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FACTORS AFFECTING THE RECRUITMENT OF JUVENILE CARIBBEAN SPINY LOBSTERS DWELLING IN MACROALGAE

Mark J. Butler IV, William F. Herrnkind and John H. Hunt

ABSTRACT

In south Florida, Caribbean spiny lobsters (*Panulirus argus*) settle and spend their first few months in macroalgae or seagrass. After a few months, these “algal-phase” juveniles emerge from vegetation and, as “postalgal-phase” juveniles, seek refuge in crevices, often dwelling in groups. The importance of crevice shelters in determining the abundance of postalgal-phase juvenile spiny lobsters has been studied, but we know little about the processes affecting lobster distribution and survival during their cryptic algal-dwelling phase. We found that postlarval supply varied independently of changes in the structure of macroalgal settlement habitat. For this reason, postlarval supply alone can not reliably predict local settlement density. Changes in the size of macroalgal patches in particular tend to increase the variability in settlement density among locations and times. Field and mesocosm experiments indicate that social interactions and individual movements are unlikely to alter the general distribution of algal-phase lobsters established at settlement. But if algal-phase lobsters are aggregated at scales $<1 \text{ m}^2$ (e.g., due to patchy settlement), they experience higher mortality than non-aggregated lobsters, as revealed in field experiments where lobsters were tethered alone or in pairs and at varying inter-individual distances. Field manipulations of settlement density indicate that recapture (survival) of microwire tagged algal-phase juveniles is positively associated with features of the habitat that affect lobster density (e.g., site area, macroalgal patch size), but survival and growth of lobsters are unrelated to artificially manipulated settlement density. Collectively, these results imply that the population dynamics of juvenile *P. argus* dwelling in macroalgae are not typically regulated by density-dependent processes, although density-dependent predation may be locally important in patches when settlement is episodically high.

Extreme variance in recruitment, defined as the number of new individuals within a population that survive to a specified size, age, or ontogenetic stage, is characteristic of marine animals with “open” populations whose meroplanktonic larval stages drift for weeks or months in the water column. Many of these species also have complex life histories with multiple developmental stages requiring distinctly different habitats (Roughgarden et al., 1988). Therefore, understanding the processes affecting recruitment of such species requires information on larval availability, larval settlement, ontogenetic shifts in stage-specific habitat requirements, changes in nursery habitat availability and structure, and other factors that might alter post-settlement survival and growth.

A recurrent theme in the marine ecological and fishery literature centers on the extent that recruitment is limited either by larval settlement or post-settlement processes (Underwood and Fairweather, 1988; Grossberg and Levitan, 1992). A significant relationship between larval settlement and recruitment to some later life stage is typically considered evidence for supply-side (“recruitment”) population regulation and also the absence of density-dependent post-settlement mortality (Connell, 1985; Doherty and Williams, 1988). If post-settlement events, such as inter- or intraspecific competition or predation, are to regulate population density, then it is generally believed that they must act in a density-dependent manner (Hughes, 1990). If so, the relationship between larval settlement and recruitment is destroyed so that the age structure of recruits no longer reflects prior settlement. Yet, the

results of at least one mathematical model indicate that a settlement “signal” can persist in a population’s age structure despite density-dependent mortality, especially where settlement density is low or density-dependence is weak (Holm, 1990).

The literature describing the relative importance of pre- and post-settlement processes in regulating populations of marine organisms is rich with examples from crustacea. Barnacle populations on rocky shores in California (USA) (Gaines and Roughgarden, 1985; Possingham and Roughgarden, 1990) and spiny lobster populations in Western Australia (Chittleborough and Phillips, 1975; Pearse and Phillips, 1988; Caputi et al., 1995) are strongly affected by variation in larval (or postlarval) supply, a large part of which is driven by alterations in coastal currents. The recruitment of clawed lobsters in New England (USA) (Wahle and Steneck, 1991; Incze and Wahle, 1991), stomatopods in Panama (Steger, 1987), and Dungeness crabs in Washington (USA) (Eggleston and Armstrong, 1995) are thought to be limited by post-settlement mortality, notably the availability of suitable shelter for protection from predators. Similarly, shelter availability is critical to the recruitment of spiny lobsters in the Caribbean (Herrnkind and Butler, 1986; Butler and Herrnkind, 1992; Eggleston et al., 1990; Mintz et al., 1994; Field and Butler, 1994) and in Hawaii (Parrish and Polovina, 1994; Polovina et al., 1995), where it appears to regulate recruitment by setting thresholds (i.e., a local carrying capacity) for late-stage juveniles and subadults. One hypothesis is that recruitment is limited above these shelter-imposed thresholds, but below them the population fluctuates in response to larval supply (Forcucci et al., 1994; Polovina et al., 1995; Herrnkind and Butler, 1994; Butler and Herrnkind, 1997).

In this paper we examine the relationship between postlarval supply, settlement habitat dynamics, and early post-settlement processes that are likely to affect the distribution and survival of algal-phase juvenile Caribbean spiny lobster (*Panulirus argus* Latreille) in the Florida Keys (USA). We do this by drawing inference from: 1) field observations of postlarval supply and changes in macroalgal habitat structure that may alter settlement density, 2) mesocosm experiments that test whether algal-phase lobsters are gregarious, which could alter their post-settlement distribution, 3) field experiments testing whether residency in macroalgae is affected by short-term changes in prey availability, 4) tethering studies that test if cryptic algal-phase lobsters experience higher mortality when aggregated, and 5) field experiments that directly test whether microwire-tagged lobsters released into the wild experience density-related differences in growth or survival.

METHODS AND MATERIALS

THE COMPLEX LIFE CYCLE OF THE CARIBBEAN SPINY LOBSTER. The Caribbean spiny lobster supports the most economically important fishery in Florida (Hunt, 1994) and is heavily fished throughout its range from Bermuda to southern Brazil. It has a complex life cycle requiring three distinct habitats: coral reef (adults), open ocean (larvae), and shallow, vegetated coastal zone (juveniles). The early life history and ecology of *P. argus* is reviewed elsewhere (Herrnkind et al., 1994), so we only summarize the ecology of life history stages relevant to this study, namely the postlarval and early benthic juvenile stages.

