

A Case for Shelter Replacement in a Disturbed Spiny Lobster Nursery in Florida: Why Basic Research Had to Come First

WILLIAM F. HERRNKIND

*Department of Biological Science, Florida State University
Tallahassee, Florida 32306-1100, USA*

MARK J. BUTLER, IV

*Department of Biological Sciences, Old Dominion University
Norfolk, Virginia 23529-0266, USA*

JOHN H. HUNT

*Florida Marine Research Institute, Florida Department of Environmental Protection
Marathon, Florida 33050, USA*

Abstract.—Basic research on the settlement and postsettlement ecology of spiny lobster *Panulirus argus* has led to an application with the potential to replace lost natural refuge with artificial shelters intended for the vulnerable small juvenile stages. We began investigating ecological processes regulating juvenile spiny lobster recruitment in the Florida nursery in the mid-1980s. An unprecedented massive die-off of sponges in the middle Florida Keys followed cyanobacterial blooms in 1991–1993, ultimately affecting about 300 km² of a region providing approximately one-fifth of total juvenile recruitment. Before 1991, crevices in sponges provided diurnal refuge from predators for about 70% of juveniles <50 mm carapace length. On the basis of sampling done before and after sponge loss, we estimated that juvenile abundance declined by 30–50% on spongeless sites without alternative shelter, resulting in a decrease of annual nurserywide potential of up to 10%. Results of a field experiment evaluating the relative influences of the magnitude of settlement and availability of crevice shelter on juvenile recruitment, fortuitously begun before the sponge die-off, showed that juvenile survival and abundance were sustained on small 0.02- to 0.07-ha test sites provided with supplemental artificial shelters (slotted concrete blocks). In the absence of sponges, survival of microwire-tagged juveniles on the shelter-supplemented sites was about six times higher than that on unsupplemented sites. On the basis of our earlier ecological findings, we devised a feasibility study to test whether the artificial shelters could replace lost sponge shelter for juvenile lobsters on a large scale. It took the form of a field experiment using 240 shelters spread over 1-ha sites located amid hard substrate denuded of sponges. The shelters provided substitute crevices, supporting juvenile lobster recruitment approximating that in areas with good sponge cover. This outcome exemplifies the essential value of initial basic research that provides understanding of the ecological processes regulating individual survival and, ultimately, the character and dynamics of the fishery population. Such an approach, and the information it provides, is necessary to successful rehabilitation of essential habitat or restocking of natural populations. Moreover, conducting basic research can help prevent the waste of precious time, funds, income, and human effort that typically has occurred in past failed attempts that were undertaken with insufficient knowledge. We urge the fisheries-ecology discipline and support agencies to promote strongly the primacy of research on basic processes.

Historically, efforts to increase stocks of lobsters (spiny and clawed), as well as other fishable species, have been driven by immediate socioeconomic goals and have constituted either direct, large-scale stocking of small juveniles or habitat enhancement by construction of “reefs” of natural or man-made materials (Conan 1986; Nonaka and Fushimi 1994; Bannister and Addison 1998). The practitioners, whether scientists or entrepreneurial fishers, usually began with limited knowledge of ecological and early life history requirements of the target species. Initial ecological and recruitment research was rarely undertaken, being deemed

too time consuming, too expensive, methodologically unfeasible, or unnecessary. Instead, enhancements or stocking usually proceeded without preliminary field testing and seldom incorporated effective follow-up monitoring designed to evaluate their effect. Most of these costly long-term efforts failed to accomplish the expected outcome, such as a markedly larger catch (Addison and Bannister 1994; Bannister and Addison 1998), or there remained serious questions as to whether an apparent effect was beneficial, for example, whether artificial habitat increased productivity or simply attracted individuals already recruited in the surround-

ing habitat (Cruz and Phillips 1994). Often, the role of the researcher has been to try, post hoc, to discern the impact of extensive activities in an already altered situation, without undisturbed controls and lacking data on initial conditions (Briones et al. 1994; Phillips and Evans 1997). Present widespread and serious socio-economic and conservation needs (e.g., to sustain or replenish stocks and ensure availability of essential habitat) demand more effective, anticipatory, and strongly inferential research approaches (Phillips and Evans 1997).

Our research on the settlement and postsettlement ecology of Caribbean spiny lobster *Panulirus argus* in Florida, begun in the 1980s, has led to an application with the potential for artificial replacement of natural refuge lost in an unforeseen, widespread sponge die-off that affected about 20% of the lobster nursery habitat in the early 1990s. The application was a logical extension of knowledge gained during research on factors regulating recruitment of lobsters in the Florida Bay nursery, which sustains the extremely valuable and heavily fished adult population. The basic research we conducted during the decade preceding the sponge die-off was predicated on the rationale that one must know the ecological linkages between juvenile lobsters and those processes and habitat features that determine individual survival and population abundance. This knowledge is essential to solving problems of resource management and conservation. The nature of initially unforeseen linkages, in this case the extreme significance of crevice refuge to survival at a critical juvenile stage and its interaction with postlarval supply, would probably not have emerged without a broad ecological perspective and an initially open-ended research agenda. This is one of a number of recent examples for fished species demonstrating the value of investing in basic research, which alone can provide relevant, applicable knowledge (Caddy 1986; Blankenship and Leber 1995; Cobb 1995).

