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MACROALGAE (RHODOPHYTA: *LAURENCIA* SPP.) AS HABITAT FOR YOUNG JUVENILE SPINY LOBSTERS, *PANULIRUS ARGUS*

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ABSTRACT

Field surveys were conducted in the middle Florida Keys to better document habitat used by newly settled juvenile spiny lobsters, *Panulirus argus*. Early benthic stages were most numerous in locations where they resided in or beneath macroalgal clumps of red algae *Laurencia* spp. Macroalgae provide refuge and support an abundant, diverse fauna preyed upon by young lobsters. Postlarval settlement occurred at monthly intervals, indicating continuous use of the algal microhabitat by successive settlement classes. Patterns of resource use were well defined ontogenetically. From settlement (6 mm carapace length) through approximately 17 mm CL, young lobsters remained within algal clumps, thereafter moving to the substrate to take residence in various den structures. The transition from algal to den dwelling was accompanied by a shift from solitary to aggregate habitation. However, this apparent change in sociality was not rigidly fixed ontogenetically but depended in part on the local distribution of shelter and food.

The western Atlantic spiny lobster, *Panulirus argus,* supports major commercial fisheries in south Florida, the Bahamas, Brazil, Cuba, and other regions of the Caribbean (Bowen, 1980). The spiny lobster life history has several stages (larval, postlarval, early benthic juvenile, juvenile, and adult), each characterized by distinctive behaviors and habitat use (Kanciruk, 1980). Phyllosome larvae spend 6 to 12 months in the oceanic plankton, then metamorphose offshore into the puerulus, or postlarva, a brief (weeks), non-feeding, swimming stage which migrates shoreward, eventually settling in nearshore shallows (Lyons, 1980). Settlement occurs at 6 mm carapace length (CL), as measured from the base of the supraorbital spines to the posterior edge of the cephalothorax. Upon settling, previously transparent pueruli acquire dark pigmentation and within days molt into the first juvenile stage. Distinctive color patterns of young juveniles represent a combination of cryptic and disruptive features. Body colors include shades of brown, black, and purple. The antennae and pereopods are banded white, while a broad white stripe extends along the dorsal midline of the carapace and abdomen.

Combined with small size, body coloration renders young juveniles exceedingly difficult to observe amidst benthic vegetation. Consequently, information on specific habitat requirements, behavioral–ecological relationships, and population characteristics for the period immediately following settlement is limited. Although such information is available for equivalent stages of some other palinurids, habitation patterns appear to be dependent on the ecological characteristics of particular regions. For example, juvenile *Panulirus cygnus* concentrate in dense aggregations on protected, algal-fouled reefs along the coastal shallows of western Australia (Chittleborough, 1970), whereas recently settled *P. interruptus* reside solitarily in nearshore beds of the surfgrass *Phyllospadix* along the coast of southern California (Engle, 1979).

Witham et al. (1964) reported catching postlarval and juvenile *P. argus* (up to 25 mm CL) from algal-fouled mangrove roots and algal masses collected from shallow seagrass beds in the St. Lucie Estuary in eastern central Florida. Algae were predominantly rhodophycean macrophytes. The region sampled is north of