Following a prolonged oceanic larval period of 9 months or more, the phyllosome larvae metamorphose near the continental shelf break into non-feeding, strongly swimming puerulus postlarvae. Postlarvae enter Florida Bay, the major spiny-lobster nursery in Florida, over a period of a several days every lunar cycle, usually at night during new-moon flood tides. They settle and metamorphose on macroalgae-covered hard-bottom habitat, particularly among clumps of the ubiquitous red macroalga *Laurencia* spp. and, less frequently, in seagrass. In the Florida Keys, juvenile spiny lobsters exhibit

three behaviorally and ecologically distinct phases following settlement: algal-phase, postalgal-phase, and subadult. The algal-phase juveniles (5 - 15 mm carapace length; CL) remain for a few months in vegetation, where they are sheltered from predators and have abundant prey. Upon reaching 15-20 mm CL, they emerge from settlement habitat and, as postalgal juveniles, take up daytime refuge under crevices provided by rocks, sponges, octocorals, or other structures. Approximately 1 yr after settling the juveniles become nomadic within the nursery and after 2 yr, they mature and migrate seaward to the reef tract.

ESTIMATING POSTLARVAL SUPPLY AND MACROALGAL STRUCTURE. We estimated monthly changes in postlarval supply from the number of postlarval spiny lobsters collected from five Witham-type surface collectors deployed approximately 200 m offshore of the southwest end of Long Key, FL, adjacent to Long Key Channel. The collectors were sampled 7 d after each new moon from June 1991 - August 1992. Details of their construction and sampling is described elsewhere (Heatwole et al., 1992; Phillips and Booth, 1994). Tidal currents from Long Key Channel surge into Florida Bay and pass over an area just south of the Arsnicker Keys (Herrnkind and Butler, 1994) where we monitored macroalgal habitat structure (described below). This channel therefore serves as an important "source" of postlarvae for our macroalgal monitoring sites and the Witham collectors we deployed near the channels are likely to yield good estimates of postlarval supply to the region (Herrnkind and Butler, 1994).

Monthly changes in macroalgal habitat structure were monitored at 27 separate hard-bottom sites, each surrounded by seagrass and situated approximately 0.5 km south of the Arsnicker Keys in Florida Bay. The sites were spread roughly east-west over an area > 2 km². The size of the sites ranged from about 200 - 1000 m² and all were 2 - 3 m deep. In June 1991, we established four haphazardly selected, non-overlapping permanent transect locations within each site by driving stakes into the substrate at the ends of each transect. Transects varied in length depending on the configuration of the site. Divers visited each site once a month from June–November 1991, February–March 1992, and June–August 1992, stretched underwater tape measures between each set of stakes, and then measured the length (cm) of all substrate types lying under the tape. When a patch of red macroalgae *Laurencia* spp. was encountered, the divers also measured its height (cm) from the substrate every 0.25 cm along the tape. Data from the four replicate transects were then used to calculate the mean (and 1 SD) percent cover, patch size, and height of macroalgae at each site during each sample month. During some months, our observations were precluded by dense blooms of cyanobacteria (Butler et al., in press), so the data set is temporally discontinuous.

The monthly correspondence between postlarval supply and the three separate measures of macroalgae structure (i.e., percent cover, patch size, patch height), averaged across sites, were examined using the Pearson correlation statistic. In addition to the standard estimate of postlarval supply derived from the Witham collectors, we created two additional indices of potential settlement density by expressing postlarval supply (numerator) in terms of macroalgal percent cover and patch size (separate denominators) for each site. Postlarval supply/percent cover provides a relative estimate of postlarval density per site, whereas postlarval supply/patch size provides an index of crowding. Macroalgal height was not included as an index because it is positively correlated with the percent cover of macroalgae ($r = 0.82$, $P < 0.001$) and, therefore, not independent.

ESTIMATING GREGARIOUSNESS. This experiment was conducted in September, 1988, at the Keys Marine Laboratory on Long Key, FL in nine 2.5 m diameter x 0.3 m tall plastic tanks with sand covered bottoms. We recirculated sea-water through each tank and covered them with shade-cloth. Two 2-liter clumps of *Laurencia* spp., collected fresh from the field, were placed 1 m apart in the center of each tank. Between 16:00 and 18:00 h, two algal-phase lobsters (5.5 - 11.4 mm CL) were released on the open sand in the center of each tank. Forty-eight hours later, the macroalgal clumps were recovered with a fine-mesh handnet and the frequency of lobster cohabitation within macroalgal clumps was recorded.

A chi-square goodness-of-fit test was used to evaluate whether the frequency of cohabitation or solitary habitation by lobsters in macroalgal clumps differed from a random distribution. Greater than expected cohabitation would suggest that algal-phase lobsters are gregarious. Less than expected

cohabitation would suggest that lobsters are anti-social. A random distribution of lobsters would indicate that lobsters in this ontogenetic stage are asocial, neither preferring the company of conspecifics nor avoiding it.

RESIDENCY OF ALGAL-PHASE LOBSTERS IN RESPONSE TO FOOD AVAILABILITY. The presence of prey in macroalgal clumps (Marx and Herrnkind, 1985b) reportedly can affect the small-scale dispersal and residency patterns of algal-phase juvenile *P. argus*. We tested this hypothesis in a field experiment conducted in July, 1986, at a hard-bottom site 1.5 m deep and approximately 50 m offshore (north) of the Keys Marine Laboratory on Long Key, FL. The 14 m x 16 m site was devoid of any prominent physical structures other than sparse sprigs of calcareous green macroalgae, which we removed by hand. We then anchored 42 2-liter clumps of *Laurencia* spp. to the sea floor 2 m apart in a 6 x 7 array using monofilament and lead weights. Prior to placement on the bottom, every other clump in the array was rinsed in sea-water to reduce the number of lobster prey (e.g., amphipods, isopods, copepods, gastropods, echinoderms, etc.) dwelling in the macroalgae. Thus, half the clumps contained natural prey densities (high food treatment) and half contained a reduced number of prey (low food treatment). We did not control for artifacts caused by the rinsing procedure (e.g., rinse the high food treatment macroalgal clumps and then to replace the prey) because it was shown to have no significant impact by Marx and Herrnkind (1985b). Forty-two algal-phase lobsters, obtained from Witham surface collectors, then received unique paint marks on their legs before each was implanted individually by divers into each of the macroalgal clumps in the array. After 24 h, we retrieved each clump in a fine-mesh hand net; the clumps were dismantled in the laboratory and we recorded the number and identification of those lobsters found. Two trials of this experiment were conducted.

