POPULATION ECOLOGY OF *PAGURUS MACLAUGHLINAE* GARCIA-GOMEZ (DECAPODA: ANOMURA: PAGURIDAE) IN THE INDIAN RIVER LAGOON, FLORIDA

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ABSTRACT

Pagurus maclaughlinae is an abundant component of sea-grass macrobenthos in Florida waters. As a grazer on sea-grass blades, it may play an important role in sea-grass ecology by reducing epiphyte cover on the blades. Population dynamics, habitat selection and utilization patterns, and interactions with a decapod predator were examined in field collections and laboratory experiments.

At a site north of Link Port in the Indian River Lagoon, Florida, *P. maclaughlinae* was more abundant in beds of *Thalassia* as compared to those of *Syringodium* or *Halodule*. In the laboratory, *Syringodium* was selected in preference to *Thalassia* and *Halodule*, and choice was not influenced by presence of a predator. Sea grass with epiphytes was significantly selected over unfouled substrates. Recruitment occurred in October–February and in May–July, and the overall male/female ratio was close to 1, although month to month variation occurred. High percentages of ovigerous females were found in the fall and in the spring, and female maturation occurred at a CL of approximately 1.25–1.50 mm. *Cerithium muscarum, Modulus modulus,* and *Nassarius vibex* constituted ~94% of the 13 species of gastropod shells used. Shell utilization differed between sexes, ovigerous and nonovigerous females, and among size classes. Predation experiments with the blue crab *Callinectes sapidus* suggested that predation rate was independent of shell species, that the presence of *Thalassia* offered significant protection against predation compared with bare sand, and that predation rates were not different between sea grasses.

Pagurus maclaughlinae Garcia-Gomez is a very abundant component of the macrobenthos associated with sea grasses in the Indian River Lagoon and in Florida waters in general (Provenzano, 1959; Grizzle, 1974; Heck, 1976; Gore *et al.,* 1981; Greening and Livingston, 1982; Virnstein *et al.,* 1983). It was recently recognized as a separate species of the Provenzanoi group of hermit crabs (Garcia-Gomez, 1982). This species was earlier misidentified as either *Pagurus annulipes* (Stimpson) or *Pagurus bonairensis* Schmitt (=*P. stimpsoni* A. Milne Edwards and Bouvier) (Lemaitre *et al.,* 1982).

While most species of hermit crabs are omnivorous detritivores (Orton, 1927; Caine, 1975, 1976), there are deviations from this feeding mode (Boltt, 1961; Caine, 1975; Markham, 1977; Caine, 1980). *Pagurus maclaughlinae* appears to be a grazer of sea-grass epigrowth. The feeding activities of hermit crabs may affect other organisms in the community (e.g., Lowery and Nelson, 1988). Given its abundance, *P. maclaughlinae* may thus be important to the structure and composition of the associated animal and sea-grass communities.

Although the larval stages of *P. mac-laughlinae* have been thoroughly described by McLaughlin and Gore (1988), little information on the population dynamics of this species is available. As a first step toward the understanding of the ecological role of *P. maclaughlinae,* this study focused on the seasonal abundance, size–frequency distribution, recruitment, shell utilization, sex ratio, and reproductive cycle of this species. In addition, habitat utilization patterns in the field were examined, while some aspects of habitat selection, and the role of blue-crab predation in this process were examined in the laboratory. Predation experiments were performed because the blue crab, an aggressive predator, occurs abundantly within the same habitats as *P. maclaughlinae.*

MATERIALS AND METHODS

Field Studies. — To investigate seasonal changes in population characteristics, monthly samples of *P. maclaughlinae* were collected north of the Harbor Branch Oceanographic Institution (HBOI), Link Port, Florida, between 21 August 1985 and 23 October 1986. The bottom of the shallow bay sampled consisted of fine to muddy sand with large patches of the sea grasses *Thalassia testudinum* Banks ex König and *Syringodium filiforme* Kützing in Hohenacker. A narrow band

Table 1. Sampling program north of Link Port, Harbor Branch Oceanographic Institution. Dates indicate when qualitative and number of 1-m² quantitative samples were collected within the different habitats. Salinity is presented as ppt and temperature in °C.

Number	Date	Salinity	Water temperature	*Thalassia*	*Syringodium*	*Halodule*	Bare sand
1	21 Aug. 1985	—	—	Qualit.			
2	20 Sep. 1985	—	27.0	Qualit.			
3	18 Oct. 1985	24.0	28.0	Qualit.			
4	22 Nov. 1985	32.5	25.7	Qualit.			
5	8 Dec. 1985	27.0	17.5	5 Quant.			
6	15 Jan. 1986	23.0	16.4	4 Quant.			
7	14 Feb. 1986	22.0	18.3	3 Quant.	3 Quant.	4 Quant.	
8	12 Mar. 1986	32.0	27.0	3 Quant.	3 Quant.	3 Quant.	3 Quant.
9	15 Apr. 1986	34.7	26.9	3 Quant.	3 Quant.	3 Quant.	
10	15 May 1986	34.0	26.2	3 Quant.	3 Quant.	3 Quant.	
11	13 Jun. 1986	35.9	32.1	3 Quant.	3 Quant.	3 Quant.	
12	15 Jul. 1986	28.0	32.1	3 Quant.	3 Quant.		3 Quant.
13	15 Aug. 1986	27.5	31.8	3 Quant.	3 Quant.	3 Quant.	
14	18 Sep. 1986	27.0	28.0	3 Quant.		3 Quant.	
15	23 Oct. 1986	23.0	24.8	3 Quant.	3 Quant.	3 Quant.	

of *Halodule wrightii* Ascherson was also found close to the shoreline (see Virnstein and Carbonara, 1985). The study site was not significantly influenced by tides. Quantitative dip net (4 × 3-mm mesh) samples were taken within a 1 × 1-m, weighted PVC pipe frame. The frame was tossed at random and stabilized on the bottom by four PVC pipes in the corners of the frames. Quadrats were sampled with a straight-sided dip net until no further hermit crabs were collected in 3 consecutive, intensive trials. Because of poor weather conditions, no samples were taken in *Syringodium* in September 1986, and in *Halodule* in July 1986 (Table 1).

Samples were sieved (2-mm mesh) in the field and kept in a solution of 2% MgCl in sea water for 1 h before being transferred to 4% neutralized Formalin. They were identified to species in the laboratory, and sexes were separated by counting the pleopods. Carapace length (CL) was measured by using a stereomicroscope equipped with an ocular micrometer.