The first of three sections to follow synthesizes our research on spiny lobsters in south Florida, emphasizing the progression from initially descriptive studies and short-term experiments to developing and testing general hypotheses by large-scale field manipulations that provide inferences at the regional and population level. Amid this work, in 1991–1993, the massive loss of sponges introduced an unplanned “grand” test of hypotheses about the respective effects of variable postlarval supply to the nursery and

the abundance of shelters on postsettlement survival. The second section describes and provides an initial assessment of results of a large-scale field test of the effectiveness of replacing lost sponge shelters with artificial structures. The third section reviews and discusses various lobster enhancement efforts, identifies types of research needed to provide baseline data for validly assessing effects of habitat changes, and culminates in a prospectus asserting that basic research on ecological processes must receive the highest priority if we expect to achieve success in habitat rehabilitation in the face of large-scale changes in ecological and populational conditions.

Florida Spiny Lobster Recruitment Research

Life History

The Caribbean spiny lobster supports major commercial fisheries over its range from Brazil to Bermuda. In the Florida Keys it is the focus of both intensive commercial trapping and recreational diving, and it alternates with shrimp as the state’s most economically important marine species (Harper 1995). As a large, long-lived, abundant, and widely ranging benthic predator of sedentary mollusks and crustaceans, it is ecologically significant in all the coastal habitats it occupies (Kanciruk 1980). The complex life history of this species requires three distinct habitats (Figure 1; Marx and Herrnkind 1983; Herrnkind et al. 1994; Lipcius and Cobb 1994). Adults potentially can live for several decades, congregating in reef crevices and frequently migrating about the coastal shelf. Mating and spawning occur in spring on oceanic reefs; the phyllosome larva develops as it drifts in the open ocean for an estimated 6–9 months before metamorphosing into the puerulus postlarva. The nonfeeding pueruli move through inlets into Florida Bay every month on nightly flooding tides at new moon phase, then settle within days amid benthic vegetation (Herrnkind et al. 1994).

After metamorphosis, the benthic instars remain within vegetation for several months until attaining about 15–20 mm carapace length (CL), when they take up daytime shelter in sponge crevices or rocky substrate but forage in the open at night. At about 50 mm CL, about one year after settlement, the juveniles leave the initial nursery habitat and move nomadically about the bay for the next year, ultimately migrating offshore to the reefs, where they