EFFECT OF AGGREGATION ON SURVIVAL OF ALGAL-PHASE LOBSTERS. Three separate tethering experiments were conducted to address different questions (listed below as 1 - 3) concerning the effects of aggregation on the probability of lobster mortality by predators.

1. Does the mortality of solitary algal-phase lobsters differ from that measured for lobsters aggregated in pairs? In July, 1986, we obtained algal-phase lobsters from Witham collectors and tethered them alone ($n = 30$) or in pairs ($n = 15$ pairs; 30 lobsters total) in seagrass and macroalgal habitat located approximately 50 – 100 m offshore (north) of the Keys Marine Laboratory on Long Key, FL. Our tethering protocol is described elsewhere (Herrnkind and Butler, 1986; Smith and Herrnkind, 1992). After 24 h, the number of lobsters found alive or missing in each treatment was recorded, and a log-linear categorical analysis was used to determine if lobster condition (i.e., alive vs. missing) was independent of tethering condition (i.e., solitary vs. paired).

2. Does the distance between pairs of lobsters affect the probability that one or both individuals are killed? Pairs of algal-phase lobsters were tethered in July 1986, 1990, 1991, and 1995 in seagrass and macroalgal habitat at the same location near the Keys Marine Laboratory. Pairs of tethered lobsters were separated by either 25, 75, or 200 cm, forming three treatment groups. Again, lobster presence or absence was recorded after 24 h and the data were analyzed using log-linear categorical analyses that tested whether lobster survival was independent of distance between individuals and experimental trial (year).

3. Does the spatial pattern of predation on tethered lobsters differ with respect to the spatial scale over which lobsters are distributed? Algal-phase lobsters were tethered in seagrass in three separate 5 x 5 arrays. Inter-individual distances were 25, 75, and 200 cm. Thus, arrays of 25 lobsters covered 1, 9 and 100 m², respectively. After 24 h, lobster presence or absence was recorded as was their position within the array. We used a Monte-Carlo based simulation model and statistic (C) designed for analysis of spatial patterns on grids (Stapanian et al., 1982) to determine if the occurrence of predation was random, clumped, or uniform when lobsters are aggregated at the three different densities. The density of lobsters in the three arrays corresponded to densities of 25 lobsters m⁻² in the small array, 2.78 lobsters m⁻² in the 9 m² array, and 0.25 lobsters m⁻² in the 100 m² array. The two lower densities are comparable to previously published natural densities of about 0.03 lobsters m⁻² (Marx and Herrnkind, 1985b; Herrnkind and Butler, 1994) and recently recorded settlement densities in the range of 2 – 4 lobsters m⁻² (M. Butler, W. Herrnkind, J. Hunt, R. Bertelsen, unpubl. data), whereas the highest density (= smallest array) is considerably greater than any recorded.

FIELD MANIPULATIONS OF ALGAL-PHASE LOBSTER DENSITY. We directly tested for the possible effects of increased density on algal-phase juvenile lobster population dynamics in two separate field experiments that differed in protocol.

The first experiment ran for 20 d and we manipulated lobster density by altering site size rather than the number of lobsters released. The second experiment continued for over a year and lobster density was manipulated by releasing two different numbers of lobsters into sites with natural boundaries and which varied in size. Thus, the experiments differed both in the way settler density was manipulated and duration of the experiment. The first experiment was designed to reveal short-term density effects occurring during the first three weeks that lobsters resided in macroalgae, whereas the second assessed the effect of density over the entire algal-dwelling period and the early postalgal phase when lobsters were finally collected.

The first experiment was conducted in July, 1990, 1 km north of the northeast tip of Grassy Key, FL and just west of Tom's Harbor Channel and Channel Key. Four separate circular macroalgal-covered sites (1.5 m deep) were established by removing all vegetation and structure (e.g., rocks, sponges) from a 2 m wide belt surrounding the sites; two sites were 100 m² and two were 50 m². Algal-phase lobsters obtained from Witham collectors were then implanted into the sites: 25 lobsters added per site. It was impossible to search all the macroalgae to search for algal-phase lobsters, so after 20 d we removed all of the macroalgae from 30% of the bottom at each of the four sites. That is, we sampled the same proportion of area in each site. Divers sampled by gathering algae in mesh bags at 2 m² areas haphazardly selected on each site. The bags of macroalgae were then meticulously searched at boatside.

