POPULATION DYNAMICS OF JUVENILE CARIBBEAN SPINY LOBSTER, *PANULIRUS ARGUS*, IN FLORIDA BAY, FLORIDA

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ABSTRACT

Despite a wealth of information on the growth and population dynamics of sub-adult and adult Caribbean spiny lobsters (*Panulirus argus*), there is far less information about younger juveniles under natural conditions. Here we describe growth and population dynamics of juvenile spiny lobsters (12–68 mm carapace length, CL) that we have studied for 14 months (October 1988–December 1989) using mark-recapture techniques in a hardbottom community in Florida Bay, Florida. We also monitored the supply of postlarvae into the region in 1988 and 1989 using Witham-type surface collectors in an effort to link peak periods of settlement of postlarvae with subsequent cohorts of juveniles. Field estimates of growth were the highest ever reported for this species, averaging 0.95 mm CL·wk^{-1} (range: 0.35–1.25 mm CL·wk^{-1} for individuals 20–25 mm CL and 40–45 mm CL, respectively). These results indicate that lobsters in some areas in Florida Bay can reach Florida's legal harvestable size (76 mm CL) 1.5 years after settlement. Season and lobster size had significant effects on growth rates; slower growth occurred during the winter and among small individuals. Differences in growth among size classes resulted from changes in molt increment, whereas seasonal differences were a result of changes in intermolt interval. Using mark-recapture techniques, we estimate that the density of juvenile spiny lobsters <45 mm CL in this prime nursery habitat was 454·ha^{-1}, that the mean monthly probability of survival (reflecting actual mortality plus emigration) was 0.51, and that an average of 131 lobsters entered the population through recruitment and immigration each month. Recruitment of juveniles was significantly correlated ($r = 0.83$) with the supply of postlarvae to the region 8 months earlier. This relationship is stronger than was previously believed, and may only be manifested in areas with superior nursery habitat.

The Caribbean spiny lobster (*Panulirus argus*) is heavily fished from Bermuda to Brazil and is of great economic importance to many countries throughout its range. It is, for example, the most economically valuable fishery in Florida (Hunt, 1994). For this reason, the population dynamics of adult *P. argus* have been studied in a number of Caribbean regions (Peacock, 1974; Olsen et al., 1975; Lyons et al., 1981; Davis and Dodrill, 1989; Lozano-Alvarez et al., 1990; and others); however, many aspects of the early life history of *P. argus* and many other species of spiny lobster are not well known (Kanciruk, 1980; Herrnkind et al., 1994). Yet, information on early life stages is crucial if we are to understand recruitment and population regulation of spiny lobsters, or if we hope to properly manage these fisheries and the nearshore nursery areas that sustain them.

Currently, we know that *P. argus* postlarvae (5–7 mm carapace length; CL) settle into the nearshore habitats of the Florida Keys throughout the year, at night, around the time of new moon (Little, 1977; Marx, 1986). Settlement of postlarvae is greatest in architecturally complex substrates, especially hardbottom habitat covered by red macroalgae *Laurencia* spp. (Marx and Herrnkind, 1985; Butler and Herrnkind, 1992a). Shortly after settling, postlarvae metamorphose into juveniles and remain within the benthic algae for several months (Herrnkind and Butler, 1986; Butler and Herrnkind, 1991). Once juveniles reach 15–20 mm CL, they emerge from the algae (hereafter called their "post-algal stage") and take up refuge in crevices under sponges, octocorals, and other

structures (Andree, 1981; Herrnkind et al., 1994). Juveniles become nomadic at about 45 mm CL and wander within nursery areas; eventually, they migrate offshore to reefs where they dwell as adults (Kanciruk, 1980; Lyons et al., 1981; Herrnkind et al., 1994).

Several factors make it difficult to distinguish cohorts in population data or to obtain fishery-independent estimates of various population parameters within the heavily fished waters of the Florida Keys. These factors include: year-round settlement, the great mobility of large juvenile (>45 mm CL) and adult lobsters, lack of isolated populations, and variable growth induced by fishery techniques (e.g., use of sub-legal size lobsters in traps as attractants; Lyons et al., 1981; Gregory and Labisky, 1986; Hunt and Lyons, 1986; Davis and Dodrill, 1989). Here we describe a mark-recapture study of the growth and population dynamics of a semi-isolated population of post-algal stage juvenile *P. argus* in relation to the regional supply of postlarvae. We provide new information on growth rates in the field and various population parameter estimates for post-algal stage juvenile *P. argus,* and we link peaks in the supply of postlarvae to subsequent juvenile cohorts.

METHODS

Site Description.—Our mark-recapture study site was located within Florida Bay in a hardbottom community (<2 m depth) on the north-west side of Fiesta Key (24°50.50'N, 80°47.80'W). The 0.5-ha site was surrounded by a thick *Thalassia testudinum* seagrass meadow and an emergent carbonate mud bank. Because postlarval *P. argus* settle preferentially in hardbottom habitat and the movement of small juveniles is thought to be minimal (Herrnkind and Butler, 1986; Yoshimura and Yamakawa, 1988), the configuration of this site yielded a well-defined hardbottom area that we could completely sample in one day and in which we could be assured to find a relatively distinct population of juvenile lobsters for study. We considered this hardbottom site near Fiesta Key to be prime *P. argus* nursery habitat because of the prolific macroalgae available for settling postlarvae and the abundant shelter (large sponges and octocoral complexes) for post-algal stage juveniles. The site is also adjacent to a large channel between Long Key and Lower Matecumbe Key and is readily accessible to postlarvae arriving from offshore.