Caribbean Spiny Lobster Life Cycle

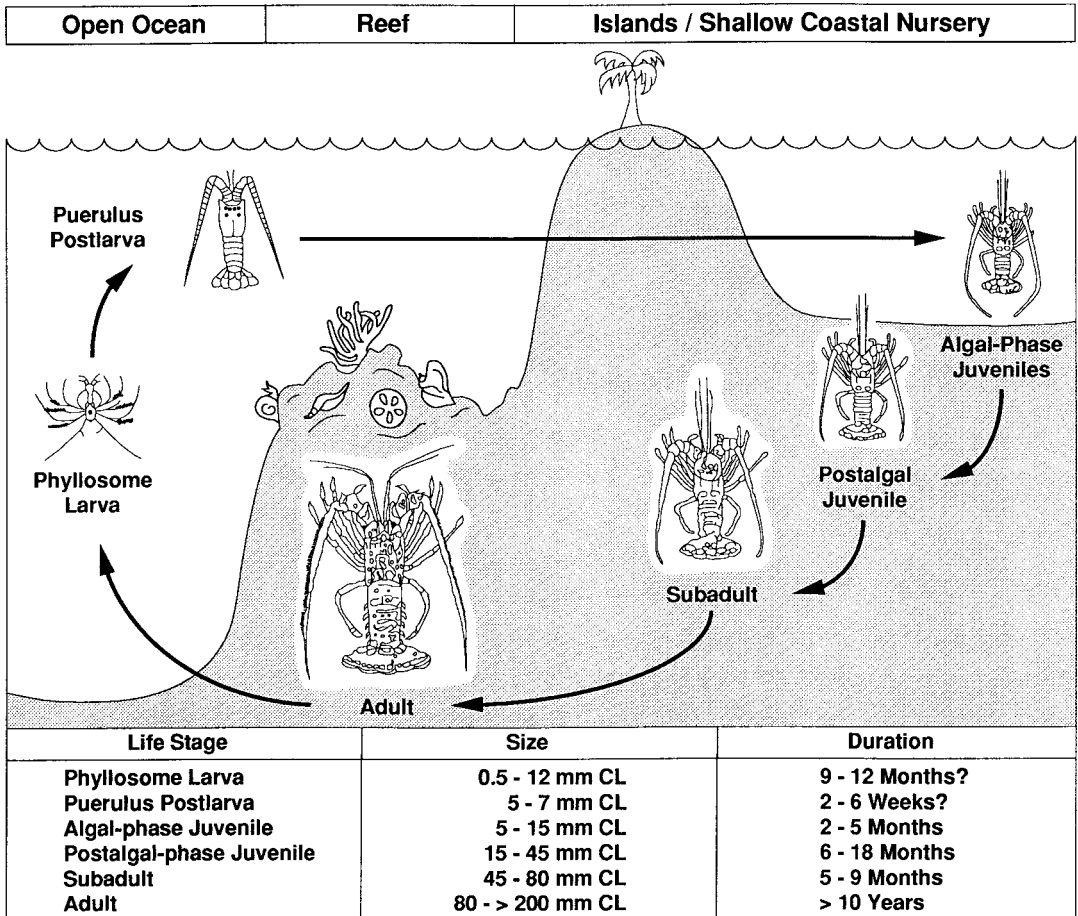


FIGURE 1.—Diagram summarizing the stages of the life cycle of the Caribbean spiny lobster *Panulirus argus*, showing size, duration, and habitat of each stage in Florida waters (Butler and Herrnkind 1997). Present evidence suggests that late-stage phyllosome larvae and the subsequent puerulus postlarvae that settle in the region originate from as yet unspecified locations in the Caribbean Sea. Florida-born larvae have an unknown fate. (Reprinted from Canadian Journal of Fisheries and Aquatic Sciences with permission of the NRC Research Press, Ottawa, Canada.)

attain sexual maturity (~78 mm CL or “legal” size; Herrnkind 1980). Annual fishing mortality is estimated at >90%, and the removal of the large majority of adults each fishing season, particularly the large fecund females, has reduced the reproductive capacity of the Florida population to approximately 12% of its prefishery level (Kanciruk 1980; Lyons et al. 1981). Because postlarvae settling in the Florida nursery arises from parental stocks at as yet unspecified locations elsewhere in the Caribbean basin (Ehrhardt 1994), it is imperative that those recruits be assured appropriate nursery habitat.

The Missing Stage Revealed

In the early 1980s, the descriptive ecology of preadult and reef-dwelling *P. argus* was emerging, but the settlement microhabitat and postsettlement ecology remained unknown (Herrnkind 1980; Kanciruk 1980). Meanwhile, western Australian fisheries ecologists used their growing knowledge of the nursery ecology of *P. cygnus* to predict the fishable population several years into the future (Phillips et al. 1994). Impelled by the Australians’ success, an intensified search for the “missing” postsettlement stage of *P. argus* got underway with

the support of Florida Sea Grant. James Marx, working in the Florida Keys, discovered highly dispersed, newly settled postlarvae and first benthic instars residing solitarily within and under large, attached clumps of foliose red algae *Laurencia* spp. (Marx 1983; Marx and Herrnkind 1985a). These algal-phase juveniles remain within algae at all times, feeding on abundant small mollusks and crustaceans (Marx and Herrnkind 1985a; Herrnkind et al. 1988). Their outline-disruptive dark and light bands and stripes make them almost invisible to a human observer even when they are exposed atop variegated vegetation. The solitary algal lifestyle gives way to frequent crevice cohabitation with other juveniles at about 15–20 mm CL (i.e., the postalgal stage; Childress and Herrnkind 1996), during which time the banded pattern becomes indistinct and the characteristic benthic-phase spots and coloration appear. Marx's discovery and initial observations made it feasible to undertake simultaneous research efforts to investigate the recruitment process in the nursery and to specify the biological characteristics of the uniquely specialized but poorly understood early benthic stage.

Ecological insights, later leading to recruitment hypotheses, came from early mesocosm and aquarium experiments aimed at elucidating basic behaviors and their probable functions during the early ontogenetic period. Choice tests with presettlement pueruli and first benthic instars showed that both phases strongly, but not exclusively, preferred to reside in algae instead of sea grass *Thalassia testudinum*, long thought to be the predominant settlement microhabitat (Herrnkind and Butler 1986). Substrates with interstices among fibrous structure, whether natural or artificial, were strongly preferred. In mesocosms, algal-phase juveniles avoided exposure but left clumps with (experimentally manipulated) low prey abundance to cross open bottom at night (Marx and Herrnkind 1985b). In the field, however, large contiguous algal patches contained an apparent overabundance of prey for the typically solitary juveniles, which are spaced an average of 1 per 36 m² of vegetated substrate (Marx and Herrnkind 1985a; Herrnkind et al. 1988); i.e., food was unlikely to be limiting in typical settlement habitat.

Field experiments showed that juveniles in large, dense algal patches had significantly lower mortality, day and night, than those in small algal clumps or in sea grass, although being in any structure was greatly superior to being in the open (Herrnkind and Butler

1986; Smith and Herrnkind 1992; Childress and Herrnkind 1994). Amid vegetation, the wide spacing and solitary isolation of algal-phase juveniles further promoted evasion of predators (Butler et al. 1997). Despite the refuge afforded by vegetation, numerous predatory species frequented nursery habitat and preyed on juveniles. Predators included snappers *Lutjanus* spp., sting rays *Dasyatis americana*, toadfish *Opsanus tau*, Caribbean reef octopus *Octopus briareus*, and swimming crabs *Portunus* spp. and *Callinectes* spp., among others (Smith and Herrnkind 1992). Larger juveniles that seek crevice refuge still suffered about the same relative predation while foraging away from refuge at night as the smaller algal juveniles experienced while within vegetation. Crevices in a variety of structures such as sponges, rock crevices, and narrow slots in partition concrete blocks offered equal protection (Childress and Herrnkind 1994). Thus, juvenile lobsters are at high risk of predation throughout the early benthic period, especially when they are foraging, seeking shelter, or otherwise exposed.