The second experiment was conducted from June 1991–August 1992 at 18 of the 27 natural hard-bottom sites (193 - 722 m² area) near the Arsnicker Keys where we were also monitoring changes in macroalgal habitat structure (described earlier in the section, Estimating Postlarval Supply and Macroalgal Structure). Once a month from June–December 1991, we collected algal-phase juvenile lobsters from Witham collectors, marked them with internal microwire tags, and then implanted each tagged lobster directly into clumps of macroalgae on each of the sites. Nine sites received high levels of enhancement ("High Seed" treatment; 182 lobsters added site⁻¹ total) which was four times as many tagged lobsters as implanted in the nine "Low Seed" treatment sites (46 lobsters added site⁻¹ total). Microwire tagging has only minor effects on the survival and growth of juvenile spiny lobsters and has been used in estimating growth of juvenile lobsters in the field (Lellis and Pardee, 1991; Phillips et al., 1992). The number of lobsters implanted on high and low density sites varied among months in accordance with natural fluctuations in postlarval supply to our Witham collectors. Divers searched each site and collected all lobsters found each month from June 1991–August 1992. We searched for lobsters around structures that provide shelter for postalgal-phase juveniles (e.g., sponges, corals, solution holes, and rock crevices); macroalgae was not searched, so we primarily recovered postalgal-stage juveniles. All the lobsters collected were measured, and evaluated for the presence of a microwire tag. Untagged lobsters and tagged lobsters < 25 mm CL were returned to the site. As described earlier (see section on Estimating Postlarval Supply and Macroalgal Structure), we also surveyed the macroalgal habitat on each site each month to follow changes in habitat structure that might be associated with the recapture of tagged lobsters. The results of this experiment were evaluated by comparing the number and sizes of microwire tagged lobsters recovered from high seed and low seed treatment sites (Mann-Whitney Rank sum test), and by examining (best-fit multiple regression) whether the proportion of tagged lobsters that were recaptured could be predicted from variables describing the experimental conditions at each site (e.g., number of tagged lobsters added to site, number of untagged lobsters captured, area of the site, macroalgal percent cover, macroalgal patch size, and height of macroalgae).

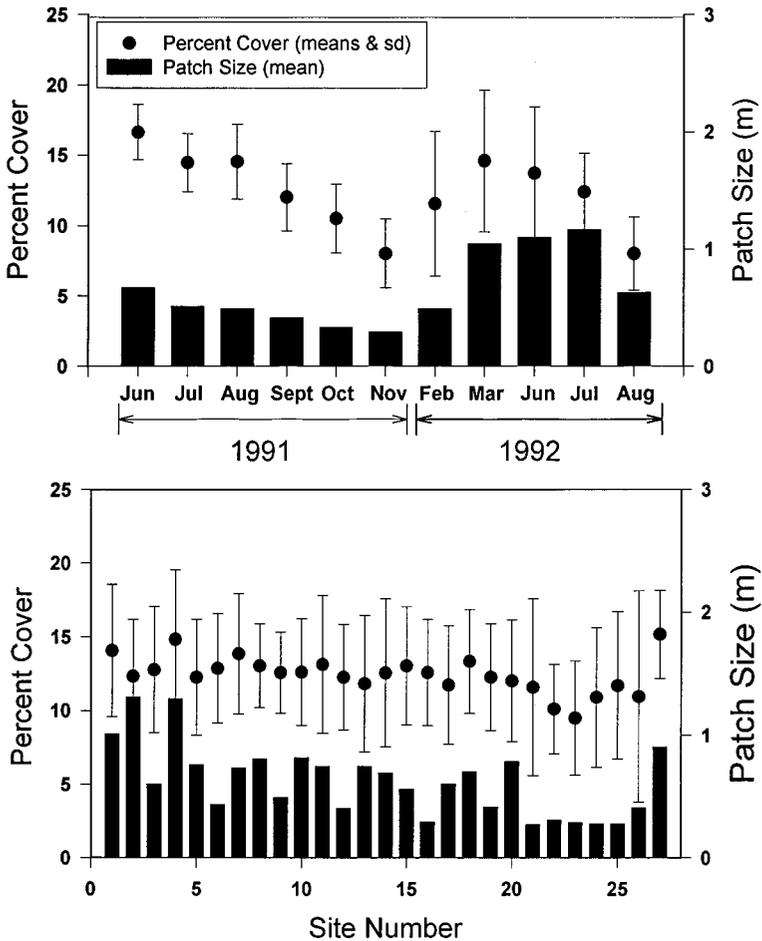


Figure 1. (top panel) A comparison of the temporal variation in percent cover (points and error bars are means \pm 1 SD) and patch size (histogram; means) of red macroalgae (*Laurencia* spp.) among 27 sites near the Arsnicker Keys in Florida Bay, FL (USA) that were monitored monthly from June - November 1991 and in February, March, and June - August 1992. (bottom panel) A comparison of the spatial change in percent cover (points and error bars are means \pm 1 SD) and patch size (histogram; means) of red macroalgae (*Laurencia* spp.) among 27 sites near the Arsnicker Keys in Florida Bay, FL (USA) that were monitored monthly from June - November 1991 and in February, March, and June - August 1992.

RESULTS

ESTIMATING POSTLARVAL SUPPLY AND MACROALGAL STRUCTURE. Macroalgal percent cover and height are highly correlated ($r = 0.82$, $P < 0.001$) and nonindependent, so only the percent cover of macroalgal was considered further in these analyses. The percentage of the bottom covered by red macroalgae and macroalgal patch size did not vary appreciably among nearby sites at the Arsnicker Keys when data were averaged across months (Fig. 1b), but the mean percent cover and patch size of macroalgae on 27 sites varied considerably among sample dates (Fig. 1a). Ours is the first reported time-series of data describing changes in macroalgal habitat structure in Florida Bay.