Nearshore hardbottom habitats are characterized as areas of exposed carbonate bedrock overlain by a thin veneer of sediment and populated by patchily distributed sponges, octocorals, and benthic macroalgae. Over 20 species of sponges have been recorded at the Fiesta Key site, including several large sponges that serve as shelter for spiny lobsters (Sullivan et al., 1992). Vase sponges (*Ircinia campana*), stinker sponges (*Ircinia felix*), green sponges (*Haliclona viridis*), and massive loggerhead sponges (*Speciospongia vesparium*) are all common at the Fiesta Key site. Loggerhead sponges, which are an important shelter for juvenile spiny lobsters in south Florida, are also the most abundant large sponge at this site (7.7 individuals·20 m^{-2} in 1989; Sullivan et al., 1992). The hard corals at this site are primarily small species (e.g., *Siderastrea radians*), but octocorals, some of which serve as shelter for lobsters, are abundant (30 individuals·20 m^{-2} in 1989) and include *Pseudopterogorgia americana, Pterogorgia quadalupensis,* and *Pterogorgia anceps* (Sullivan et al., 1992). There is also a dense, diverse assemblage of green algae (*Penicillus* spp., *Halimeda* spp., *Caulerpa* spp.), brown algae (*Dictyota cervicornis*), and red algae (*Laurencia intricata*) at the Fiesta Key site that at times covers more than 90% of the bottom (Sullivan et al., 1992).

Field Study Methods and Analyses.—We collected lobsters biweekly in October 1988 and November 1988, then monthly from December 1988 through November 1989. Lobsters were caught by SCUBA divers (using hand nets), who methodically searched potential shelters of juveniles (i.e., sponges, octocoral complexes, hard corals, solution holes) within pre-defined sections of the site. The entire hardbottom area was searched during each census, which required 4–6 diver h per census. Carapace length (recorded to the nearest 0.1 mm), sex, type and number of injuries, and tag number (for recaptured individuals) were recorded for every lobster caught. The distal portion of one pleopod was also removed from each lobster for microscopic analysis to determine molt stage (Lyle and MacDonald, 1983). Lobsters >20 mm CL were tagged with sphyrion anchor tags inserted in the dorsolateral extensor muscle between the cephalothorax and abdomen. After the first few sampling periods, the sphyrion anchor was modified (by removing one end of the wire hook anchor) to reduce injury to small lobsters. Molting lobsters were not tagged. Divers released tagged lobsters individually next to

sponges, octocorals, or other shelters. On three occasions (June, July, August 1989) we censused the lobster population 1 day after our regular census to evaluate the replicability of our capture success.

We calculated growth rates of juveniles by dividing the increase in carapace length of recaptured individuals by the number of days between recaptures (Munro, 1983; Hunt and Lyons, 1986; Davis and Dodrill, 1989); 1-day recapture intervals were not used for these estimates. Daily growth rates were then converted to weekly rates. Using criteria established by Hunt and Lyons (1986), only changes in carapace length exceeding 1 mm were considered to be growth. Summer was defined as occurring between May and October, and the remaining months were considered winter, again following procedures established by Hunt and Lyons (1986).

Munro's (1983) method for determining intermolt interval was not appropriate for these data because our sampling interval (2–6 weeks) approximated one intermolt period, which violates a critical assumption of that technique. Instead, we plotted each observation of change in carapace length against time at large for each size class (Fig. 1). These plots enabled us to estimate those observations representing a single molt. When plotted this way, the data points clustered into groups that we interpreted as representing single and multiple molting events. Only single-molt observations were used to estimate molt increments for each size class. We then calculated intermolt interval (in weeks) by dividing, for each size class, the mean molt increment (mm CL) by the mean growth rate (mm CL/wk). We also used information obtained from microscopic analysis of pleopodal setae to independently estimate intermolt interval. If a lobster was within molt stages D–AB (i.e., premolt through recent postmolt) at one capture date and was discovered to be within the same molt-stage grouping on the subsequent capture date, we then estimated intermolt interval based on time at large and the change in size of the lobster (i.e., whether it might have molted one or more times); only single molt episodes were used for this determination.

We also estimated the monthly supply of postlarvae to the region from January 1988 to November 1989 using an array of three modified Witham surface collectors (Witham et al., 1964; Heatwole et al., 1992) located <1 km seaward of Big Pine Key, Florida. Collectors were sampled weekly and the number of postlarvae and juveniles found on each collector were recorded.

A four-factor model 1 ANOVA was used to examine the independent and interactive effects of sex, season, injury, and size on growth of juvenile lobsters. Data were $\ln(X + 1)$ transformed prior to the analysis to meet assumptions of normality and homogeneity of variances among groups. Jolly-Seber estimates of population size, population addition, and probability of survival were determined using a model suggested by Jolly (1965) and a computer program adapted from that model (model A; J. E. Hines, U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland). We used Pearson's correlation coefficient to investigate the potential relationship between the supply of postlarvae, lagged by several different monthly increments (i.e., 6–9 mos.), and recruitment of juvenile lobsters to the 30–35 mm CL size class. We chose this juvenile size class because at this stage juvenile lobsters are easily detected and, therefore, most accurately censused. Movement of palinurid lobsters also increases with size (Kanciruk, 1980; Gregory and Labisky, 1986; Yoshimura and Yamakawa, 1988), so individuals of this size are more likely to have remained in our study than large individuals.