Settlement: Pattern without Predictability

Two aspects of the above information were directly relevant to questions about crustacean recruitment generally and to the Florida lobster nursery in particular: the highly dispersed spacing of both settling postlarvae and algal-phase instars, and the extreme vulnerability of shelterless, small, postalgal-phase juveniles. The most applicable hypotheses were (1) recruitment success was directly dependent on the numbers of postlarvae entering the nursery (a "supply side"-dominated process; Fairweather 1991; Fogarty et al. 1991), and (2) recruitment was regulated by variable availability of settlement and postsettlement habitat (a "demographic bottleneck"; Caddy 1986; Wahle and Steneck 1991). The applicability of either hypothesis could not be established from data available in the late 1980s (Marx 1986; Herrnkind et al. 1988), so in 1988 we undertook long-term, large-scale experimentation designed to discriminate their respective roles in a productive nursery area of the middle Florida Keys.

To determine the large-scale spatiotemporal pattern of postlarval settlement, we measured numbers of planktonic postlarvae arriving from offshore at four inlets of a 200-km² region of the middle Keys while also measuring the numbers settling successively greater distances downstream into the bay (Figure 2); the project ran a total of 6 months over 3

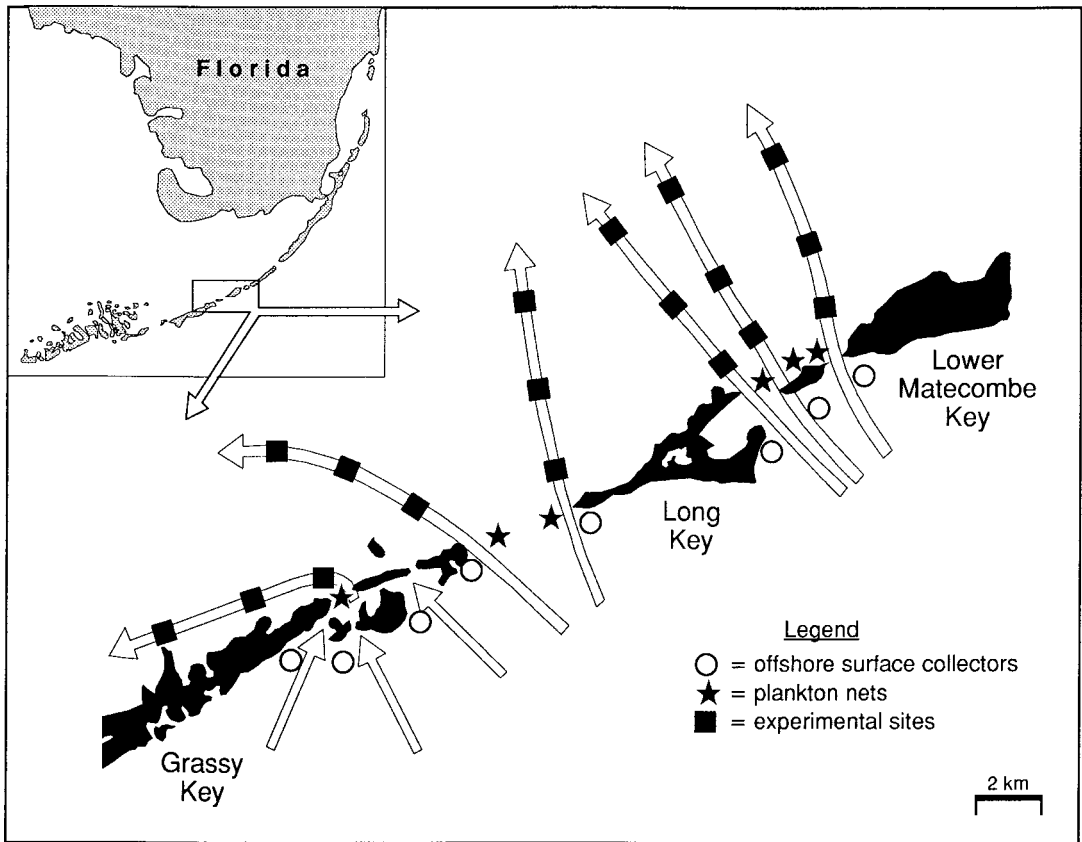


FIGURE 2.—Diagram of the middle Florida Keys showing current paths, postlarval monitoring stations, settlement sites, and adjacent benthic juvenile sampling locations for Caribbean spiny lobster during the summers of 1988–1990. Although overall downstream settlement reflects the relative number of arriving postlarvae, local settlement patterns are unpredictable because of spatiotemporal variability in postlarval abundance and settlement habitat. For more details, see text and Herrnkind and Butler (1994). (Reprinted from *Crustaceana* with permission of Brill, Leiden, the Netherlands.)