Temperature and salinity measurements were taken outside the sea-grass meadows at approximately 10 cm in water of about 0.5-m depth. The salinity was measured in the field by means of a refractometer.

Laboratory Studies. — The laboratory studies were performed at the Indian River Marine Science Research Center, Vero Beach, Florida, to determine: (1) whether *P. maclaughlinae* tends to aggregate, (2) whether selection of sea-grass species corresponds to field occurrence, (3) whether the presence or absence of epiphytes are an important factor concerning sea-grass selection, and (4) whether the predator *Callinectes sapidus* Rathbun, which is abundant within the same habitat as *P. maclaughlinae*, could affect hermit crab population or habitat utilization pattern.

Small Scale Distribution Patterns. — One set of experiments was performed in June 1988 to determine whether *P. maclaughlinae* showed tendencies toward dispersion or aggregation. A glass aquarium (30 × 60 cm, 30 cm high) was filled with approximately 5 cm of beach sand. A grid (made of 2-mm diameter galvanized wire), covering the whole bottom area of the

aquarium, was placed on the sand. This divided the bottom of the tank into 18 squares of equal size (10 × 10 cm). One plant of *Thalassia testudinum*, with 3 blades, was placed in the middle of each square. The specimens used in the study were all adults (sexes not determined) collected within the meadows of *Thalassia* at Link Port in the morning of the experimental date. One specimen of *P. maclaughlinae* was placed on the sand close to each plant of *Thalassia* in each square and left undisturbed. The number of hermit crabs within each square was then observed after 3 h. This experiment was repeated with new hermit crabs 3 times. A corresponding experiment, with the same number of replicates, was also performed, but with all 18 hermit crabs placed in the middle of the tank at the beginning of the experiment. The aquarium was supplied with filtered (30 μm) sea water, except during the experimental period, when the water was shut off.

Habitat Distribution Pattern Experiments. — A second set of experiments examined several factors potentially involved in determining the habitat distribution pattern of *P. maclaughlinae*. All experiments used aquaria (30 × 60 × 30 cm) with the tank divided in half with a plastic partition to form a 30 × 30 cm experimental arena. In the first experiment (repeated 3 times), one compartment per tank was planted with 3 monospecific sea-grass plots (10 × 10 cm) in the corners of the tank. The fourth corner was bare sand in order to determine whether the crabs actively avoid this habitat. Each plot contained a varied number of blades which gave approximately equal blade surface areas (450 cm²). Position of each plot within a tank was determined at random, and 6 replicate tanks per experiment were used. The number of blades for each sea-grass species was determined from blade number versus surface area regressions given by Stoner (1980). For each experiment, 20 hermit crabs per replicate were placed in the center of each experimental area, and the number of crabs in each plot type was counted after 24 h.

A second habitat choice experiment examined the importance of the presence of epiphytes on the sea-grass blades. Only *Syringodium* and *Thalassia* were

tested, because the blades of *Halodule* proved too fragile for manipulation of epiphytes. Four treatment plots (10 × 10 cm) were established in the corners of one-half of an aquarium. One treatment used natural sea-grass blades which were briefly immersed in fresh water to remove mobile animals, but were otherwise unmanipulated. A second treatment used natural blades which were briefly immersed and were then cleaned of all epiphytic algae using a foam dishwashing pad. The surface of the sea-grass blades did not appear to be damaged by this procedure. The third treatment used artificial sea-grass blades which mimicked the morphology of the sea grass being tested. The fourth treatment used artificial sea grass which was left under water for 1 week at the same site where the natural sea grasses had been collected. The artificial *Thalassia* was composed of 100 1.3-cm wide strips of nylon ribbon, while the artificial *Syringodium* was composed of 50 lengths of 50 lb (26.8 kg)-test monofilament fishing line, both cemented to petri dish bases. Twenty hermit crabs were released into each of 6 aquaria (3 with *Syringodium* and 3 with *Thalassia*), and the numbers in each plot were counted 24 h later. Because habitat choice experiments demonstrated a clear preference of *P. maclaughlinae* for sea grass versus bare sand, animals that remained on bare sand were excluded from the analysis. The final habitat distribution experiment examined whether the presence of a predator would alter the choice of *P. maclaughlinae* for a particular sea-grass substrate. Sea-grass plots for *Thalassia, Syringodium,* and *Halodule* were established in 3 corners of each of 4 replicate aquaria as above. In the fourth corner, a diagonal partition (0.5-mm nylon mesh) was established and 1 *C. sapidus* (blue crab) was placed behind the barrier. Twenty-five hermit crabs were placed on bare sand in the center of the tank and the number of hermit crabs in each sea-grass plot was counted after 24 h.

The habitat preference and predator avoidance experiments were analyzed using a one-way ANOVA and a posteriori Welsch Step-Up procedures (Sokal and Rohlf, 1981). The epiphyte experiments were analyzed using a two-way ANOVA with replication where the 2 factors were fouling (a = 2) and sea-grass type (b = 2). Analyses used the arcsine square root transformation for percentage data.

Predation Experiments.—Predation on *P. maclaughlinae* by the blue crab *C. sapidus* was examined in a series of aquarium experiments. The blue crabs were collected in meadows of *Thalassia* in the Indian River Lagoon using a seine. *Pagurus maclaughlinae* were collected from the site of the population studies.

The experiments were performed in the compartmentalized aquaria described above. The compartments were supplied with a constant flow of filtered (30 μm) sea water, except during the 24-h experimental period, when the water supply was shut off. The blue crabs were placed in separate holding tanks immediately after collection and were held without food for 24 h before the experiments were started in order to acclimate to the experimental containers. Repeated experimental trials were carried out with individual blue crabs on successive days. This procedure was deemed acceptable, since observations of blue crabs held in the laboratory showed no decrease in feeding rate over time. This observation was confirmed by the experimental results which showed no decrease in consumption rates of blue crabs in successive trials.

Twenty hermit crabs, 10 crabs each carrying the shells of *Modulus modulus* L. and *Cerithium muscarum* Say, were transferred to the experimental containers 1 h before the blue crabs. All shells were measured by means of calipers (maximum length and width), and the size distribution of gastropod shells was similar in all experiments. For practical reasons, it was not possible to determine the sizes of the hermit crabs occupying these shells. Each experiment lasted for 24 h. All surviving hermit crabs were removed and new ones were added before new experimental runs were started.