RESULTS

Population Dynamics.—We measured 1,441 lobsters (including recaptures) ranging in size from 11.5 mm to 74.4 mm CL (mean ± 1 SE = 35.5 ± 0.3 mm; modal CL = 34.1); 444 of the 749 lobsters tagged were recaptured and 75% of the lobsters captured were less than 40.1 mm CL. The size-frequency distribution of lobsters at the Fiesta Key site indicates that this habitat is used almost exclusively by juvenile lobsters (Fig. 2). For example, lobsters >50 mm CL represented <10% of the total population, suggesting that lobsters emigrate once they reach this size. Only two lobsters were recaptured and reported outside the study site (each by fishermen), and both exceeded 55 mm CL upon recapture.

Between October 1988 and August 1989, Jolly-Seber population estimates indicated a mean abundance of 227 individuals on the site (Table 1), yielding an average lobster density of approximately 454 individuals·ha^{-1}. On average, 131 new individuals recruited to the population during monthly sampling intervals, which represents both settlement and immigration (Table 1). Given the isolation of the site, the periodic peaks in the abundance of small juveniles (<30 mm CL) that appeared at the site (Fig. 2), and the limited mobility of juveniles, we suspect that settlement within the site accounts for most of these new recruits. Jolly-Seber
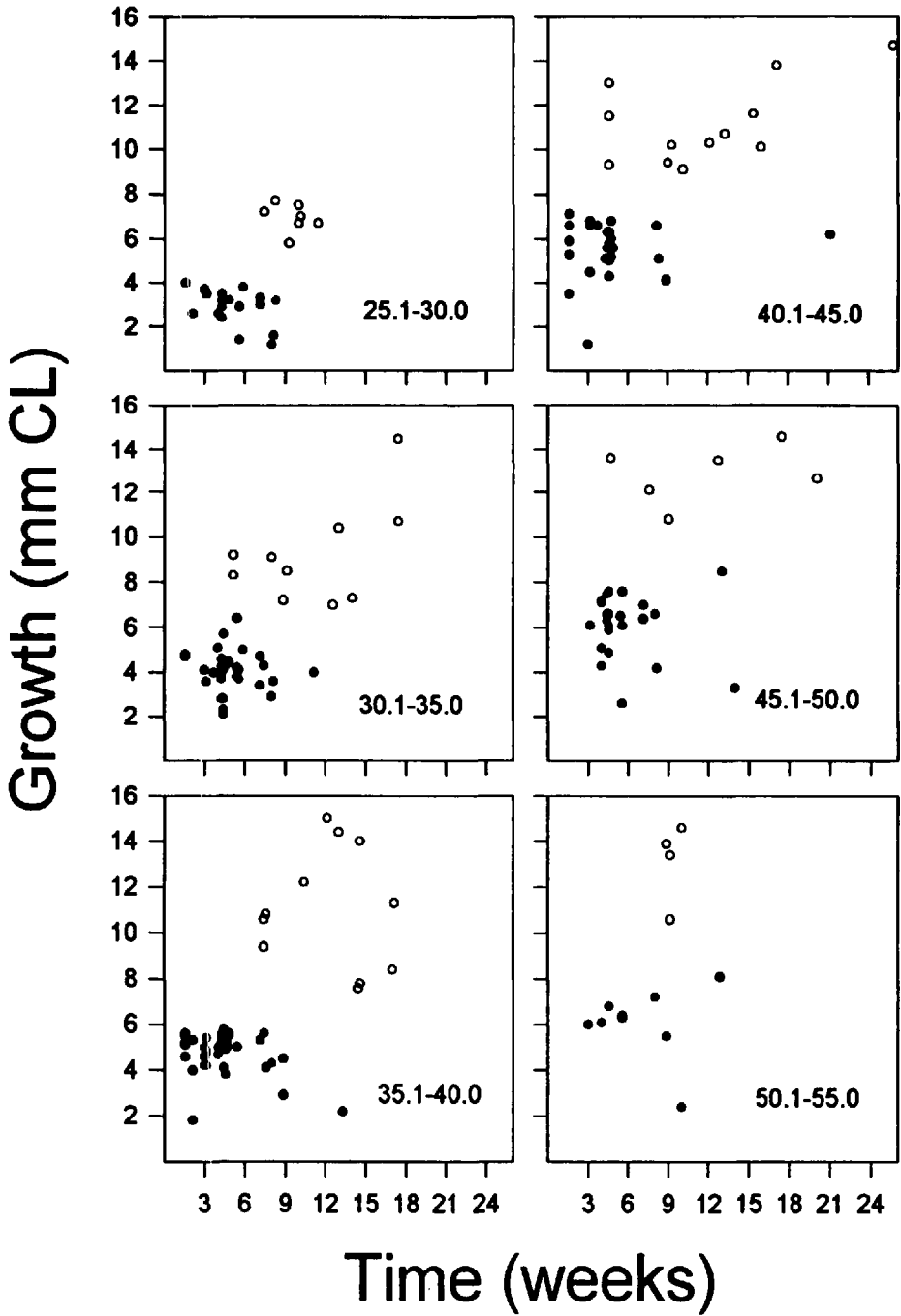
Figure 1.   Growth of juvenile spiny lobsters, by 5-mm CL size classes (size class identified within each panel), near Fiesta Key, Florida from October 1988–November 1989. Solid circles indicate values identified as single-molt observations.
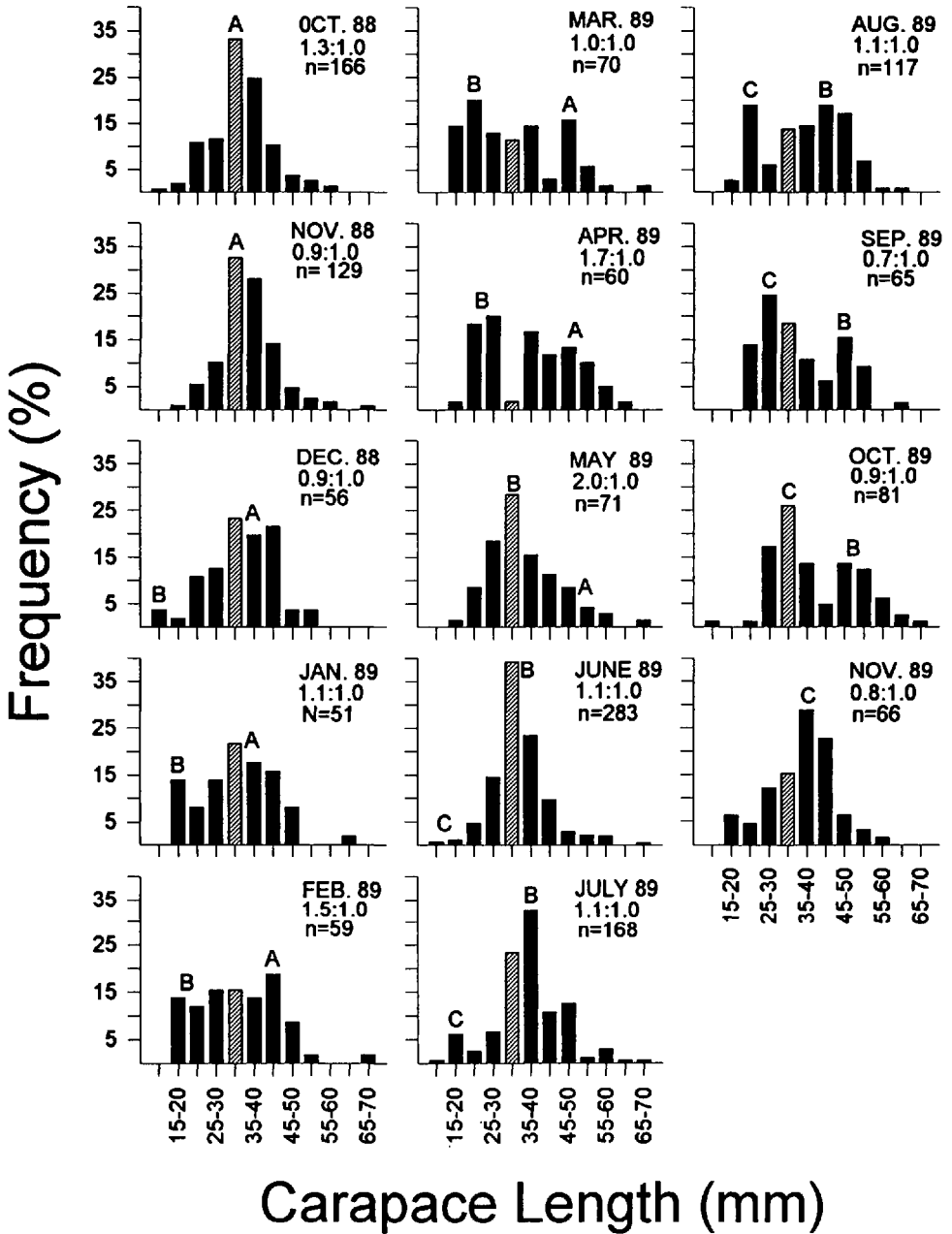
Figure 2. Monthly size-frequency distributions of juvenile spiny lobsters near Fiesta Key, Florida. Sex ratios (female: male) and sample size (N) are given below the month within each panel. The letters above the histograms represent the March 1988 (A), October 1988 (B), and February 1989 (C) cohorts based on records of the influx of postlarvae into the region. Hatched bars indicate the 30–35 mm CL size class in each panel.