summers from 1988 to 1990 (Herrnkind and Butler 1994). We also compared the magnitude and spatial pattern of settlement on each site to the abundance of small crevice-dwelling juveniles in the surrounding area. Not surprisingly, the numbers of postlarvae settling on our benthic collectors downstream of an inlet reflected the numbers that had just passed through it. Despite this general pattern, the distribution and abundance of settlers was patchy and locally unpredictable from month to month and among the experimental settlement sites. Although areas with abundant, large algal patches, sponges, and other crevice-bearing shelter consistently harbored the highest numbers of small juveniles, algal abundance in most locations fluctuated markedly by season or from year to year. In short, we could identify sites where juvenile recruitment was generally high

or low, on the basis of habitat structure and proximity to inlets supplying postlarvae, but we could not predict short-term or small-scale recruitment patterns. Presumably, variability in both postlarval supply and macroalgal distribution created a continually shifting mosaic of settlement (Butler et al. 1997).

We proposed a conceptual model (Figure 3; Herrnkind and Butler 1994) to explain this spatiotemporally unpredictable pattern of juvenile recruitment on the basis of the relative settlement and survival of arriving postlarvae (support capacity) in a variable system. It was apparent that on poor habitat (sparse algae, few crevice shelters), even large numbers of settling postlarvae cannot yield many juveniles because they suffer very high postsettlement predation. Over time there is unlikely to be any close correspondence between regional

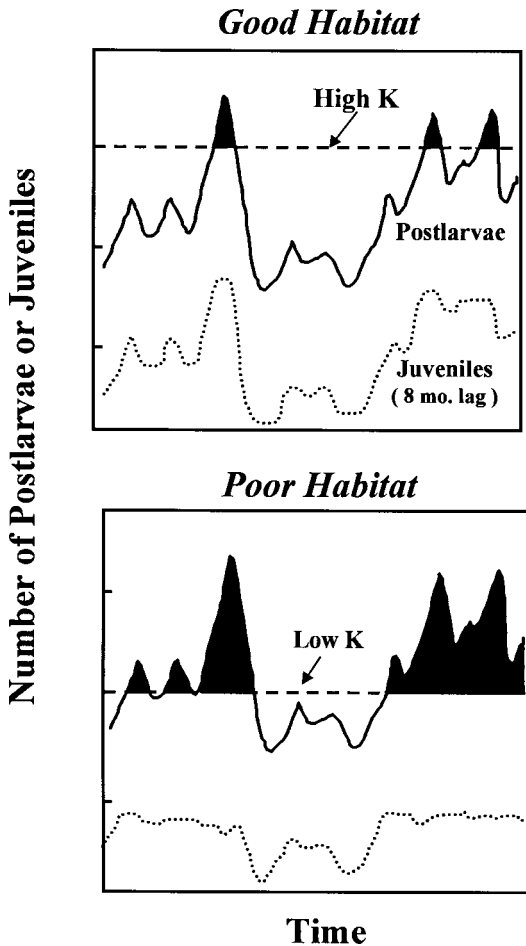


FIGURE 3.—Graphic conceptual model of the relationship between the number of postlarvae settling on “good” (many crevices) and “poor” (sparse crevices) nursery habitat. In good sheltering habitat, with a high carrying capacity (K), mortality crops excess recruits (black area) only when settlement is extremely high, so at other times, settlement is reflected by and closely correlated with later juvenile abundance. However, on habitat of low carrying capacity, there is high mortality after even moderate settlement, so the relationship between numbers of postlarvae and later juvenile abundance is decoupled.

postlarval supply and juvenile recruitment on such sites. Contrarily, numerous settlers on good nursery habitat (abundant algal and crevice refuge) will have comparatively high survival rates through the algal and postalgal period, so juvenile abundance will later be reflected as correspondingly higher compared to periods of low postlarval abundance. However, both postlarval numbers and settlement conditions vary over time and location independently in the Florida nursery. During times when few postlarvae arrive in

an area, even sites with rich nursery habitat will exhibit relatively low juvenile recruitment. Juvenile recruitment will also be reduced at previously productive locations during episodes of low algal production, even when postlarvae are abundant. According to the model, we would expect to see a long-term, high correlation between postlarval abundance and subsequent juvenile abundance only on shelter-rich sites that sustain extensive algal cover. This pattern has been documented on one of our long-term sites that is particularly rich in algae and sponge crevices, which has sustained for a decade the highest juvenile densities of any censused natural site (Forcucci et al. 1994; Butler et al. 1997; Childress and Herrnkind 1997). Nonetheless, predictions of this model needed to be experimentally tested on an appropriate spatial scale.

The importance of both algal condition and postlarval numbers to subsequent juvenile recruitment was demonstrated in a year-long experiment in which, each month, we added differing known numbers of microwire-tagged first benthic instars (total of either 46 or 182 per site) to 18 isolated 200- to 1,000-m² sites ($n = 9$ sites per density treatment), with naturally varying but known amounts of algal cover (Butler et al. 1997). The number of recovered tagged juveniles gave a direct estimate of survival on each site, whereas the ratio of untagged to recaptured juveniles of the same size (a proxy for age) at each census allowed us to back-calculate the number of natural settlers there. Results showed that postsettlement survival in algae was not strongly density dependent even at our artificially inflated settlement levels. Algal patch size varied nearly threefold over the study period; regional postlarval abundance also varied but independently of algal dynamics. Proportional survival and growth, however, were comparable at the two settlement-density treatments, whereas total juvenile recruitment (tagged plus untagged) was correlated with algal patch size on the site. We concluded from this study that the initial numbers of settlers and condition of the habitat together influenced how many juveniles survive to make the transition into the crevice-dwelling phase.