Three different types of habitats were also used in the predation studies, namely bare sand, *Thalassia,* and *Syringodium.* The depth of the sand layer in all aquaria was approximately 5 cm. The predation experiments were designed to examine several main questions:

(1) Is survivorship on bare sand different for *P. maclaughlinae* carrying shells of *Modulus* versus *Cerithium*? Experiment 1a: Four blue crabs with carapace widths (CW) of 71.7 mm, 68.2 mm, 84.4 mm, and 67.6 mm were used. Three trials were carried out for each crab, except the 84.4-mm crab ($N = 2$). Trials were pooled for each crab to obtain mean percentage of survivorship of hermit crabs in the two shell species and statistically analyzed with a paired t-test ($N = 4$) with arcsine square root-transformed data. Experiment 1b: Three trials were run with 7 small blue crabs (mean CW 39.1 mm, SD = 2.2 mm) in a single compartment. Data were compared with a paired t-test (arcsine square root-transformed data).

(2) Is survivorship higher for *P. maclaughlinae* in the presence of *Thalassia* as compared with bare sand? Experiment 2a: In addition to the 3 trials with bare sand, 3 replicate trials with the 71.7-mm CW blue crab from experiment 1a were carried out with *Thalassia* added. Five plants (3 blades each) were placed in the compartment with 1 in each corner and 1 in the middle of the compartment. Percentage survivorship for hermit crabs in both shell types combined was compared in the 2 treatments with a t-test (arcsine square root-transformed data). Experiment 2b: Three blue crabs (81.5; 91.5; 87.1-mm CW) were used for these experiments which were carried out in 6 compartments where 3 had bare sand bottom and 3 had a patch of *Thalassia* (field density) covering 25% of the bottom surface (in one corner). After the termination of the first part of the experiment after 24 h, the blue crabs were switched to the other "habitat" (after removing all hermit crabs and adding new ones). Percentage survivorship for hermit crabs in both shell types combined was compared in the 2 treatments with a paired t-test (arcsine square root-transformed data).

(3) Is survivorship higher in beds of *Syringodium* versus those of *Thalassia*? Two aquaria, each with two compartments, 1 of which contained *Thalassia* (field density) and 1 of which contained *Syringodium* (field density), were used. One blue crab (CW = 75.0, 70.0, 83.8, and 89.9 mm) was placed in each compartment according to the procedures described above. After 24 h, blue crabs were removed, surviving hermit crabs were counted, and a new set of hermit crabs was added to each compartment and allowed to climb on the sea grass for one h. Each blue crab was then placed in a compartment with the other sea-grass species for a sec-

ond experimental trial. Percentage survivorship for hermit crabs in both shell types combined was compared in the 2 treatments with a *t*-test (arcsine square root-transformed data).

RESULTS

Field Studies

Size-Frequency Distribution.—For graphical presentations the individuals were divided into size classes (CL) of 0.05-mm intervals (Fig. 1). Males reached greater size than females in most months (Fig. 1), and females tended to have a uni- or bimodal distribution, while males tended to have either a bimodal or polymodal distribution. For months in which the larger size classes were dominated by males (August and October 1985, February, March, April, July, and August 1986), the size–frequency distribution of males and females was significantly different ($R \times C$ tests of independence (G), $P < 0.05$).

Recruitment.—The monthly percentages of individuals in the samples with a CL ≤ 1.00 mm are shown in Fig. 2. Recruitment occurred mainly in October–February and May–July, with the highest values recorded during the latter period (Figs. 1, 2).

Sex Distribution.—Among the 1,244 individuals collected with a CL ≥ 1.00 mm the male/female ratio was close to 1 (50.9% males and 49.1% females). Seasonal differences were recorded in this ratio, however (Fig. 3). Significant deviations from a 1:1 sex ratio were observed only in August 1985, July and August 1986 when males occurred in greater proportion, and in March 1986 when females were more abundant (G tests of goodness of fit to 1:1 ratio, $P < 0.05$).

Ovigerous Females.—The percentage of ovigerous females (≥ 1.5-mm CL) varied seasonally (Figs. 1, 4). The percentage was high ($>50\%$) in August, September, October (1985), and in February–June (1986), and low ($<25\%$) in December (1985), January, July, and August (1986). The data suggest that female maturation occurred at approximately 1.25–1.50-mm CL.

Shell Species Utilization.—Gastropod shell utilization was determined for *P. maclaughlinae* in size classes (CL) of 0.25-mm intervals. Class 1 represents all individuals with a CL ≤ 0.75 mm and class 10 represents all individuals with a CL >2.75 mm. The gas-

tropod shells used by *P. maclaughlinae* were recorded for 2,404 individuals from the entire study period. No study was performed concerning the composition and number of empty available shells in the field. A total of 13 gastropod species was utilized, of which two could not be identified. *Cerithium muscarum, Modulus modulus,* and *Nassarius vibex* Say constituted 93.6% of the shells used (Fig. 5). Females used more shells of *C. muscarum* than males, but males used more shells of *M. modulus* than females (Fig. 6). Overall shell utilization patterns were significantly different between sexes ($R \times C$ test of independence, G test; $G = 80.88$, *d.f.* $= 7$, $P < 0.001$). Ovigerous females (≥ 1.50-mm CL) utilized more shells of *C. muscarum* and fewer shells of *M. modulus* as compared to nonovigerous females within the same size group (Fig. 7) ($R \times C$ test of independence (G test); $G = 13.69$, *d.f.* $= 4$, $P < 0.01$).

Cerithium muscarum strongly dominated in size class 1–3 males (≤ 1.25-mm CL), while *M. modulus* dominated in males larger than size class 6 (>2.00-mm CL, Fig. 8). *Cerithium muscarum* dominated among females in size classes 1–5 (≤ 1.75-mm CL), but *M. modulus* was the dominant species for the largest size class (>2.75-mm CL) for females (Fig. 8). The use of shells of *N. vibex* was similar in both sexes, except that no size class 1 females (≤ 0.75-mm CL) carried these shells. The percentage of shells of *N. vibex* used was also notably lower in size class 8 males (2.26–2.50-mm CL) compared to the same size class females.