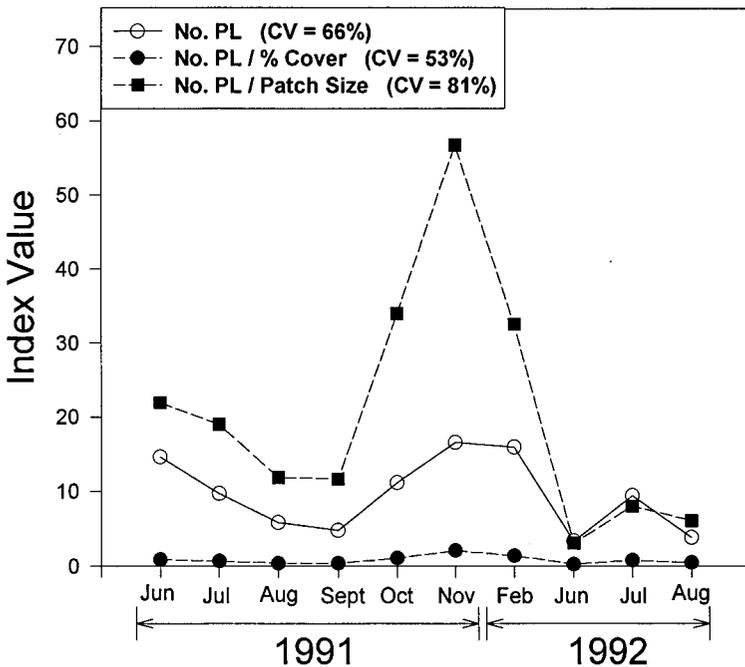


Figure 2. Graph showing the temporal fluctuations in three related indices representing the potential magnitude of postlarval settlement in hard bottom habitat in the south-central Florida Bay near the Arsnicker Keys, FL (USA). The three indices are: 1) mean number of postlarvae/Witham collector (No. PL), 2) mean number of postlarvae/Witham collector/mean percent cover of macroalgae (No. PL / % cover), and 3) mean number of postlarvae/Witham collector/mean macroalgae patch size (No. PL / patch size). The coefficient of variation (CV) for each index calculated among sampling dates is also shown and demonstrates that “No. PL” varies the least among months, whereas “No. PL/patch size” varies the most.

Postlarval supply to the region, determined from collections of postlarvae caught on Witham collectors, also varied substantially among months as indicated by a CV of 66% (Fig. 2), but it varied independently of changes in macroalgal percent cover ($r = 0.10$, $P = 0.76$) and patch size ($r = -0.29$, $P = 0.36$). Thus, the two indices of postlarval supply that reflect local differences in macroalgal habitat structure (i.e., no. postlarvae/percent cover of macroalgae, no. postlarvae/macroalgae patch size), give a different impression of the magnitude of temporal change in postlarval settlement, although the general pattern of high and low settlement periods is retained (Fig. 2). When postlarval supply is expressed as the number of postlarvae/Witham collector/percent cover of macroalgae (No. PL/% cover), the month-to-month variance is reduced (CV = 53%) compared to the variance attained from measuring postlarval supply on Witham collectors (CV = 66%). But when changes in macroalgal patch size are incorporated in an index of postlarval supply (i.e., number of postlarvae/Witham collector/macroalgal patch size; No. PL/patch size) the variance is accentuated (CV = 81%), suggesting that settlement density per clump of macroalgae or “crowding” can vary remarkably among months (Fig. 2).

ESTIMATING GREGARIOUSNESS. The results of the experiment indicate that algal-phase *P. argus* are asocial because the distribution of individuals in the two clumps of macroalgae did not differ significantly from a random distribution ($X^2 = 0.0871$, $P = 0.7679$). Lobsters

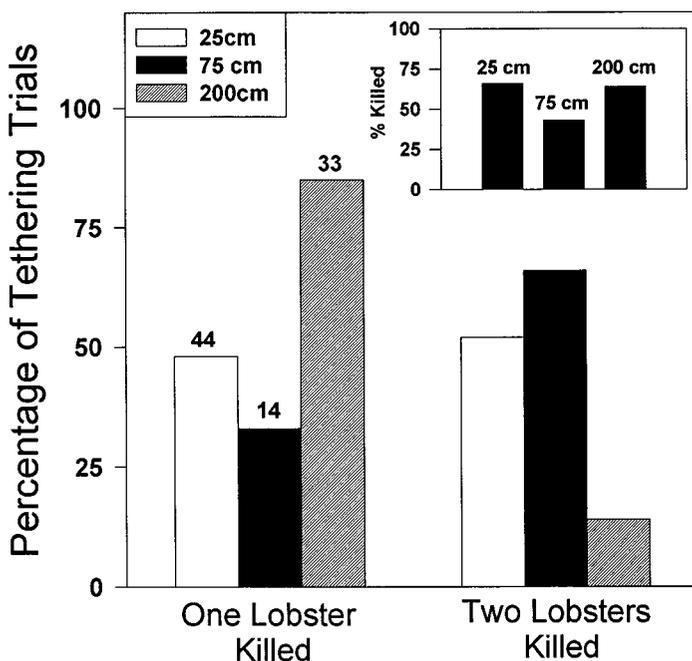


Figure 3. (inset) The total percentage of algal-phase lobsters killed when tethered 25 cm, 75 cm, and 200 cm from one another ($n = 91$). (large graph) The relative frequency (percentage of tethering trials) where at least one lobster was killed when pairs of lobsters are tethered 25, 75, and 200 cm apart. The number of lobster pairs tethered at each distance is given above the first set of histograms. The figure illustrates that the chance that both lobsters in a pair are killed is significantly reduced when individuals are separated by 200 cm.

were found together 11 times and solitarily 12 times. Twenty seven replicates of this experiment were completed, but four were omitted because lobsters either died or could not be located at the end of the trial.

RESIDENCY OF ALGAL-PHASE LOBSTERS WITH RESPECT TO FOOD AVAILABILITY. The presence of algal-phase lobsters (i.e., dispersal) did not differ between experimental trials or between macroalgal clumps that had reduced prey densities versus unmanipulated clumps that had typical prey densities ($X^2 = 1.02$, $df = 1$, $P = 0.31$). Therefore, prey availability within macroalgae did not affect the spatial distribution of lobsters dwelling in macroalgae. However, we suspect that the differences in prey density that we initially established diminished by the end of the experiment due to rapid recolonization by prey of the macroalgal clumps.

EFFECT OF AGGREGATION ON SURVIVAL OF ALGAL-PHASE LOBSTERS. Although *P. argus* postlarvae are thought to prefer settlement in macroalgae (Marx and Herrnkind, 1985a; Herrnkind and Butler, 1986), settlement also occurs in seagrass (M. Butler, W. Herrnkind, and J. Hunt, unpubl. data). Mortality in these two habitats can differ (Herrnkind and Butler, 1986), but in this set of experiments we found no difference in lobster mortality in seagrass versus hard-bottom ($X^2 = 0.21$, $df = 1$, $P = 0.65$), nor was there a significant three-way interaction between the mortality of lobsters tethered at different distances from one another in the two different habitats ($X^2 = 0.02$, $df = 1$, $P = 0.88$). Therefore, we do not consider habitat effects any further and interpret the results as they pertain to the effect of aggregation on lobster mortality.