Crevices: Refuge from the Predator “Gauntlet”

Support for the shelter-bottleneck hypothesis came from an experiment in 1988–1989 designed to test the influence of settlement magnitude and available crevice shelter—for postalgal juveniles—

on recruitment. We added artificial shelters to 6 isolated, 0.05-ha algal and hard-bottom sites and also added algal-phase juveniles to 3 of those sites; 3 other unmanipulated sites served as controls (Butler and Herrnkind 1992, 1997). Twelve artificial shelters (each consisting of two cement partition blocks), each 10 cm W × 20 cm H × 40 cm L, were set haphazardly on each of the six sites. These shelters each provided a total of 6 narrow holes (4 cm W × 2 cm H) and were capable of housing a maximum of about 15 small juveniles (Childress and Herrnkind 1996) up to 50 mm CL. To three of the six isolated sites, we also added an average of 26 postlarvae per site monthly for 6 months. We censused all sites bi-weekly, counting, measuring, tagging, then releasing all collected juveniles <50 mm CL.

We expected that a substantial number of the added algal-phase juveniles would survive within the algae, thus supplementing the natural settlement and increasing the numbers of postalgal juveniles censused several months later as they moved into crevices. Instead, the numbers of small postalgal juveniles <35 mm CL increased markedly on all shelter-supplemented sites but not on unmanipulated sites (Butler and Herrnkind 1997). Juvenile numbers were statistically similar in the two experimental treatments. The artificial shelters (cement blocks) housed 76% of all juveniles <45 mm CL collected on the manipulated sites; each occupied block housed 1–6 juveniles (mean ~2) of the same size range as those in nearby sponge crevices (mean ~32 mm CL). Tag-recapture data indicated high on-site residency for juveniles <35 mm CL and gradually increasing emigration and immigration thereafter. This outcome suggested that lack of crevice refuge can potentially constrain the number of lobsters in the nursery, given otherwise sufficient numbers of settlers and protective vegetated substrate.

Experimental support of the “bottleneck” hypothesis was significant both to understanding recruitment of obligate crevice-dwelling species generally (Caddy 1986; Wahle and Steneck 1991) and particularly to understanding the processes within the Florida lobster nursery. In addition, the potential to increase the proportion of surviving settlers on vegetated but crevice-poor substrate simply by adding artificial shelter was likely to have appeal to those interested in increasing the fishable population (Fee 1986; Moe 1991).

We believed that the initial study was an insufficient test and that much more needed to be learned about the basic ecological processes involved be-

fore anyone set out to attempt such a large-scale intercession. Therefore, in 1991 we undertook a longer and more extensive experiment incorporating several levels of both available shelter and settler numbers so as to discriminate their respective influences better.

This study included three levels each of added settlers and shelter blocks. We also used microwire tags to mark the introduced algal-phase juveniles so we could assess survival, growth, and natural settlement. The study incorporated 27 isolated sites (each ~200–1,000 m²) in a completely crossed 3 × 3 factorial design potentially allowing interpretation of main effects and interactions. Algal cover could not be effectively regulated but was measured monthly along with number, size, and gender of crevice-dwelling juveniles; identification of juvenile shelter and number of conspecifics in each shelter also occurred monthly.

Small postalgal juveniles were initially few on all the test sites but increased in number and grew in size between June and October 1991 (Figure 4a). This is a characteristic seasonal pattern in the Florida nursery, probably caused by the acceleration of growth rates with rising temperatures, so many of the winter and early spring settlers make the transition into the crevice-dwelling stage over summer and early fall (Lellis and Russell 1990; Forcucci et al. 1994; Herrnkind et al. 1997b). Recapture of sphyrion-tagged postalgal juveniles demonstrated site fidelity until ~45 mm CL and negligible movement between sites (W. Herrnkind, M. Butler, and J. Hunt, unpublished data). Recovery of microwire-tagged juveniles indicated a survival rate during the first benthic year of ~1–4% (Herrnkind and Butler 1994; Butler et al. 1997).

Housing Shortage in the Nursery

The preceding experiment, started in June 1991, was disrupted the following November by an unprecedented massive bloom of cyanobacteria, which reduced visibility to <1 m and curtailed assessment of the sites until February 1992 (Figure 5). In the wake of the bloom, we found that approximately half of the marked sponge dens had disappeared from the study sites and throughout hundreds of square kilometers of the surrounding region; sponge crevices formerly had housed >60% of all postalgal juveniles (Butler et al. 1995; Herrnkind et al. 1997b) but afterward housed only 25%. The total number of juveniles on the experimental sites did not decrease, but the proportion in shel-