Habitat Utilization.—The quantitative samples collected between December 1985 and October 1986 showed that the mean density of *P. maclaughlinae* was highest in *Thalassia testudinum,* somewhat lower in *Syringodium filiforme,* and very low in *Halodule wrightii* (Fig. 9). The mean densities were significantly different in each sea-grass habitat (T' method of multiple comparisons), $P < 0.05$ (Sokal and Rohlf, 1981); *Thalassia*: 45.3 ind·m^{-2} (SD $= 25.3$, $N = 36$), *Syringodium*: 28.5 ind·m^{-2} (SD $= 19.3$, $N = 24$), *Halodule*: 3.7 ind·m^{-2} (SD $= 6.5$, $N = 25$). The abundance of *P. maclaughlinae* differed seasonally, with peak values in February–March, July–August, and October, with the highest values during the
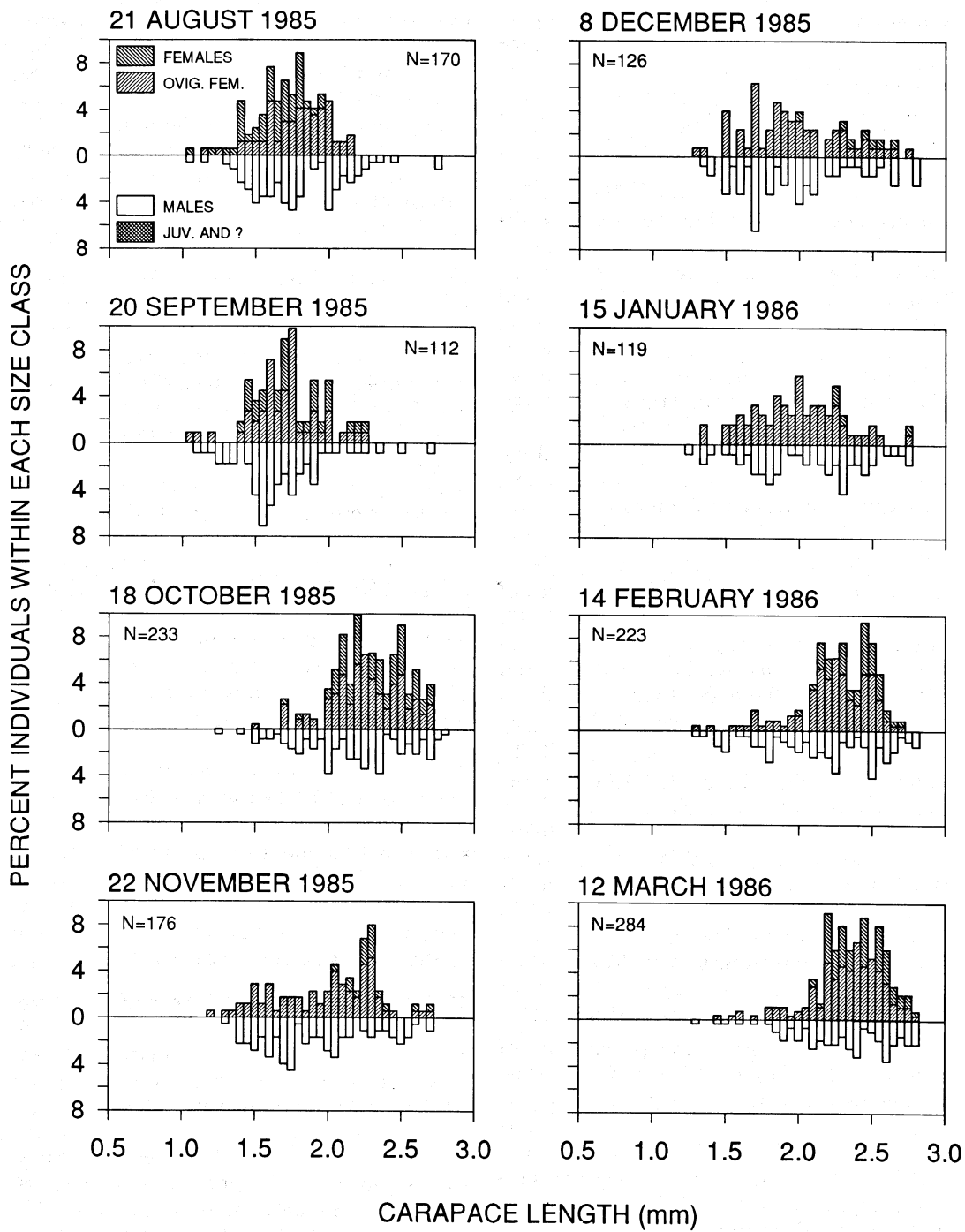
Fig. 1.   Size-frequency distribution in carapace length of all individuals (*N*) of *Pagurus maclaughlinae* collected at each sampling date. Cross-hatched bars denote juvenile specimens or individuals where the sex could not be determined.
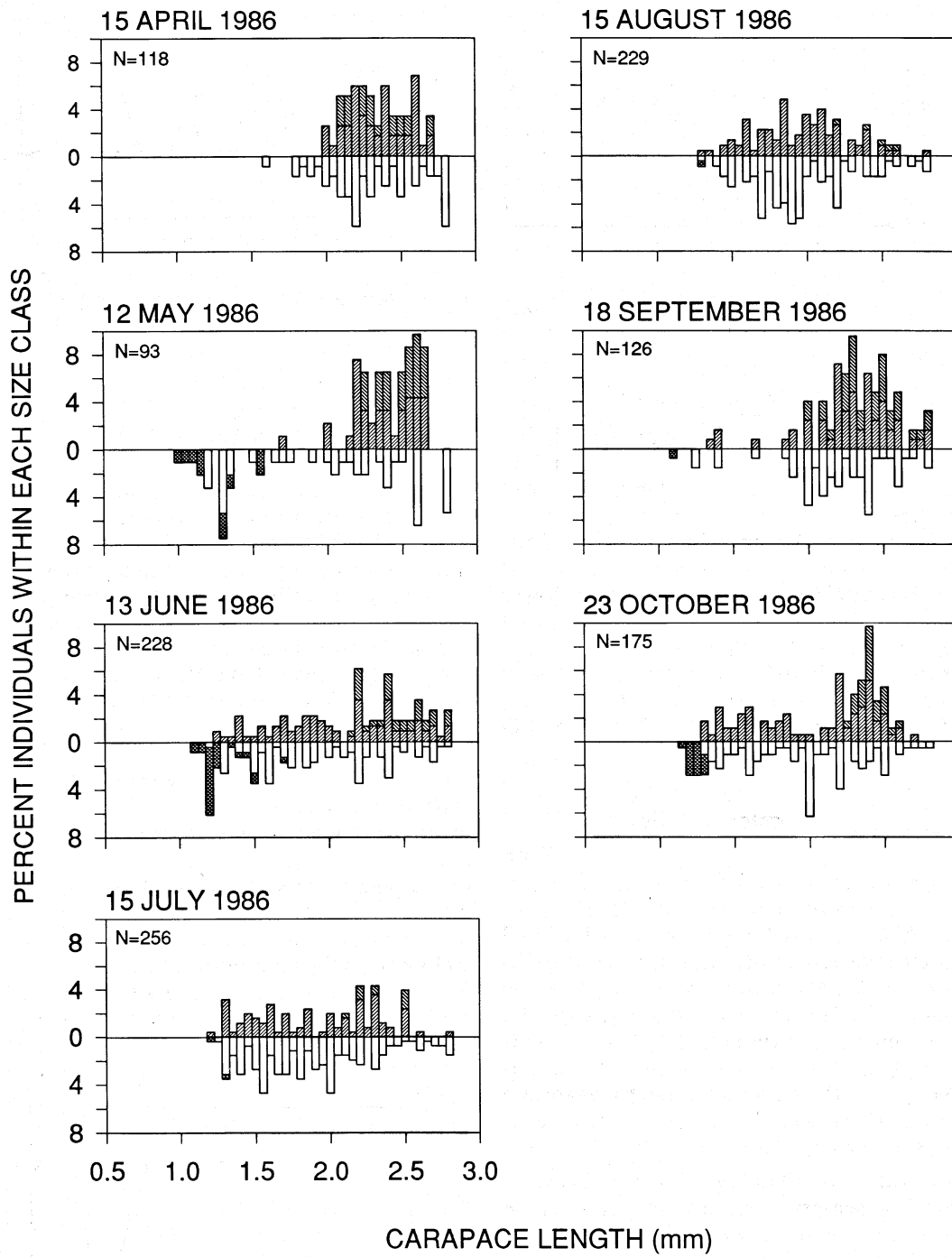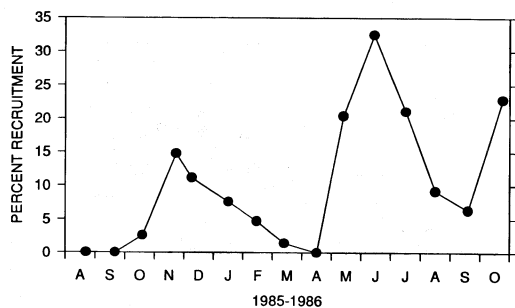
CARAPACE LENGTH (mm)