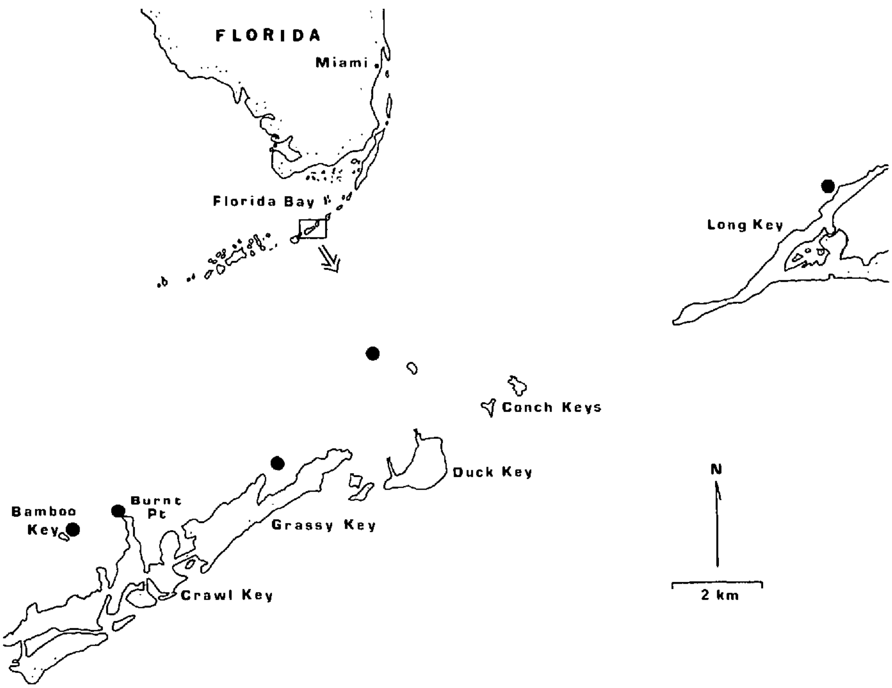


Figure 1. Symbols denote sites in the middle Florida Keys where early post-settlement spiny lobsters, *Panulirus argus*, inhabited clumps of red algae, *Laurencia* spp.

the major concentration of Florida spiny lobsters and may not represent typical habitat. Eldred et al. (1972) and Davis (1979), monitoring commercial bait trawls in Biscayne Bay, observed substantial catches of lobsters between 11 and 30 mm CL. Sampled habitat consisted of sand and mud substrate with seagrasses, calcareous green algae, and the red alga *Laurencia obtusa* although the microhabitat actually occupied could not be specified. Andree (1981) discovered populations of somewhat older juveniles ($\bar{x}$ = 20 mm CL) within shallow, algal-fouled rubble zones on the bayside of Elliot Key in Biscayne National Park. Lobsters resided solitarily in small crevices amidst benthic vegetation dominated by calcareous green algae and various red algae, primarily *Laurencia* spp. Foraging was strictly nocturnal and confined to the narrow zone of algal-fouled rubble within which the animals took shelter. Fecal content analyses indicated a diverse diet, with frequent occurrence of gastropod, bivalve, and crustacean material.

We undertook to expand the breadth of knowledge concerning the habitat requirements of young *Panulirus argus* immediately after settlement. Specific objectives were to (a) determine the settlement habitat in the Florida Keys, (b) obtain basic information describing the population characteristics of young juveniles, and (c) determine the nature of their microhabitat requirements. This information is of interest both with respect to contemporary questions about animal–resource relationships and for fishery management.

Materials and Methods

Habitat surveys were made in the middle Florida Keys (near Marathon) from May through September 1982 and in August 1983 in areas of densely vegetated or otherwise structurally complex substrate at depths from 1–5 m. All surveys were conducted during daytime by skin or SCUBA diving.

Table 1. Mean abundances and sizes (length in mm) of major groups of organisms obtained by rinsing six 2.5 liter clumps of *Laurencia* spp. (Standard deviations are shown to the right of the mean values)

Group	$\bar{x}$ per patch	$\bar{x}$ size (mm)
Gastropoda	94 ± 19	2.8 ± 2.4
Isopoda	25 ± 12	5.9 ± 1.9
Amphipoda	18 ± 12	4.0 ± 0.9
Caridea	18 ± 9	7.7 ± 1.8
Holothuroidea	21 ± 12	7.9 ± 3.6
Ophiuroidea	10 ± 3	2.2* ± 0.8
Polychaeta	12 ± 8	10.4 ± 4.9

* Diameter of central disc.

We recorded all young lobsters found from settlement stage to 20 mm CL as well as habitat characteristics including depth, distribution of substrate, and type and degree of vegetation.

Newly settled lobsters were especially abundant in *Laurencia* spp. clumps near Burnt Point on the bayside of Crawl Key (Fig. 1). This area was sampled at least once weekly from 22 May through 28 September 1982. Lobsters up to 20 mm CL were collected by fine-mesh hand nets and immediately transported to boatside holding tanks. The carapace length, dwelling resource used, and type of occupancy displayed (solitary vs. aggregated) was recorded. To prevent subsequent recapture, all collected animals were released several miles away in similar habitat.