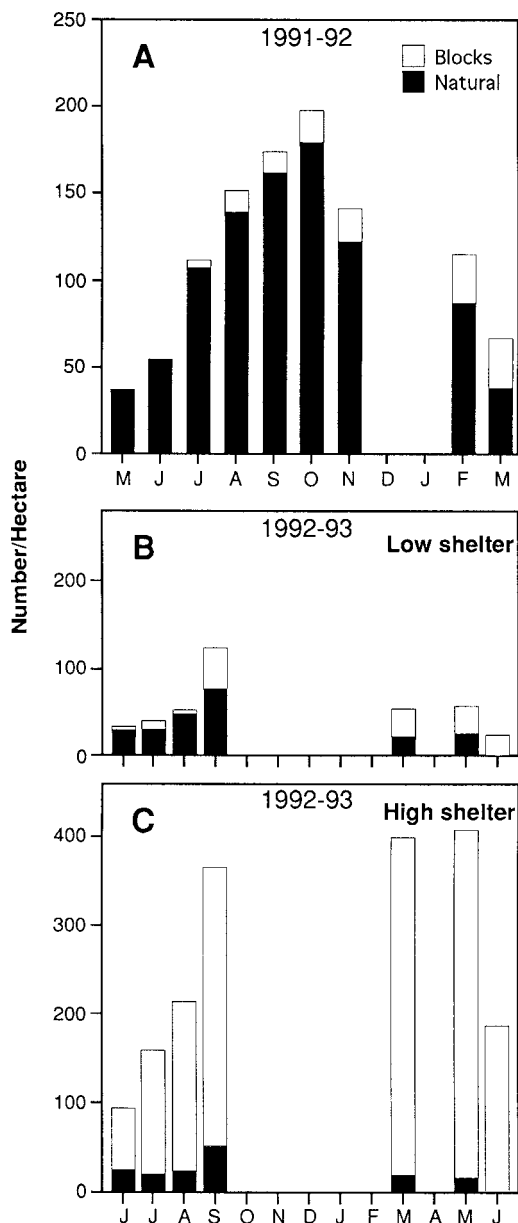


FIGURE 4.—(A) Mean numbers per hectare of juvenile spiny lobster <35 mm carapace length (CL) on 9 sites in the middle Florida Keys with primary sponge or other natural crevices between May 1991 and March 1992. Numbers increase through early fall as algal juveniles grow and leave the settlement vegetation to become crevice dwellers. A sponge-killing cyanobacterial bloom lasted from November 1991 through January 1992; about one-half of sponge dens were obliterated. (B) Numbers of juveniles <35 mm CL on 8 sites, affected by the 1991–1992 bloom, with mainly natural crevices between June 1992 and June 1993. A second bloom from October 1992 through February 1993 destroyed all sponges on the sites. (C) Numbers of lobsters during the same period as (B) on eight sites supplemented with concrete shelter blocks.

ter blocks, 24% before sponge loss, increased to 49% following this first bloom. We began a revised experiment incorporating 24 sites in June 1992, only to have it curtailed by an even larger, longer-lasting bloom from October 1992 through February 1993. This time all large, lobster-sheltering sponges died. We found only small numbers of postalgal juveniles on spongeless test sites without artificial shelters; those few individuals occupied rock crevices and occasional coral heads.

The extreme sponge loss across hundreds of square kilometers of a productive nursery region raised the specter that a refuge shortage might cause increased juvenile mortality and a subsequent decline in the adult population. Eventual repercussions to the fishery became a primary concern. In spring 1993, we set out to assess the change in the juvenile distribution, abundance, and shelter within the affected area. Our field studies in the bloom-swept region for the previous five years (e.g., Herrnkind and Butler 1994; Field and Butler 1994; Forcucci et al. 1994) provided data for before-and-after comparisons of algal and sponge cover, juvenile abundance, age structure, and types of shelter occupied.

Regionally, spongeless hard-bottom patches with few alternative crevice-bearing shelters harbored only about half the number of juveniles (<50 mm CL) they had housed in their previous, sponge-rich condition (Herrnkind et al. 1997b). On sites that retained some sheltering sponges or had numerous rock or coral crevices, juvenile abundances were actually about 40% higher than during the several-year period before the blooms, although some of this increase probably came from local immigration by larger, nomadic juveniles. Nevertheless, the presence of the entire juvenile size range showed that settlement and recruitment had continued across the affected region throughout the bloom period. The use of den structures reflected the available housing choices; for example, rock and coral crevices accounted for about 70% of dens, and sponges accounted for <20%. This pattern was echoed by conditions on the experimental sites provided with supplemental artificial shelter. There, juvenile numbers were as high as or higher than prebloom levels, but the vast majority of juveniles occupied shelter blocks (Butler et al. 1995; Herrnkind et al. 1997a).