Fig. 1. Continued.

Fig. 2. Percentage of individuals of *Pagurus maclaughlinae* with a carapace length ≤ 1.00 mm on each sampling date.

Fig. 3. Male/female ratio among individuals of *Pagurus maclaughlinae* with a carapace length ≥ 1.00 mm on each sampling date.

summer. Low abundances were recorded in April–May, and in *Thalassia* also in December–January, the only habitat sampled in these months.

Comparison between bare sand and *Thalassia/Syringodium* ($N = 6$, 12 March and 15 July 1986) found a significant lower abundance of *P. maclaughlinae* on bare sand (0.7 ind·m⁻², SD = 0.8) versus the two sea grasses which did not differ significantly from each other (*Thalassia,* 70.7 ind·m⁻², SD = 18.4, *Syringodium,* 45.2 ind·m⁻², SD = 24.6), T' method.

Laboratory Studies

Small-Scale Distribution Patterns. — Both laboratory experiments examining the small-scale distributional patterns of *P. maclaughlinae* showed a random distributional pattern (variance/mean ratio, $P < 0.05$) (Elliott, 1977). Most crabs were found on the plants of *Thalassia* and only a few on the sediment surface (none buried into the sediment). There does not appear to be a tendency for *P. maclaughlinae* to aggregate within *Thalassia,* at least within the parameters of the experiment.

Habitat Distribution Pattern Experiments. — Sea-grass species choice. — Three experimental trials were run, in which *P. maclaughlinae* was offered a choice among the three sea-grass species or bare sand. In all three trials, significant differences were observed for the mean percentage of hermit crabs within a substrate type (Table 2). For all three trials combined, the largest number of crabs were found in patches of *Syringodium* followed by patches of *Thalassia* and
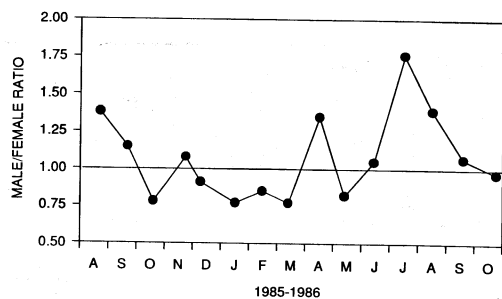
Halodule, and then bare sand. Statistical comparisons indicated, however, that the trials differed in which means were significantly different from each other.

In trial 1, all means were significantly different with the majority of crabs choosing *Syringodium,* followed by *Thalassia* and *Halodule,* with very few crabs in bare sand (Table 2). In trial 2, hermit crabs were removed and replaced, but the same sea-grass blades were left in the tanks to allow evaluation of whether previous occupation of the sea grass would alter crab choice. The mean percentage of crabs selecting *Syringodium* and *Thalassia* did not differ significantly, although *Syringodium* again had the highest percentage of crabs. The percentage in *Halodule* was significantly less than the other sea grasses and no crabs were found in bare sand (Table 2). It is likely that the crabs grazed the epiphytes sufficiently in the first trial to affect the relative attractiveness of the *Syringodium* in the second trial.
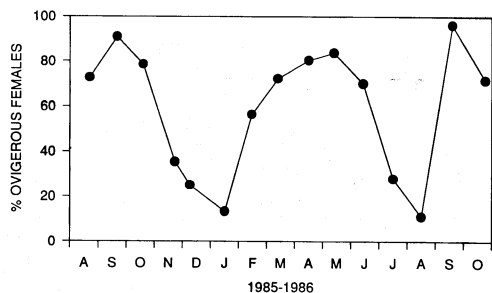

Fig. 4. Percentage of ovigerous females versus total females among individuals of *Pagurus maclaughlinae* with a carapace length ≥ 1.5 mm on each sampling date.
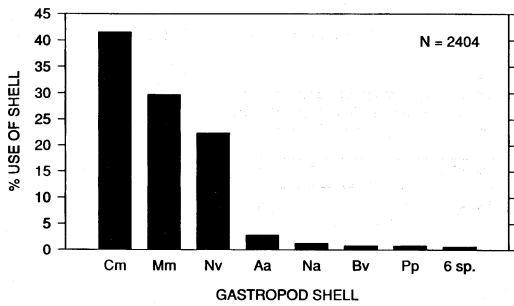
Fig. 5. Gastropod shell use among 2,404 individuals of Pagurus maclaughlinae collected between August 1985 and October 1986. Cm = Cerithium muscarum, Mm = Modulus modulus, Nv = Nassarius vibex, Aa = Anachis avara, Na = Nassarius acutus, Bv = Bittium varium, Pp = Pyrgocythara plicosa, 6 species (=Mitrella lunata, Eupleura caudata, Rissoina catesbyana, Cerithiopsis greeni, gastropod sp. A, gastropod sp. B).