Quantitative descriptive information for Burnt Point was obtained by tossing a 1-m^2 frame of plastic pipe at random within the habitat. Relevant resources within the frame were counted (sponges, ledges, etc.) and all rhodophycean algae removed and measured volumetrically. All volume measurements were done above water using the natural packing of the algal clumps as collected. A total of 21 tosses were performed; in eight samples algae were sorted to major species prior to measurement. Spot surveys were carried out to estimate the total area of habitat occupied by lobsters, while intensive sampling of a representative 300 m^2 area provided density estimates.

Faunal associates of *Laurencia* spp. were quantified by rinsing six 2.5-liter clumps of algae and sorting the organisms obtained to major groups. Rinsing consisted of gently and repeatedly shaking small handfuls of algae in a bucket of seawater. The sorting technique used was inefficient for fauna below 1 mm in total length, therefore reported abundances are conservative. The diet of recently settled lobsters was determined by examining 25 stomachs of juveniles 6–8 mm CL collected at night after they had foraged in *Laurencia* clumps.

RESULTS

Recently settled *P. argus* were found at several locations along the bayside of the middle Florida Keys (Fig. 1). The young lobsters resided within or underneath macroalgal masses dominated by red algae *Laurencia* spp. The coarse, relatively wide algal branches formed an open lattice-work facilitating the movement of young lobsters within the clumps. In addition, the intricate branching supported a heterogeneous mixture of algal epiphytes, attached fauna (hydroids, bryozoans, etc.), and diverse gastropods, crustaceans, and other potential prey readily consumed by small juvenile lobsters (Tables 1 and 2).

Species composition varied among collection sites, but productive algal clumps were generally dominated by *Laurencia obtusa* and *L. poitei*, with sparser amounts of *L. intricata*. At the bayside Grassy Key site, however, the few animals collected were from a gorgonian skeleton overgrown exclusively by *L. intricata*. Habitat surveys on the oceanside were generally unproductive. We found a single animal, 13 mm CL in a crevice within a shallow, sparsely vegetated coral rubble zone off Conch Key. Four hours of subsequent sampling revealed no additional animals less than 20 mm CL. This absence is noteworthy because artificial habitats in the immediate vicinity regularly collected postlarval *P. argus*. Several juveniles between 7 and 15 mm CL were collected from the exposed rhizomes of undercut seagrass beds near Grassy Key. Extensive searching in adjacent areas revealed this to be a relatively uncommon habitat. In general, the oceanside has relatively

Table 2. Food items observed in stomachs of young juvenile spiny lobsters (6–8 mm CL) which had been foraging in *Laurencia* spp. (Frequencies of occurrence in 25 samples are indicated in parentheses)

Group	Species
Gastropoda (96%)	*Rissoella* sp.
	Tricolia spp.
	Arene sp.
	Marginella sp.
Crustacea (80%)	Ostracods (3 spp.)
	Isopoda
	Erichsonella floridana
	Flabellifera (1 sp.)
	Asellota (1 sp.)
	Anthuridea (1 sp.)
	Amphipoda
	Tanaidacea
	Copepoda (1 sp.)
	Paguroidea (1 sp.)
Echinodermata (8%)	Ophiuroidea (1 sp.)
	Holothuroidea (1 sp.)

little densely vegetated substrate as compared to the bayside. Early benthic lobsters were consistently found in greatest number at Burnt Point where the following information was obtained.

Habitat Description.—*Laurencia* clumps were patchily distributed at 2–3 m depths near shore in structurally complex substrate characterized by numerous sponges, gorgonians, and dense calcareous green algae. Such structures stabilized and provided attachment sites for red algae. Although the substrate was generally hard, direct holdfast attachment by red algae appeared to be inhibited by heavy layers of silt and detritus. Shoreward, in shallower water, algae were sparse and usually unattached, presumably due to disruptive wave action. Habitat offshore had reduced algal growth amidst thick particulate substrate patchily overgrown by seagrasses.