Table 1. Mark-recapture statistics and Jolly-Seber population estimates for the juvenile spiny lobster population in a 0.5-ha site near Fiesta Key, Florida from October 1988–November 1989. Population estimates include: population size (N), population addition (B; the number of individuals recruiting or immigrating into the population during the sampling interval), and the probability of survival (PHI; the number of individuals surviving or emigrating into the population during the sampling interval). Values that cannot be calculated using the Jolly-Seber method are represented by a "—." Data from sampling dates that were not incorporated into the Jolly-Seber model are indicated by a "*."

					Jolly-Seber estimates (± 1 SE)		
Date	Total caught	Diver h	Percent-age re-captured	Tagged released (No.)	Popl. size (N)	Popl. addition (B)	Prob. survival (PHI)
10/07/88	88	6	—	86	—	—	0.19 (0.10)
10/18/88*	78	5	26	74	114 (23)	90 (35)	0.62 (0.16)
11/02/88	56	5	32	56	92 (44)	110 (56)	0.22 (0.09)
11/17/88*	73	4	25	73	254 (96)	106 (53)	0.26 (0.09)
12/15/88	56	5	16	54	130 (58)	36 (30)	0.48 (0.11)
01/06/89	51	4	37	51	97 (23)	107 (41)	0.71 (0.17)
02/03/89	59	5	27	54	176 (49)	86 (43)	0.64 (0.17)
03/03/89	70	4	27	67	195 (53)	176 (90)	0.78 (0.25)
04/06/89	60	4	25	60	324 (117)	142 (78)	0.44 (0.14)
05/12/89	71	4	18	71	286 (90)	407 (173)	0.92 (0.28)
06/02/89	153	6	15	147	670 (218)	14 (33)	0.18 (0.05)
06/03/89*	130	6	67	124	—	—	—
07/03/89	87	6	40	76	133 (28)	102 (41)	0.53 (0.17)
07/04/89	81	6	70	57	—	—	—
08/04/89	65	5	34	59	167 (56)	—	—
08/05/89*	52	6	69	47	—	—	—
09/12/89	65	5	35	23	—	—	—
10/16/89*	80	4	16	13	—	—	—
11/16/89*	66	4	2	1	—	—	—
Means	76	5	32	63	227 (74)	131 (65)	0.51 (0.15)

estimates of the probability of survival (reflecting actual survival and emigration) ranged from 0.18–0.94 and averaged 0.51 between sampling intervals of about 1 month (Table 1).

A significant correlation ($r = 0.83$; $P < 0.001$) between the abundance of juveniles in the 30–35 mm size class and prior influx of postlarvae only occurred when we lagged the influx by 8 months. Three prominent peaks in the number of juveniles (within the 30–35 mm size class) at our site further illustrate the relationship between settlement of postlarvae and the abundance of post-algal stage juveniles (Fig. 2). In June 1989, the 30–35 mm CL size class was at its maximum 8 months after the October 1988 peak in the influx of postlarvae (Figs. 2, 3). The peak for the 30–35 mm CL size class in October 1989 occurred 8 months after the influx of postlarvae that occurred in February 1989. Similarly, a peak in the influx of postlarvae in March 1988 corresponded with a large number of individuals in the 30–35 mm CL size class 8 months later in November 1988. These data indicate, for the first time, the relationship between the timing of the influx of *P. argus* postlarvae as measured on Witham collectors and recruitment to the juvenile lobster population.

Growth.—The mean (± 1 SE) growth for lobsters (N = 273 recapture observations; 203 individual lobsters) was 0.95 mm CL·wk^{-1}(±0.05 mm CL/wk), but growth was strongly dependent on initial size and season. Growth rates increased as size increased from 20 mm CL to 35 mm CL, leveling off at over 1 mm CL·wk^{-1} (Fig. 4). Results from an ANOVA testing the effects of sex, season, injury, and size on growth indicated a significant effect of season and size, but
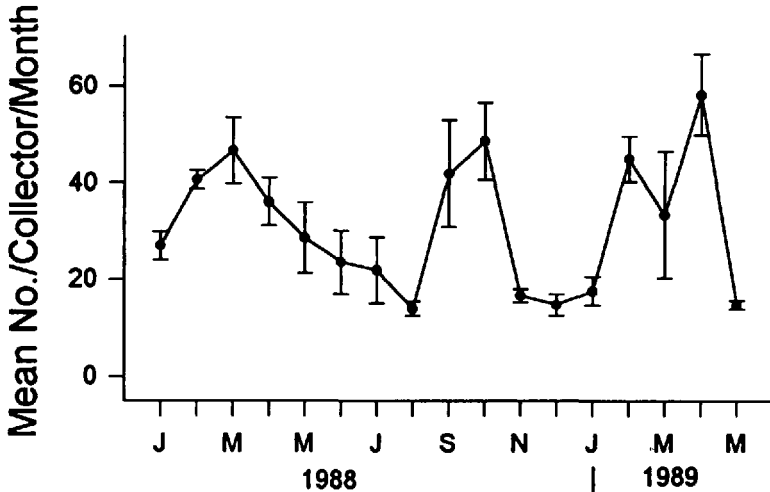
Figure 3. Monthly influx (means ± 1 SE) of spiny lobster postlarvae near Big Pine Key, Florida in 1988 and 1989 as measured by settlement on three Witham collectors, except for the March and April 1989 data, which are from two collectors.

no significant interactions (Table 2). Tukey's *a posteriori* multiple comparison test indicated a significant difference in growth between the 20–25 mm and 50–55 mm CL size classes; all other comparisons were non-significant. These estimates indicate that lobsters settling at this site can reach Florida's legal harvestable size as soon as 1.5 years after settlement.

Molt increment increased as initial size increased until the mean increment reached a maximum of about 6 mm, and intermolt interval fluctuated between 4 and 6 weeks, with a mean of 4.75 weeks (Fig. 5). Examination of pleopods for molt stage allowed intermolt interval to be determined for 23 post-algal stage lobsters; these values ranged from 4 to 5 weeks. Furthermore, examination of pleopods indicated no seasonal difference in the proportion of lobsters in the intermolt stage (stage C; 70% in winter and 67% in summer). Comparisons of seasonal growth indicated that lower growth rates in winter were a result of a longer intermolt interval rather than a smaller molt increment (Table 3).