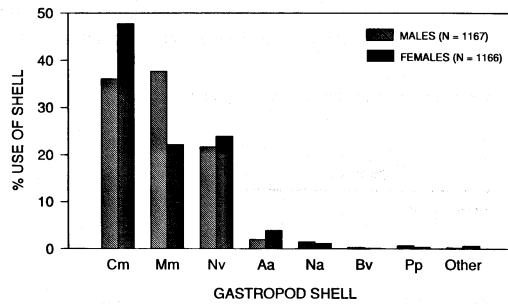Fig. 6. Gastropod species use versus sex for Pagurus maclaughlinae. See Fig. 5 for explanation of species abbreviations.

The sea grasses were replaced after trial 2 and a third trial was done. Again, significantly more crabs were found in *Syringodium*, and significantly fewer crabs were found in bare sand, while the percentage in *Thalassia* and *Halodule* were intermediate and did not differ from each other (Table 2).

Epiphyte choice experiments.—Results of the experiments comparing clean and fouled surfaces with both natural and artificial sea grasses are given for *Syringodium* and *Thalassia* in Table 3. There was no difference in selection of real versus artificial *Syringodium*, while there was a highly significant preference for fouled surfaces compared to clean ones. The interaction term was not significant (Table 3). The situation for the experiment with *Thalassia* was more complex. Again, there was no significant difference between real and artificial sea grasses in terms of hermit crab abundance, while there was a highly significant preference for fouled substances over clean ones. The interaction term was significant, however, presumably caused by the relatively similar values for fouled and clean, real sea-grass blades, while fouled and clean artificial sea grasses were extremely different.

Predator presence experiment.—Hermit crabs selecting sea-grass substrata in the presence of a blue crab predator had a highly significant preference for *Syringodium* versus the other two sea-grass species (Table 4). There was no significant difference in the selection of *Thalassia* versus *Halodule*.

Predation experiments.—Predation experiments (Table 5) indicate that (a) predation rate was not dependent on the type of shell used by P. maclaughlinae (*Modulus* and *Cerithium*) (experiment 1a survivorship: *Modulus* = 28.2%, *Cerithium* = 43.6%; experiment 1b survivorship: *Modulus* = 72.8%, *Cerithium* = 61.2%), (b) the presence of *Thalassia* offered protection against predation compared with bare sand (experiment 2a survivorship: sand = 23.3%, *Thalassia* = 45.0%; experiment 2b survivorship: sand = 37.5%, *Thalassia* = 66.6%), and (c) predation rates of blue crabs were not different between the two sea-grass habitats, *Thalassia* and *Syringodium* (experiment 3 survivorship: *Syringodium* = 53.3%, *Thalassia* = 36.7%).

DISCUSSION

The high abundance of P. maclaughlinae found within the study area and its feeding

Table 2. Summary data for habitat preference experiments for *Pagurus maclaughlinae*. F values are for one-way ANOVA with arcsine square root-transformed percentage data. Means presented are back-transformed percentages. Horizontal lines under means indicate values not significantly different at $P < 0.05$ (Welsch Step-Up procedure).

Trial number	F	d.f.	Treatment means (%)			
			Sand	Halodule	Thalassia	Syringodium
1[a]	45.2[b]	3,20	0.2	14.7	25.5	58.8
2[a]	48.2[b]	3,20	0.0	21.6	36.5	40.2
3	18.8[b]	3,16	6.1	24.4	24.4	44.0

[a] Same sea-grass blades used.
[b] $P < 0.001$.

Table 3. Summary data for epiphyte-choice experiments for *Pagurus maclaughlinae*. *F* values are for two-way ANOVA with arcsine square root-transformed percentage data. Means presented are back-transformed percentages.

| | Mean percentage of blade type selected | | | |
| | Fouled | | Clean | |
Experiment	Real	Artificial	Real	Artificial
Syringodium	36.7	34.6	15.3	8.0
ANOVA	*d.f.*	*F*		
Fouled versus clean	1,8	7.89**		
Real versus artificial	1,8	0.43		
Interaction	1,8	1.92		
Thalassia	27.6	44.1	21.8	4.1
ANOVA	*d.f.*	*F*		
Fouled versus clean	1,8	18.68**		
Real versus artificial	1,8	0.64		
Interaction	1,8	11.07*		

* $P < 0.05$.
** $P < 0.01$.

behavior indicates that it is a very important component within these sea-grass systems. Noteworthy in this context is that only one other hermit crab species, *Clibanarius vittatus* (Bosc), was found during the whole study period (4 specimens). Therefore, as suggested by Gore *et al.* (1981) and Virnstein *et al.* (1983), *P. maclaughlinae* appears to be the dominant hermit crab in the sea grasses in this region of the Indian River.

As shown in Figs. 2, 4, recruitment peaked in November–December and May–July, while the highest ratio of ovigerous females was found in September–October and March–June. Ovigerous females with eggs ready for hatching were mainly found in September–October, February–March, and

June. The development time of the four zoeal stages through the megalopa stage is between 14 and 22 days (McLaughlin and Gore, 1988); this suggests that the period between hatching and when recruitment was recorded in the samples varied between approximately 1.5 and 2.5 months, provided that the recruitment occurred from the population that was being studied.

High densities were recorded in the spring and in the summer both in *Thalassia* and *Syringodium* (Fig. 9). As shown in Fig. 2, the high values during the summer were probably due to recruitment during this period.

Hermit crabs are, with few exceptions, dependent on the empty shells of gastropods. These are often found in limited supply (Fotheringham, 1976; Kellogg, 1976;

Table 4. Summary data for predator presence experiment for *Pagurus maclaughlinae*. *F* values are for one-way ANOVA with arcsine square root-transformed percentage data. Means presented are back-transformed percentages. The horizontal line under means indicates values not significantly different at $P < 0.05$ (Welsch Step-Up procedure).