Table 1. Results of Monte-Carlo simulation analysis testing (C statistic; Stapanian et al., 1982) whether the pattern of predation on algal-phase juvenile *P. argus* tethered in three different sized 5 x 5 arrays is significantly different from a random distribution.

Grid type	K (# predation events)	Calculated C statistics	Upper and lower 95% bounds for C	P	Distribution
1 m ²	5	1.50	1.64-6.94	<0.05	clumped
9 m ²	15	4.48	3.34-5.18	>0.05	random
100 m ²	12	5.01	3.01-5.31	>0.05	random

The first tethering experiment was designed to test whether mortality differed between algal-phase lobsters tethered alone or in pairs. The results of the log-linear analysis were non-significant ($X^2 = 2.37$, $df = 1$, $P = 0.12$), even though 73% of the paired lobsters were killed whereas only 53% of the solitary lobsters were killed.

In the second experiment, we found that the mortality of algal-phase lobsters tethered in pairs differed significantly ($X^2 = 9.48$, $df = 4$, $P = 0.05$) among pairs tethered at three different distances from one another (i.e., 25, 75, and 200 cm apart). The total mortality in the three treatments did not differ (Fig. 3, inset), but those tethered closer together (i.e., 25 and 75 cm) experienced more "double" predation events than those tethered 200 cm apart (Fig. 3). As depicted in Figure 3, this effect is perhaps best evaluated by only examining cases where mortality occurred (i.e., a predator(s) encounters a tethered lobster) and then testing whether the likelihood that the predator will eat one or both lobsters is independent of distance between the lobsters. This result is also significant ($X^2 = 9.31$, $df = 2$, $P = 0.01$). That is, both individuals in pairs separated by 25 or 75 cm are significantly more likely to be killed if one individual is detected by a predator, than are pairs of individuals that are separated by 200 cm (Fig. 3).

In the third tethering experiment, we evaluated whether the spatial pattern of predation on tethered lobsters differed with spatial scale. When lobsters were tethered 25, 75, and 200 cm apart in three separate 5 x 5 arrays measuring 1, 9, and 100 m² (respectively), the Monte Carlo simulation indicated that predation was significantly patchy within the smallest array (1 m²), but random within the larger two arrays (Table 1).

FIELD MANIPULATIONS OF ALGAL-PHASE LOBSTER DENSITY. In the first experiment, less than 10% of the algal-phase lobsters added to the two large (100 m²) and two small (50 m²) macroalgae-covered sites were recovered three weeks later. Four of the 50 lobsters added to the two large sites were recovered and only 2 of the 50 added to the two small sites were recovered. These results are consistent with what might be expected if density-dependent survival were at play - twice as many lobsters were recovered on the larger sites with the lower density of lobsters. However, we can draw no strong conclusions about density-dependence because of the few individuals recaptured. Better inference comes from the second, long-term experiment.

The results of the second experiment are summarized in Table 2. The areas of the sites that were randomly allocated to the two lobster density treatments differed substantially, so the actual enhancement densities of the high enhancement treatment was five times that of the low treatment, rather than the four-fold difference originally intended. The proportion of the microwire-tagged juvenile lobsters recaptured in the sites enhanced with high densities of settlers versus low densities of settlers (2.9:1) was somewhat lower than would be expected if survival and emigration were unrelated to settlement density (5:1). On average,

Table 2. Summary of results from the second field experiment where algal-phase lobster densities were artificially manipulated (two treatments: high density, low density) at 18 hard bottom sites (n = 9 sites/treatment) near the Arsnicker Keys, Florida.

	High density sites	Low density sites
No. lobsters added/site	182	46
Enhancement ratio (weighted by site area)	5.0	1
Recapture ratio	2.9	1
Percentage recaptured	3.2 %	4.3 %
Mean (SD) No. lobsters recaptured/site	5.8 (3.4)	2.0 (2.1)
Mean (SD) size lobsters Recaptured/site	24.0 mm CL (9.3)	25.1 mm CL (10.9)

3.2% of the microwire-tagged lobsters were recovered during the year-long study period at the high density sites compared to a 4.3% recovery of lobsters on the low density sites. The mean size of the microwire tagged lobsters at recapture did not differ between the two treatments (Mann-Whitney Rank Sum $t = 292.0$, $df = 12, 49$, $P = 0.1492$), but this general result obscures more subtle differences that may have occurred through time. Most of the lobsters recovered from the low density treatment were captured late in the experiment (Fig. 4) and their average size was consistently smaller than that for lobsters in the high density treatment.

The best-fit multiple linear regression analysis revealed that nearly 60% of the variance ($r^2 = 0.59$) in the proportion of tagged lobsters that were recaptured could be explained from a linear combination of three of the independent variables we tested: total density (tagged + untagged) of lobsters ($P = 0.0026$), area of the site ($P = 0.0231$), and the mean size of macroalgal patches on the site ($P = 0.0645$). Recapture success was positively related to all three variables in the equation:

$$\% \text{ recapture} = -0.288 + 1.03 (\text{lobster density}) + 0.0003 (\text{site area}) + 0.142 (\text{patch size})$$

DISCUSSION

It is well known that the influx of postlarval *P. argus* in Florida varies considerably from month to month (Little, 1977; Heatwole et al., 1992; Forcucci et al., 1994; Acosta et al. in press). What is not generally appreciated is that the structure of the macroalgal settlement habitat also varies over short time intervals and among nearby locations. We found that postlarval supply and the abundance of macroalgal settlement habitat varied independently at sites in central Florida Bay. One possible consequence of independent and simultaneously fluctuating postlarval supply and settlement habitat availability is more variable settlement, including locally higher settlement densities than predicted from postlarval supply alone. This means that variation in settlement estimated by postlarval supply (i.e., catch of postlarvae on artificial collectors) is further altered by changes in settlement habitat structure, notably the percent cover and patch size of macroalgae in the nursery area. This increases the likelihood of density-dependent regulation of algal-phase juvenile populations during certain periods of time or at sites where postlarval influx is high and macroalgal habitat is sparse.