DISCUSSION

This is the first field study to focus on population dynamics of post-algal stage juvenile *P. argus* within prime nursery habitat. Prior field studies have relied primarily upon tag returns, mostly from fishermen, of larger sub-adult or adult lobsters recaptured over broad areas (Lyons et al., 1981; Waugh, 1981; Hunt and Lyons, 1986; Lozano-Alvarez et al., 1990). The growth rates reported here are 25% greater than the highest previously reported for juvenile *P. argus* in Florida or the Caribbean (e.g., 0.76 mm CL·wk⁻¹; Davis and Dodrill, 1989). Davis and Dodrill (1989) concluded that the rapid growth they observed in Florida Bay was a consequence of the abundant food and shelter in the region. We believe that our growth rates are higher than those previously reported because prior studies (1) sampled large areas encompassing many different habitats of varying nursery quality, and (2) sampled primarily large juvenile and sub-adult lobsters much larger than those we studied.

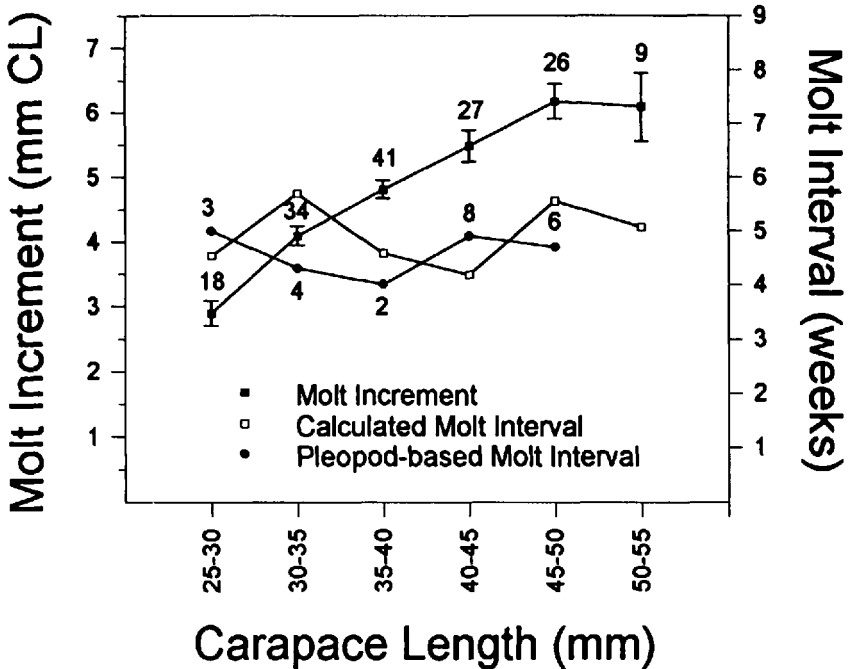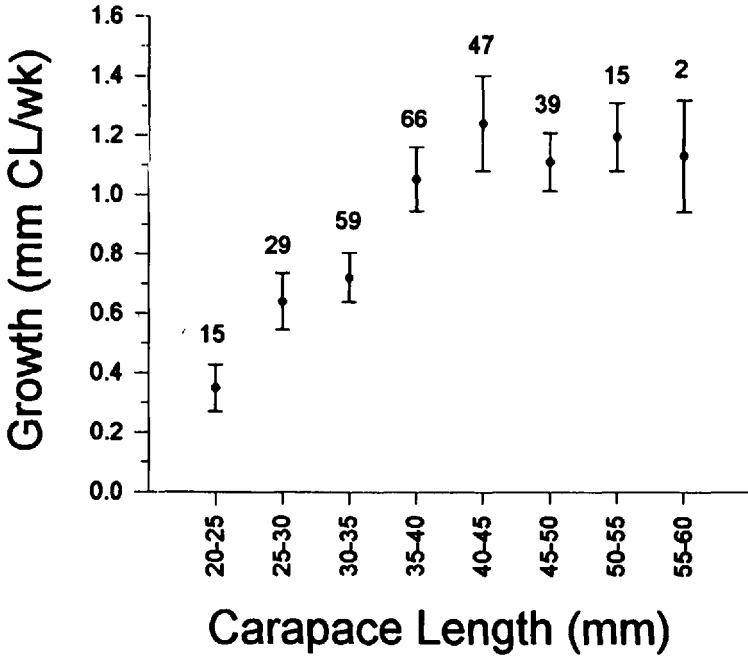Even higher growth has been reported for algal-dwelling and early post-algal

Figure 4 (upper). Mean (± 1 SE) weekly growth of recaptured juvenile spiny lobsters near Fiesta Key, Florida. Sample sizes are listed above the value for each size class.

Figure 5 (lower). Molt increment (mean ± 1 SE), calculated molt interval, and molt interval determined from examination of pleopods from juvenile spiny lobsters at Fiesta Key, Florida. Sample sizes for the molt increment and calculated molt interval are based on the number of lobsters recaptured in that size class, whereas those for pleopod determined molt interval are based on pleopodal sampling.

Table 2. Results of a four factor model I ANOVA testing the effects of sex, season, injury and size on growth of juvenile spiny lobsters near Fiesta Key, Florida. All data were $\ln(x + 1)$ transformed.