Laurencia spp. grew most luxuriantly where stabilizing structure and attachment substrate were abundant (Table 3). Gorgonians were frequently engulfed by algae, the extended fronds stabilizing clumps attached at the substrate to calcareous green algae or other stable surfaces. Clumps commonly exceeded 0.5 m thick, covered some 0.75 m^2 bottom area and harbored in excess of 10 liters of algae.

Patterns of Habitation.—Size-related patterns of habitation were well-defined (Table 4), reflecting ontogenetic changes in both the type of dwelling resource used (algae or dens) and occupancy (solitary or aggregated). Animals from initial settlement through 9 mm CL were found off the substrate dwelling solitarily within the deeper recesses of algal clumps. Single clumps often contained more than one small lobster although the individuals were dispersed within the structure. Volume appeared to be critical, because most recently settled lobsters were collected from large clumps (10 to 15 liters).

Lobsters from 10–17 mm CL were usually found on the substrate, residing solitarily under an algal clump and backed against a sponge, small coral, gorgonian base, or clump of *Halimeda* spp. Even large clumps contained only a single lobster of this size range, indicating increased dispersion as lobsters moved from within the algae to the substrate. The latter part of this size range (14–17 mm CL) appeared transitional, lobsters occasionally occupying dens without algal overgrowth such

Table 3. Abundance estimates of resources at Burnt Point as mean numbers (simple counts or volume) per m^2 random sample

Resource	$\bar{x}$ per sample
Gorgonacea*	2.3
Porifera†	0.60
Halimeda spp.‡	0.14
Stony corals, ledges, holes§	0
Laurencia obtusa	4.3 liters
Laurencia poitei	2.6 liters
Unidentified algae	0.6 liters

* Minimum height of 45 cm.
† minimum height of 20 cm.
‡ minimum diameter of 30 cm.
§ present in the habitat but not observed in the m^2 frame during 21 random tosses.

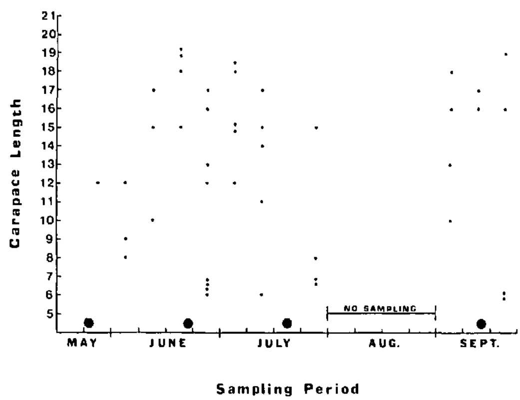
as rock holes, ledges, or depressions at the bases of sponges or corals. The transition to den dwelling, virtually complete by 18–19 mm CL, was accompanied by the first appearance of aggregations of similarly sized conspecifics. High quality dens allowing protective withdrawal, e.g., ledges or holes, were sparse (Table 3), possibly inducing juveniles 19 mm CL and larger to emigrate. The concomitant shift in both dwelling resource and co-occupancy, which appeared between 16 and 19 mm CL, was marked, suggesting an intimate relationship between these two features of habitation; dependence of each on size was supported statistically (separate tests; *G*-statistic, $P < 0.05$ for each case; Sokal and Rohlf 1969).

Population Structure.—Twenty-two sampling days at Burnt Point yielded 43 lobsters less than 20 mm CL ($\bar{x}$ = 13 mm). Carapace lengths of animals collected during each weekly sampling period are presented in Figure 2. Settlement over summer occurred monthly during the new moon–1st quarter lunar period as indicated by the presence of lobsters 6–7 mm CL in June, July, and September 1982. A wide distribution of sizes was always present, only the initial settlement classes being distinct (Fig. 3). The bimodality of Figure 3 indicates that initially distinct settlement classes merge over time, with the broad second peak probably comprising several previous settlements. Merging is likely caused by differences in individual growth rates, as well as somewhat different settling times within a given new moon–1st quarter lunar period. Assuming growth of 4 mm CL per month (Witham et al., 1968), the 14–15 mm CL midpoint of the second peak suggests that substantial recruitment occurred in April. Sample sizes are too small to compare monthly settlement magnitudes or to analyze size frequency changes over time. It is clear, however, that initial nursery habitat is used continuously by successive settlement classes.