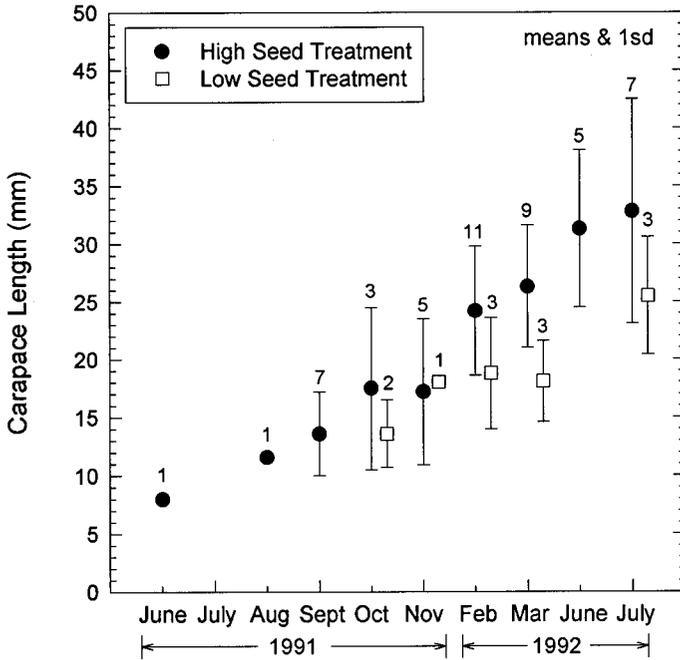


Figure 4. Growth of microwire tagged and recaptured juvenile lobsters represented by the change in mean (± 1 SD) carapace length through time in two experimentally enhanced lobster density treatments: high seed treatment and low seed treatment (nine experimental sites/treatment). The number of recaptures on each date from which the summary statistics were calculated is shown above each point.

We followed these observations with several narrowly-focused experiments designed to test whether mechanisms exist that might alter the chance that algal-phase lobsters will aggregate or survive within the macroalgal settlement habitat. To summarize those results, we found that algal-phase lobsters are asocial, neither aggregating or dispersing in response to conspecifics. Similarly, the local depletion of prey (food) resources within patches of macroalgae did not increase dispersal from those patches as we had expected, perhaps because prey recolonization of our experimentally defaunated clumps of macroalgae was rapid. Thus, neither of these processes is likely to produce local aggregations of algal-phase lobsters. The sparse, over-dispersed or random distribution of the cryptic algal-phase lobsters may be adaptive since predation is patchy at small scales (1 m^2) and individuals clumped at scales $< 2 \text{ m}$ are more likely to be preyed upon than those more widely spaced. Finally, field manipulations of algal-phase juvenile densities suggest that higher density has little or no impact on survival or growth. But the probability of recapturing microwire-tagged juvenile lobsters, a reflection of survival and lack of emigration, was affected by macroalgal habitat, with the highest recapture rates occurring on larger sites with large patches of macroalgae.

IMPLICATIONS OF SOCIAL BEHAVIOR, PREDATION, AND PREY DISTRIBUTION FOR RECRUITMENT. Sociality is a characteristic of many adult Palinurid lobsters including *P. argus* (Herrnkind, 1980), although it has been reported in juveniles of some species as well (Berrill, 1975; Cobb, 1981). Sociality obviously increases aggregation, which is theoretically disadvantageous to cryptic animals – such as algal-phase *P. argus*. Marx and Herrnkind (1985a) speculated that algal-phase *P. argus* juveniles might be asocial or anti-social because they

are sparsely distributed in nature and rarely encountered in groups. Childress and Herrnkind (1994) found no change in the activity pattern of algal-phase lobsters when in the presence of conspecifics, suggesting that *P. argus* are asocial at this ontogenetic phase. Our own experiments lead us to believe similarly, that is, algal-phase *P. argus* appear to be asocial.

Juvenile *P. argus* undergo a dramatic ontogenetic change in color pattern. Algal-phase juveniles are generally brown, but this background color is disrupted by a wide white band running dorsally down the length of the cephalothorax and abdomen, and by alternating brown and white bands around their legs and antennae. They are very well camouflaged when perched in red macroalgae that is infiltrated with white carbonate particles, which is common in tropical benthic environments. The color pattern of algal-phase lobsters fades into the elaborate adult coloration as the animals enter the postalgal-phase and vacate macroalgae for discrete crevices. Thus, this remarkable change in coloration corresponds with a habitat-shift made by juvenile lobsters as they grow larger and less vulnerable to predators (Smith and Herrnkind, 1992).

The crypticity and ecology of algal-phase *P. argus* resembles situations described in classic studies of predation on cryptic prey and the selective advantage of a solitary existence for cryptic animals subject to predation (Tinbergen et al., 1967; Owen, 1980; Kiltie and Levine, 1992). High densities of cryptic prey favor the development of search images by predators and a concomitant increase in predation rates (Dukas and Clark, 1995). Scattered settlement by postlarval lobsters ought to be sufficient to establish a dispersed distribution, but gregariousness in algal-phase lobsters would counteract this by aggregating them. Anti-social behavior may not be necessary under these conditions where individuals are already dispersed by settlement processes (Herrnkind and Butler, 1994). An absence of any gregariousness (asociality) could suffice. Our results parallel those of Childress and Herrnkind (1994, 1996), who demonstrated that the ontogenetic shift in habitat preference, from macroalgae to crevice shelters, in juvenile *P. argus* is accompanied by a change in social behavior. Others have shown that adult and subadult Palinurids use chemical cues to locate conspecifics (*P. interruptus*: Zimmer-Faust et al., 1985; *P. argus*: D. Zimmer-Faust, pers. comm.) and it has been recently determined that this ability develops ontogenetically. Juvenile *Jasus edwardsii* > 40 mm CL use chemical cues to aggregate, whereas smaller individuals do not aggregate or respond to such cues (M. Butler, A. MacDiarmid, and J. Booth, unpubl. manuscript).

