrid isopods were present in the gill cavities of 2 to 3% of the nonovigerous individuals. This represents a large number of parasitized individuals since the greatest parasitism usually seen on decapods is about 5% (Schultz, 1969). These isopods probably were *Bopyrina abbreviata* which has been taken previously on *H. zostericola* (Schultz, 1969) and which has been found previously on *H. pleuracantha* (Rouse, 1970). No parasites were found on ovigerous individuals.

Ovigerous females were present every month in this study and their numbers (5690 individuals) were greater than any other entire species. Rouse (1970) also collected ovigerous females year-round in southwestern Florida. They were most numerous in the spring when three-fourths of the individuals were ovigerous females. However, this biased sex ratio may have been a result of using a net with a large mesh size (the size was not reported) so that smaller males were able to escape. Rouse collected the species over a wide range of salinity (9 to 61 $^{o}/oo$) and water temperature (12 to 34^{o}C). Perhaps as a result of these wide tolerances, the species is dominant at Cedar Key, where it is not limited by the extremes and fluctuations of temperature and salinity.

Males taken in this study were as small as 3.6 mm in length, while ovigerous females ranged from 5.4 to 18.4 mm. Williams (1965) reported that ovigerous females varied from 12 to 18 mm. Eng (1968) collected ovigerous females ranging from 11 to 20 mm. At Alligator Harbor, Wass (1955) observed ovigerous females to vary between 9.2 and 16 mm.

Tozeuma carolinense Kingsley

T. carolinense is known as the arrow shrimp because of its long, thin rostrum and body. Individuals collected in this study varied in coloration from nearly colorless to brownish, reddish, or bright green. Arrow shrimp are abundant throughout southeastern estuaries (Tabb and Manning, 1962; Williams, 1965; Rouse, 1970) and are associated with grassbeds in which individuals feed on faunal and floral epiphytic growths (Bryce, 1961). The species also has been taken floating on Sargassum in the open sea to a depth of 15 m (Chace, 1972). Parasitic isopods were never observed on this species, even though the species was very abundant.

T. carolinense was the second most abundant species (3899 individuals) in the present study. The species was collected every month and 588 ovigerous females were collected from April to November. The species was common, but not abundant, at Crystal River, probably due to the lack of extensive grassbeds (Lyons et al., 1969). It was the dominant caridean observed in the grassbeds in Apalachee Bay (Hooks et al., 1976), in south Florida (Rouse, 1970) and along the west coast of Panama (Heck, 1977). However, the mesh size of the nets used in these studies was larger or may have been larger (Hooks et al.--18 mm; Rouse--not reported; Heck--19 mm) than the 1.7 mm net used in the present study. The larger mesh nets would tend to retain larger species such as T. carolinense, but not smaller species like Hippolyte pleuracantha, which was most numerous at Cedar Key. On the other hand, Tozeuma carolinense may actually have been dominant in these areas. In other sections of this paper, the effects of vegetation type, the level of predation, and environmental conditions are discussed as determinants of the dominant species.

The distribution of T. carolinense may be related to temperature and/or salinity. Rouse (1970) collected individuals from areas exhibiting salinity values between 23 and 54 $^{o}/oo$ and temperature between 11 and 34^{o}C. The lower salinity and temperature occasionally observed off Cedar Key may reduce the density of T. carolinense in winter and result in an absence of ovigerous females at this time. The proportion of this species observed in July also was very low, perhaps as a result of intolerance to the high water temperature which occurred in the shallows.

The smallest individuals collected during this study were 9.6 mm. Ovigerous females ranged from 32.7 to 53.8 mm in length. Williams (1965) reported 28 to 50 mm as the range for ovigerous females. Eng (1968) collected ovigerous females ranging from 20 to 49 mm in length, while Wass (1955) observed a range of 28 to 42 mm. Perhaps a greater size range was observed in the present study at Cedar Key due to the large number of individuals observed.

Family Processidae

Ambidexter symmetricus Manning and Chace

A. symmetricus represents a newly named genus and a new species in the family Processidae which has not been well-studied (Manning and Chace, 1971). These researchers report that shrimp in this family are nocturnal and often are found in grassflats in tropical or subtropical areas. The processids are superficially similar to the Hippolytidae, although the structure of the mouth parts and the form of the rostrum are distinctly different (Manning and Chace, 1971). The rostrum in this family is a simple extension of the carapace, terminating in an apical and a subapical tooth. Examination of collections from south Florida and the west coast of Florida have indicated two different processids (which were not identified) are frequently present (Tabb and Manning, 1961; Eng, 1968; Rouse, 1970). *A. symmetricus* is distinct from other members of the Processidae in having both first pereiopods chelate.

In this study only three individuals were collected in monthly samples, one in June, one in September, and one in November. Seven other individuals also were collected in one caging experiment. Since the species is nocturnal, the few individuals taken are probably a result of diurnal sampling.

Although he was unable to identify the genus and species at the time, Eng (1968) previously collected members of the Processidae at Cedar Key which had the first pair of legs equally chelated. Only two specimens were collected during his diurnal sampling, although he collected more individuals nocturnally, including ovigerous females from March to June which ranged in size from 15 to 28 mm. Examination of the processid collection of the Division of Crustacea, National Museum of Natural History indicated that ovigerous females also have been collected in July in Biscayne Bay, in January at Alligator Harbor, and in May at Cedar Key (Manning and Chace, 1971). The lack of ovigerous females in the present sampling is believed to be a result of diurnal sampling.

Individuals taken in this study varied between 4 and 9.7 mm in length. Carapace length was from 1.1 to 2.5 mm. Manning and Chace (1971) reported that carapace length of males ranged from 2.1 to 4.5 mm and of females from 2.4 to 6.7 mm.

Processa bermudensis (Rankin)

P. bermudensis individuals generally have the first right leg chelate, but not the left (Manning and Chace, 1971). This species often has been collected at night in shallow water with Ambidexter symmetricus and has occasionally been taken with a third unidentified processid (Tabb and Manning, 1961; Eng, 1968; Rouse, 1970; Manning and Chace, 1971).

During the diurnal sampling of this study, only four individuals were collected, two in June and two in November. One of the individuals collected in June was an ovigerous female, 21.2 mm in length and with a carapace length of 4.8 mm. Nonovigerous individuals varied between 12.3 and 16.4 mm in length. Williams (1965) reported that males vary between 14 and 16 mm and that ovigerous females reach 50 mm. However, these size ranges probably included individuals which have been assigned to other genera or species since that time. Manning and Chace (1971) found carapace lengths in males measuring from 2.4 to 3.4 mm and in ovigerous females from 3.3 to 5.7 mm Ovigerous females previously have been observed off south Florida in the months of December, May, and July (Manning and Chace, 1971).

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Frank J. S. Maturo, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

F. G. Nordlie
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