Table 4. Dwelling resources and occupancy patterns of 2 mm CL size classes for juvenile lobsters collected at Burnt Point, presented as the number of lobsters observed (N = 43)

Size class	Algae*	Dens†	Solitary	Aggregated
6–7	9	0	9[1]	0
8–9	3	0	3[1]	0
10–11	3	0	3	0
12–13	5	1	6	0
14–15	3	4	5	2
16–17	4	4	6	2
18–19	1	6	1	6

* Within or beneath clumps.
† various crevices independent of algal overgrowth, such as rock, coral, large sponges, etc.



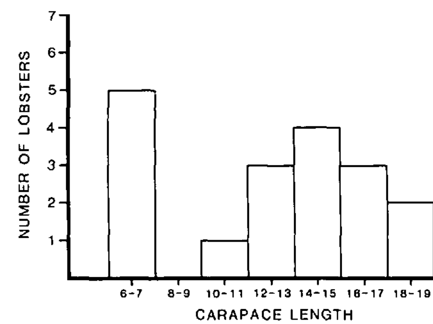


Figure 2. (Left) Carapace lengths (mm) of early post-settlement spiny lobsters collected from algal clumps at Burnt Point during each weekly sampling period from May through September 1982. The large filled circles denote the time of new moon. Lobsters 6–7 mm CL are first stage juveniles recently metamorphosed from the puerulus settling stage.

Figure 3. (Right) Size frequency of Burnt Point lobsters by 2 mm CL size classes collected during 8 sampling days between 25 June and 11 July 1982.

The total area of used habitat at Burnt Point was approximately two hectares. Intensive sampling revealed mean densities of one lobster per 36 m^2, or 278 per hectare, while greater than 50% of the algal clumps searched were void of lobsters at any time. Barren masses did not otherwise appear to differ from those containing lobsters; i.e., all were equally accessible and similar in algal composition.

Discussion

The Algal Microhabitat.—Constraints on foraging posed by predators may be a selective factor underlying the association of early benthic lobsters with *Laurencia* and other similar vegetation (Andree, 1981). Food and shelter are essentially offered in a single package, thus allowing foraging within the protective confines of an algal clump. Similar animal-resource relationships are known for other benthic decapods subject to heavy predation. Young juvenile *Panulirus interruptus* inhabit beds of the surf grass *Phyllospadix,* the dense matting and adjacent substrate providing predatory refuge as well as an abundant supply of small mollusks and other food (Engle, 1979). Young individuals of the small xanthid crab, *Pilumnus sayi,* occupy discrete heads of the bryozoan *Schizoporella pungens* which mainly provide protection from predators but also serve some trophic function (Lindberg, 1980). It is hypothetically advantageous for animals forced to compromise between resource exploitation and predator avoidance to shelter near abundant food (Morse, 1980). Macroalgae are recognized as exceptional resources in this regard (present data; Thorhaug and Roessler, 1977; Lewis, 1982).

The role of densely vegetated substrates as refuge from predation has been experimentally demonstrated by several workers. Coen et al. (1981) found that fish predation on grass shrimp was lowest in experimental arenas supplied with 100% algal cover. Similarly, Heck and Thoman (1981) reported reduced predation in areas with high seagrass density but not at lower seagrass densities, which gave no more protection than open sand. At Burnt Point, algal growth was luxuriant and most lobsters occurred in the largest clumps. It is uncertain whether this represents preferential settlement by pueruli or differential survival in microhabitats of varied quality. Selection of larger clumps is conceivably adaptive because, in addition to providing enhanced shelter, foraging area is increased and food is both more abundant and diverse. Such conditions presumably enhance growth and possibly delay emigration until the lobsters attain increased size refuge from predators.

Patterns of Habitation.—Solitary spacing should facilitate optimal resource use of the *Laurencia* clumps. Theoretically, by maintaining exclusive access to a feeding area a young juvenile reduces the foraging time required to meet nutritional demands, while simultaneously reducing exposure to predators. Dispersed spacing of young lobsters is probably mediated by agonistic behavior as suggested by their highly aggressive behavior in aquaria in which they use the antennae to lash and/or pry conspecifics (Andree, 1981 and pers. obs.). Encounters during foraging movements result in aggressive exchanges, with subsequent dispersal by the subordinate. Foraging territories in the field may be maintained via agonistic encounters arising during home range movements (sensu Burt, 1943; Stimson, 1973; Hamilton et al., 1976). The increased dispersion we observed after 14 mm CL probably resulted from more frequent encounters as growing individuals expanded their feeding range in a clump, or as food levels declined (McNab, 1963; Schoener, 1968).