Our tethering results provide an answer to the question: how far apart must individuals be before they are effectively solitary? The frequency with which “double kills” occur is significantly greater when lobsters are tethered 25 – 75 cm apart versus when they are tethered 200 cm apart. These results imply that encounters with predators are independent when lobsters are separated by 200 cm, but not by 25 – 75 cm. In simple terms, the chance that an algal-phase lobster will be killed when a predator locates and kills a conspecific is diminished when an individual is > 75 cm from its unfortunate neighbor. We have recorded initial settlement of as many as five postlarvae in single large macroalgal clump (Herrnkind and Butler, 1994); a situation likely to result in higher mortality unless dispersal occurs. While the advantage of prey separation is obvious if visual predators are involved, the same advantage is thought to apply when predators rely on olfaction or auditory cues to locate prey (Treisman, 1975).

Arranging tethered lobsters in sequentially larger arrays permitted a separate test of this hypothesis. Predation was significantly patchy in the smallest (1 m²) array where all five of the lobsters killed (out of 25) were within 25 cm of one another. The distribution of preda-

tion events in the 9 and 100 m² tethering arrays where lobsters were 75 and 200 cm apart, respectively, was not significantly different from random. Although the small-scale patterns of predation on Palinurid lobsters, or any other decapods of which we are aware, has never before been documented, similar patterns and mechanisms of predation are known among a wide variety of aquatic and terrestrial taxa (Tinbergen et al., 1967; Smith and Dawkins, 1971; Kareiva, 1982; Mellgren and Roper, 1986; Butler, 1989; Fairweather, 1988).

The use of tethering to estimate relative rates of predation under different circumstances has recently been criticized by Peterson and Black (1994) because none of the papers they reviewed tested for the possibility that treatment responses might differ in their bias. In our case, the key question is whether tethering artifacts differ when animals are tethered in pairs or alone. The most obvious artifact would be tangling of paired individuals. We never observed this in the field. We can think of no differential bias that could mar our other two tethering experiments, where animals were tethered singly in the same habitat but at different distances from one another. Thus, we are comfortable that the tethering results reported here are not appreciably confounded by tethering artifacts. Of course, it remains to be seen how the results of tethering, meant to measure relative rates of predation, compare to natural predation rates; we are presently testing this in another study (M. Butler and R. Ramsdell, unpubl. data).

We found no evidence that the distribution of algal-phase lobsters is affected by patchily distributed prey within the macroalgal habitat. Algal-phase juveniles did not disperse from clumps of macroalgae with little food or aggregate in clumps with more prey. However, Marx and Herrnkind (1985b) found that lack of food and high conspecific density (10 lobsters/1 liter macroalgae) prompted emigration of algal-phase *P. argus* tested in mesocosms. Also, in laboratory trials, algal-phase *P. argus* choose macroalgal clumps with high concentrations of natural and artificial food over clumps with little food (Herrnkind et al., 1988). Reconciliation of our field results with these from mesocosms and laboratory experiments may lie in prey recolonization rates. In both of the latter studies, low prey density patches could be maintained because there was no exogenous source of prey. This may happen in nature where deleterious environmental conditions, such as heavy siltation, reduce prey populations over a wide area (Herrnkind et al., 1988). But under normal field conditions, colonization of denuded prey patches or new substrates is remarkably rapid (Holmquist, 1994). Our impression at the time of sampling was that potential lobster prey (e.g., amphipods, isopods, etc.) in the "low food" treatment clumps were unexpectedly numerous after sitting on the sea floor for 24 h. Although locally patchy prey resources and risk of predation can have significant impacts on the distribution and foraging behavior of other marine species (Holbrook and Schmitt, 1988), we suspect that these factors are of relatively little importance in determining the small-scale distribution of algal-phase *P. argus* in nature because they are so dispersed and prey recolonization of denuded patches is so rapid.

PRE- AND POST-SETTLEMENT REGULATION OF RECRUITMENT IN CARIBBEAN SPINY LOBSTERS. The first series of experiments we conducted (discussed above) concerning juvenile lobster social behavior, aggregation and mortality, and response to local depletion in prey relied on a reductionist approach. They were designed to test specific questions about whether mechanisms exist that might produce or reduce lobster aggregation and thus their susceptibility to density-dependent influence. But those studies beg the question of whether there exists any evidence for density-dependent post-settlement regulation of juvenile lobster populations. Our manipulations of microwire-tagged algal-phase lobster density in natural hard-bottom nursery areas were designed to directly test this question.

Growth of algal-phase lobsters did not differ between the two lobster density treatments described in the second settlement enhancement experiment. Although the recovery (i.e., survival–emigration) of tagged juveniles in the high density treatment was somewhat lower than expected (i.e., observed recapture ratio in high: low density treatments 2.9:1 versus expected ratio of 5.0:1), the proportion of lobsters recaptured per site was positively associated with lobster density. This was primarily due to a strong correlation with the number of untagged lobsters collected on each site. Also, the results of the best-fit multiple regression analysis indicate that lobster recapture rates were positively correlated with variables reflecting settlement habitat suitability – namely, macroalgal patch size and height, and site area. These results indicate that regulation of algal-phase juvenile survival and emigration is not density-dependent. We suggest that features of the nursery environment that promote the survival of naturally occurring settlers also favored those that we implanted, giving rise to the positive relationship between the recovery of tagged lobsters and density of similar-sized untagged lobsters.

We conclude that for much of the time, density-dependent effects appear unlikely to contribute much to the variance in local juvenile *P. argus* recruitment. Yet, the possibility remains that where settlement density is very high, resulting in aggregations of algal-phase juvenile lobsters, density-dependent predation can occur and will thin algal-phase lobster density and contribute to their sparse distribution. Our results add to the accumulating evidence that recruitment of *P. argus* in Florida is tightly linked to a nursery habitat that is both heterogeneous and ephemeral. This may hamper predictions of adult population size (stocks) from postlarval supply unless the dynamics of the recruitment process can be coupled with information on spatial and temporal changes in nursery habitat structure.

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