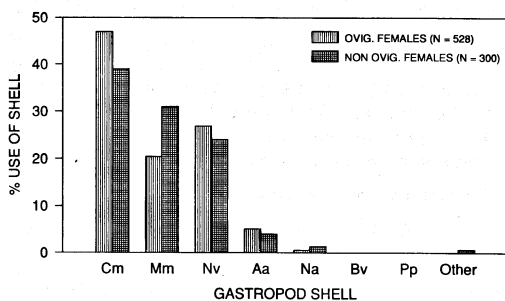| | | | Treatment means (%) | | |
			Syringo-dium	Thalassia	Halo-dule
Mean percentage selected			75.3	21.0	3.8
ANOVA	*d.f.*	SS	MS	F	
Among sea grasses	2	6,393.0	3,196.5	23.3**	
Error	9	1,235.5	137.3		

** $P < 0.01$.

Fig. 7. Gastropod species use for ovigerous and non-ovigerous females with CL ≥ 1.5 mm for *Pagurus maclaughlinae*. See Fig. 5 for explanation of species abbreviations.

Table 5. Experiments with predation on *Pagurus maclaughlinae* by the blue crab *Callinectes sapidus*. N = number of trials; t-tests used arcsine square root-transformed data). Individual experiments are described in the text.

Experi-ment	Question	N	Test	t	Significance level
1a	Is the survivorship on sand different for hermit crabs in *Modulus* versus *Cerithium* for large blue crabs?	4	paired t	−1.70	NS
1b	Is the survivorship of hermit crabs in *Modulus* different from that of hermit crabs in *Cerithium* for 7 small blue crabs?	3	paired t	1.19	NS
2a	Is the survivorship of hermit crabs in *Modulus* and *Cerithium* combined higher in the presence of *Thalassia* versus bare sand?	6	regular t	2.68	$P < 0.05$, 1 tail
2b	Is the survivorship of hermit crabs in *Modulus* higher in *Thalassia* versus bare sand?	3	paired t	1.82	NS
2b	Is the survivorship of hermit crabs in *Cerithium* higher in *Thalassia* versus bare sand?	3	paired t	1.53	NS
2b	Is the survivorship of hermit crabs in *Modulus* and *Cerithium* combined higher in *Thalassia* versus sand?	6	paired t	2.61	$P < 0.05$, 1 tail
3	Is the survivorship of hermit crabs in *Modulus* and *Cerithium* combined higher in *Syringodium* versus *Thalassia*?	6	regular t	0.75	NS

Spight, 1977; Wilber and Herrnkind, 1982). No data are, however, available on the supply of empty shells in the study area in the Indian River Lagoon. Wilber and Herrnkind (1984) showed that *Pagurus longicarpus* Say directly acquired new shells as a predatory gastropod consumed periwinkles. Shell condition has also been found to affect shell-choice behavior (McClintock, 1985). Wilber (1990) found in a study on *P. longicarpus* that shell size was a more important shell characteristic in shell selection than either shell species or shell damage. It was not within the scope of this study to evaluate these complicated questions for *P. maclaughlinae*. In one case in the present study, however, one *Modulus modulus* still contained the live gastropod behind the hermit crab (*P. maclaughlinae*, male, CL = 0.92 mm), which might indicated a short supply of suitable shells.

The total of 13 species of gastropod shells used by *P. maclaughlinae* was comparable to other species within the genus *Pagurus*. *Pagurus annulipes* (Stimpson), also within the Provenzanoi group, utilized 18 species of gastropods in North Carolina (Kellogg, 1977). Hermit crabs in the field usually occupy a distinct subset of available gastropod shell species (Hazlett, 1981), and, according to Bertness (1981a, b) the shell species selected are important regarding such factors as predation rate, resistance to thermal stress, clutch size, and growth (see below). Since the proportion of available shells in the field was not investigated, it was not possible to relate the utilization rate to shell abundance.

As shown in Fig. 8, females of *P. maclaughlinae* occupied *Cerithium muscarum* more than males, and ovigerous females also used *C. muscarum* more than nonovigerous females (Fig. 7). This contrasts with results from other studies where in free access experiments the shell preferences of males and females (also ovigerous ones) appeared similar in a given species (Bertness, 1980).

There was a clear difference in the field distribution pattern for *P. maclaughlinae* in relation to different sea-grass species in the present study. A clear preference was recorded for *Thalassia testudinum*, followed by *Syringodium filiforme*, and last by *Halodule wrightii*, with very low abundance. The difference in abundance between the three habitats is probably connected to predator
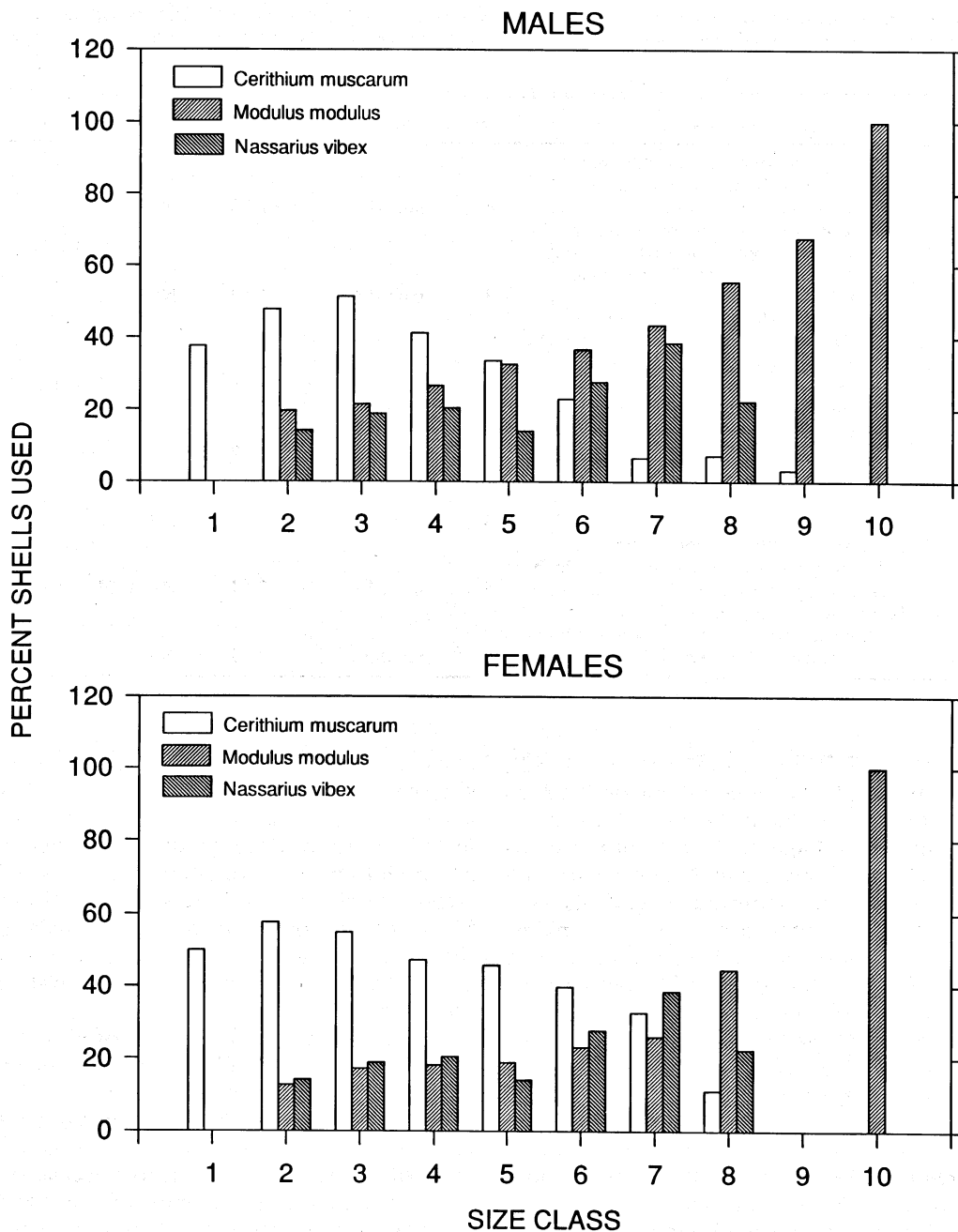
Fig. 8. Relative shell use for the three dominant gastropod species (*Cerithium muscarum, Modulus modulus, Nassarius vibex*) in different size classes for males and females for *Pagurus maclaughlinae* (see the text).