Effect	df	SS	F	P
Sex	1	0.42	3.08	0.08
Season	1	0.76	5.56	0.02
Sex × Season	1	0.18	1.35	0.25
Injury	1	0.36	2.62	0.11
Sex × Injury	1	0.10	0.75	0.39
Season × Injury	1	0.00	0.00	0.95
Sex × Season × Injury	1	0.04	0.30	0.58
Size	7	4.41	4.61	<0.001
Sex × Size	7	1.38	1.45	0.19
Season × Size	6	1.41	1.72	0.12
Sex × Season × Size	6	0.32	0.39	0.88
Injury × Size	6	0.29	0.36	0.91
Sex × Injury × Size	6	0.24	0.29	0.94
Season × Injury × Size	5	0.10	0.15	0.98
Sex × Season × Injury × Size	3	0.13	0.31	0.82
Error	218	29.79		
Total	271	39.94		

stage juvenile *P. argus* raised in the laboratory. For example, Witham et al. (1968) measured growth rates of 0.9–1.0 mm CL·wk^{-1} for lobsters held in the laboratory from the postlarval stage to 35 mm CL. These growth rates are approximately 50% greater than those we observed for lobsters <35 mm CL using our recapture data. However, the mark-recapture-based growth rates we report probably underestimate true growth because our tagging method injures lobsters. Major injuries (e.g., loss of antennae or legs) have been shown to reduce growth (Davis, 1981; Waugh, 1981; Hunt and Lyons, 1986). We are puzzled that injury did not produce a statistically significant negative effect on growth in this study (Table 2), as has been previously reported for larger juveniles (Davis, 1981; Waugh, 1981; Hunt and Lyons, 1986). Sex also had no effect on growth rates, which is in keeping with previous studies that have shown that sex-specific growth does not diverge until lobsters reach maturity, when female growth slows (Hunt and Lyons, 1986 and references therein).

Growth in crustaceans depends upon both intermolt interval and increment, which may differ with respect to their relative contributions to growth in response to environmental conditions. Waugh (1981) used various methods to determine intermolt interval for a small number of lobsters <50 mm CL on the north shore of Grand Bahama Island and reported values ranging 10.4–15.3 weeks. Hunt and Lyons (1986) reported similar intermolt intervals (i.e., 9–12 weeks) for trap-caught lobsters <55 mm CL, but most of those lobsters were >40 mm CL. Our

Table 3. Effect of season on the growth rate, intermolt period, and molt increment of two size classes of juvenile *Panulirus argus* at the Fiesta Key site in Florida Bay, Florida

Size (mm)	Season	Growth rate (mm CL·week^{-1})			Intermolt period (weeks)	Molt increment (mm CL)		
		N	Mean	SE		N	Mean	SE
≤35	Summer	76	0.71	0.07	5.1	45	3.65	0.16
	Winter	27	0.46	0.07	6.8	17	3.11	0.23
>35	Summer	132	1.19	0.08	5.0	78	5.97	0.38
	Winter	38	0.92	0.10	6.0	28	5.56	0.27

estimates of intermolt intervals are 30–50% shorter than those reported in these studies and are almost certainly attributable to the greater proportion of small juveniles in our study population and, secondarily, to the absence of fishery effects (e.g., effect of trap confinement on growth). Intermolt intervals for juvenile *P. argus* stretch in a continuum from 2–4 weeks for algal-dwelling juveniles (<20 mm CL; Lellis and Russell, 1990), to 4–6 weeks for post-algal stage juveniles (25–50 mm CL; this study), to 9–15 weeks for sub-adults (50–75 mm CL; Waugh, 1981; Hunt and Lyons, 1986). A similar continuum exists in juvenile *P. argus* molt increment, with average molt increments beginning at about 1.5 mm $CL \cdot molt^{-1}$ for algal-dwelling juveniles (Lellis and Russell, 1990), increasing to 2.5 mm $CL \cdot molt^{-1}$ for early post-algal stage juveniles (20–25 mm CL), and leveling off at about 6 mm $CL \cdot molt^{-1}$ for sub-adult lobsters.

The effect of season on growth that we observed agreed with field results reported for juvenile *P. argus* in Florida by Davis and Dodrill (1989) and Hunt and Lyons (1986): winter water temperatures reduce growth through increased intermolt periods, not through decreased molt increments. Lellis and Russell (1990) obtained highest growth of algal-dwelling *P. argus* (approximately 0.45 mm $CL \cdot wk^{-1}$) at 30°C, slower growth occurred at both higher and lower temperatures. In that study, temperature affected growth by decreasing both intermolt interval and molt increment. Waugh (1981) also observed both decreased molt increments and increased molt intervals for juvenile *P. argus* during the winter in the Bahamas. We cannot reconcile these conflicting results, but we suspect that the relative contribution of intermolt interval and intermolt increment to reduced winter growth depends on initial size, food quality, and food availability.

The density of juvenile lobsters that we report (454 lobsters$\cdot ha^{-1}$) is moderately high in comparison to that found in the few data sets available for juvenile lobsters. Population densities of juvenile spiny lobsters studied on the north shore of Grand Bahama Island ranged 546–596 individuals/hectare (Waugh, 1981). In that study, large juvenile (>45 mm CL) and sub-adult lobsters accounted for the major portion of the population. Typically, the lobster population at our Fiesta Key site was numerically dominated by the 30–35 mm CL size class. We attribute this to two factors. Lobsters of this size (30–35 mm CL) are more easily seen (and thus collected) than smaller individuals, but they are not yet nomadic at this size and so are less likely to emigrate to other areas than are larger individuals. We acknowledge, however, that our population estimates are probably biased due to tag effects on juvenile mortality. Effects of tag retention and tag-induced mortality are important factors in estimating mark-recapture population dynamics, but they are rarely known or are under-reported in studies of spiny lobsters. Under laboratory conditions, the recovery of sphyrion-tagged lobsters after 40 days is 71% (i.e., initial number tagged minus mortality and tag loss), with mortality after 14 days contributing to much of this loss (26% of the tagged lobsters; Lellis, 1991). If similar effects are manifested in the field, then we have underestimated true population size because tag loss (which contributes to overestimation) is minimal in comparison to initial tag-induced mortality (which contributes to underestimation). Tag-related mortality will also bias our estimates of population addition (settlement plus immigration) and survival (survival plus emigration). Using the Jolly-Seber model, we estimate that the probability that a juvenile lobster will survive or not emigrate in one sampling interval (about 1 month) is about 0.51, but the laboratory estimate of tag-induced mortality (Lellis, 1991) is 0.26 for a similar time period. Thus, a reasonable estimate of natural survival (plus emigration) at our field site would be around 0.80$\cdot month^{-1}$ for postalgal stage juvenile lobsters, which is similar to the survival of 0.90$\cdot month^{-1}$ (based on an estimate