The occurrence of solitary or aggregative habitation, after lobsters shift from algal to den-dwelling, seems to be regulated by the type of available shelter. At Burnt Point dens available to post-17 mm CL juveniles were sparse and patchy. The limited number of dens probably caused individuals to aggregate rather than maintain solitary dwellings. Furthermore, dens supply only partial camouflage while active defense may be facilitated by forming groups (Atema and Cobb, 1980). Andree (1981) noted a shift from solitary to aggregative dwelling at 25–30 mm CL, much later than at Burnt Point (15–20 mm CL). The critical difference appears to be that at Elliot Key, shelter was abundant and distributed throughout the habitat. We suggest that the time of ontogenetic transition from dwelling solitarily to aggregating is influenced partly by available resources. Intraspecific social flexibility in response to changing ecological circumstances is an emerging principle of behavioral ecology (Krebs and Davies, 1978; Morse, 1980); such flexibility probably allows young spiny lobsters to exploit a variety of habitats.

Population Dynamics.—Burnt Point during summer 1982 apparently had an overabundance of algal clumps relative to the number of lobsters resident at any time. *Laurencia* clumps of 2.5 liters volume, in running seawater tanks, consistently supported four to six 1st stage juveniles over a single night of foraging, yet in the field a maximum of two 1st stage juveniles inhabited algal clumps as large as 15 liters (Marx, 1983). The frequent occurrence of uninhabited clumps, combined with the occurrence of more than one recently settled lobster in the relatively few very large clumps, suggests coarse-grained selective settlement by a few recruits (Wiens, 1976).

The critical question becomes, was underutilization due to limited postlarval recruitment or poor survival of young recruits? Although estimates of predation are not available, intuitively it seems unlikely that predators could reduce early postsettlement populations so efficiently. Small, artificial habitats similar to algal clumps in size and apparent predator resistance often sustain large numbers of young juvenile *P. argus* (dozens: pers. obs.; Little, 1977; Little and Milano, 1980). Variable postlarval influx was the most likely factor limiting population size at Burnt Point during summer 1982. This proposition should be tested experimentally in the field or in large semi-field enclosures by seeding algal assemblages with pueruli and monitoring their fate over time.

Despite seemingly low densities, the estimated annual contribution to later juvenile stocks by habitats such as Burnt Point is considerable because rapid juvenile growth and the monthly influx of new pueruli cause continuous and rapid turnover of settlement classes. Given juvenile densities of 278 per hectare, and assuming growth of 4 mm CL per month (Witham et al., 1968), macroalgal habitat could contribute nearly 1,000 lobsters per hectare to the size classes above 20 mm CL each year: 20 mm − 6 mm = 14 mm (CL growth increment); 14 mm/4 mm (normal CL growth increment) = 3.5 months; 278 lobsters/hectare × 3.43 (12 mo/3.5 mo) = 954 lobsters/hectare. This extrapolation is admittedly crude, the actual contribution depending on several factors. Postlarval recruitment patterns in the Florida Keys are highly variable, peaks occurring during any season with significant regional variation during a given year (Little, 1977; Little and Milano, 1980). Contributions of settlement classes arriving during winter are likely depressed due to reduced growth (Davis, 1981) and frequent storm-caused benthic disturbances (Little and Milano, 1980). Monitoring over a full year, and preferably over consecutive years, would allow evaluation of the seasonal variability in algal microhabitat productivity, another influential factor. Irrespective of the precise values, our data imply that even small patches of rhodophycean dominated habitat contribute significant numbers of potentially harvestable lobsters. Such shallow and nearshore habitats are especially susceptible to disruption by shoreline development. Fishery attention should be given to the thorough study of this first manageable stage in the spiny lobster life cycle.

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