avoidance and/or food source (see below). The beds of *Thalassia* were very dense throughout the whole year. The blades of *Thalassia* also had a large surface area with a heavy growth of epiphytes, which appears to be the main food source of *P. maclaugh-* *linae* (Smith, 1988). The beds of *Syringo-dium* were not as dense, and the surface of the blades was smaller than that of *Thalassia. Halodule* grew only in a narrow band in shallow water along the shore line. In addition to being small in size, this sea grass
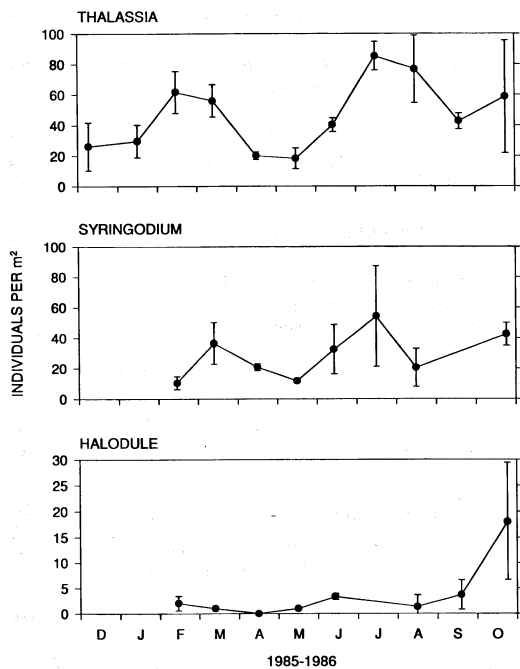
Fig. 9. Mean monthly density (± 1 SD) of *Pagurus maclaughlinae* within the three different sea-grass habitats.

grew in very patchy beds. During extreme low water the beds of *Halodule* were also completely exposed to the air. Smith (1988) found no significant differences in the abundance of *P. maclaughlinae* from a series of small (225 cm²) cores in the three sea-grass species. These cores revealed a significantly greater abundance of *P. maclaughlinae* in high biomass sea grass versus low biomass sea grass, regardless of sea-grass species. The difference in results may be largely due to the cores being too small to reflect accurately crab abundances which tend to be patchy on the scale of the samples taken.

The field distribution pattern for *P. maclaughlinae* differs from the preference for sea-grass species demonstrated in laboratory experiments where *Syringodium* was a clearly preferred substrate, whether or not a blue crab predator was present. However, in the laboratory experiments, sea grasses were provided in amounts based on equal surface areas. Clearly, hermit crab selection of sea grass involves a response to other variables than surface area. In the field, sea grasses will not be present at equivalent surface areas per unit bottom, and other factors, such as biomass per unit area or extent

of epiphyte cover, may be most important in habitat selection. The experimental work indicates that epiphyte cover is one of the important variables in habitat selection by adult *P. maclaughlinae.*

Predation pressure and physical stress were shown to be important selective pressures on hermit crabs in the Bay of Panama, influencing their intertidal distributions, shell preferences, and behaviors (Bertness, 1981b; Borjesson and Szelistowski, 1989). Some predators of hermit crabs, including gastropods, fishes, octopods, and predaceous crabs, may extract crabs directly from their shells without inflicting shell damage (Bertness, 1981b). In the present study, the blue crab predators made no attempt to extract the hermit crabs from their shells. They usually attacked the hermit crabs immediately upon encountering them. The most commonly used crushing technique was to grab the shell with one cheliped and then, with a rolling motion, to crush the outer lip of the shell with the other cheliped until the hermit crab was unable to retract any further into the spire of the shell. This technique was especially obvious with the high-spired *Cerithium muscarum.* The blue crab *C. sapidus* was very abundant within the same habitat as *P. maclaughlinae* (personal observation), and, based on the results of the predation studies, should be a significant predator on this hermit crab. The experiments suggest that the sea-grass beds (*Thalassia*) offer some degree of protection against blue crab predation, a result consistent with other studies (Heck and Thoman, 1981). Because of the small size of *P. maclaughlinae,* blue crab predation may be restricted to small and medium-sized blue crabs. Large blue crabs were not observed in the sampling area during the study period. Heck and Wilson (1987) conducted predation experiments with tethered decapods in sea-grass beds, concluding that there seemed to be little relationship between predation rates on hermit crabs and the degree of thickening or ornamentation of their gastropod shells. A study by Kuhlmann (1992) on the predation of *Pagurus longicarpus* showed that predation rate was independent of shell species, shell size, and shell damage, in contrast to results from other studies on gastropod shell predation (e.g., Palmer, 1979). Further field and laboratory experi-

ments would clarify the role of *Pagurus maclaughlinae* in the epifaunal community of sea grasses in the Indian River Lagoon.

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