of $0.85 \cdot day^{-1}$) for similar-sized lobsters observed in a tethering study in Florida Bay (Smith and Herrnkind, 1992). In contrast, Herrnkind and Butler (in press) report that only 4% of the first benthic stage (algal-dwelling) juvenile lobsters that were tagged with coded microwire tags and released within hardbottom habitat in Florida Bay survived to the post-algal stage.

Perhaps one of the most intriguing results of this study was the finding that the influx of postlarvae was correlated with recruitment of post-algal stage juveniles to the 30–35 mm CL size class 8 months later. This time lag between settlement and recruitment to the 30–35 mm size class is also consistent with growth trajectories based on intermolt interval and molt increment for algal- and post-algal phase juveniles. Although our collectors off Big Pine Key were 65 km from our Fiesta Key study site they were the only ones that were continuously monitored in the Florida Keys during the study period and we believed that they might reveal monthly fluctuations and peaks in the influx of postlarvae relevant to the entire region. Variously modified Witham collectors have been used throughout the Caribbean to estimate relative rates of postlarval influx, and in Florida postlarval catch in these collectors is strongly correlated with postlarval planktonic abundance and settlement on a regional scale (Butler and Herrnkind, 1992b; Herrnkind and Butler, in press). Furthermore, data from collectors (of a different design) at a single site in Western Australia have been used successfully to predict recruitment of *P. cygnus* to the fishery, which spans over 800 km of shoreline (Phillips, 1986).

However, several factors could conspire to weaken regional predictions of juvenile abundance (i.e., recruitment) in the Florida Keys based on the magnitude of postlarval settlement. Growth is strongly dependent upon temperature, and the low winter temperatures in Florida (typically 15–20°C) will slow the growth of juveniles that settle in the fall or winter, and will extend their ascension to the post-algal juvenile stage beyond 8 months. Deviations in temperature alone are unlikely to destroy the temporal relationship between settlement and juvenile recruitment altogether, but they will contribute additional variance to it. For example, in three separate studies at different sites in Florida Bay we have observed a particularly large cohort of small (20–25 mm CL) post-algal juveniles appearing under hardbottom shelters in May and June (this study; Butler and Herrnkind, in press; Butler, Herrnkind, and Hunt, unpubl. data); this cohort continued to numerically dominate these populations until the lobsters reached 40–45 mm CL and emigrated from the study sites. We suspect that these major spring cohorts are a consequence of one or more large influxes of postlarvae during the fall and slow growth during the winter, which essentially stacks individuals from successive fall and winter settlement events into a single size class. Under these circumstances, a relationship between postlarval supply and juvenile recruitment may still be detectable, but not necessarily on an 8-month interval.

Unpredictable spatial or temporal variation in habitat quality and the uneven dispersion of postlarvae within the Florida Bay nursery could also destroy predictions of juvenile recruitment based on the influx of postlarvae. Variation in the transport of postlarvae within Florida Bay, along with the fluctuating availability of macroalgal settlement habitat (Zieman et al., 1989), may decouple the link between the influx of postlarvae to the region and subsequent recruitment to the juvenile stage (Herrnkind and Butler, in press). In portions of Florida Bay the availability of shelter for post-algal stage spiny lobsters may also create population bottlenecks that limit recruitment to subsequent life stages (Butler and Herrnkind, in press), presumably because predation on juveniles is double for those outside of shelter (Smith and Herrnkind, 1992). The regulation of population size by

shelter availability is emerging as a common theme in crustacean ecology (Caddy and Stamatopoulos, 1990), and evidence supporting this hypothesis has been presented for palinurid lobsters (Parrish and Polovina, in press; Butler and Herrnkind, in press), homarid lobsters (Wahle and Steneck, 1991), and stomatopods (Steger, 1987), among others. In this respect, we believe that our study site near Fiesta Key represents one extreme in the continuum of nursery habitats available to spiny lobsters in the Florida Keys. We have measured spiny lobster nursery habitat structure at over 50 sites in south Florida (Herrnkind and Butler, in press; Field and Butler, in press), and the Fiesta Key site contained one of the highest coverages of *Laurencia* and sponge-octocoral densities that we have ever measured. If the availability of settlement or post-settlement habitat truly limits spiny lobster population abundance, then a strong correspondence between the supply of post-larvae and recruitment of juveniles should only be evident in areas containing prime nursery habitat, such as our study area near Fiesta Key. Determining whether this scenario accurately reflects the process of recruitment for spiny lobsters in Florida Bay will require monitoring or experimentation at additional sites of varying nursery habitat quality.

ACKNOWLEDGMENTS

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