The age structure of newly emerged postalgal juveniles (<35 mm CL) in the 1992 experiment repeated the typical seasonal pattern for the period June through September, but abundances strongly reflected the amount of shelter available on each site. That is, few juveniles were present in the natural (spongeless) treatment, substantially more in the intermediate treatment,

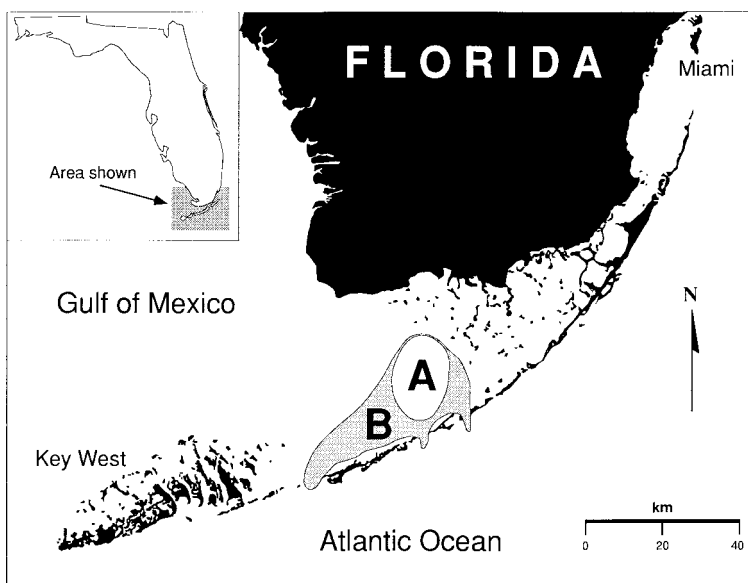


FIGURE 5.—Map of south Florida showing the approximate extent of cyanobacterial blooms in (A) fall 1991 and winter 1992 and (B) fall 1992 and spring 1993. One-half of large sponges used as dens by small juvenile spiny lobsters through the affected region were obliterated in the first bloom, and the remaining sponges were killed by the second bloom. The affected area accounts for approximately 20% of the total productivity of the main Florida nursery. Figure redrawn from Butler et al. (1995). (Reprinted from Marine Ecology Progress Series with permission of Inter-Research, Oldendorf/Luhe, Germany.)

and even higher numbers on sites with the highest shelter supplementation (Figure 4b,c; Herrnkind et al. 1997b). The same abundance pattern was present in spring 1993 after total sponge loss. Postbloom juvenile abundances on shelter-block sites in fall 1992 and spring 1993 equaled the highest levels recorded on natural unaffected sites in 1991 and approached the maximum recorded at any location (~400 juveniles <50 mm CL per ha; Forcucci et al. 1994).

The differences in abundances of small juveniles (<35 mm CL) among the sites were due to the corresponding availability of artificial shelters because the numbers occupying sparse natural crevices were similar in all treatments. Moreover, microwire tag-recovery data also indicated survival rates corresponding to shelter availability. Although an equal number of tagged early instars were released into each of the three shelter conditions, approximately six times as many were recovered as postalgal juveniles from the high-shelter (block) as from the low-shelter (natural) condition. Neither algal abundance, local variation in settlement, nor immigration of older juveniles explained the above pattern. These results extended the interpretation of the initial shelter experiment. The paucity of crevice refuge can present a “bottleneck” for small juvenile *P.*

argus over a large area of nursery as Caddy (1986) hypothesized. Observations of a high rate of occupancy of artificial crevices by small postalgal juveniles also suggested potential shelter limitation in a Mexican spiny lobster nursery (Arce et al. 1997).

Artificial Shelter on a Large Scale: The Acid Test

Rationale

The artificial shelters we had deployed for experimental purposes appeared to compensate for the lost natural sponge crevices by providing refuge for the vulnerable small juveniles as they emerged from the initial postsettlement algal microhabitat (Herrnkind et al. 1997a). From these results, a new question arose. Could the shelter blocks that served as substitute refuge on small patches in one area be effective over the range of conditions across the larger affected region?

Most nursery habitat in the Keys is distributed as large, discontinuous stretches across many hectares interrupted or separated by large sea grass meadows (Herrnkind, Butler, and Hunt, unpublished data), yet for experimental manipulations we had deliber-

ately selected small (0.05–0.10-ha) patches isolated in large and otherwise contiguous sea grass meadows. The two types of sites might differ with respect to settlement, survival, or movement of juvenile lobsters. For example, in the small corral-like patches, the effect of enhanced shelter on survival might be increased, whereas immigration might be lower than at open sites.

For a large-scale test of shelter replacement, we chose to use 1-ha arrays of the cement-block shelters at a density of 240/ha, estimated to approximate the housing capacity of crevices in regional sponge habitat. Past studies indicated that a 1-ha patch (100 m × 100 m) is sufficiently large that postlarvae settling within the array would grow through the juvenile period there until the onset of the nomadic stage (~40–50 mm CL; Forcucci et al. 1994). That is, newly emerging postalgal individuals entering the artificial shelters would be those originally recruited as postlarval settlers on that 1-ha site.

We confine the presentation below to an assessment of two key hypothetical predictions based on the postsettlement recruitment processes reviewed above (a detailed analysis of the project is being prepared). Prediction 1: numbers of small postalgal juveniles would recruit to the artificial shelter sites consistent with seasonal patterns of settlement and growth, as well as to sponge sites, but not to spongeless sites. Prediction 2: because each hectare with artificial shelters was surrounded by a much larger spongeless area of sparse crevice shelter, where larger, mobile postalgal juveniles should wander about seeking shelter, older nomadic juveniles would rapidly immigrate to and remain in residence primarily on the artificial-shelter sites and, to a lesser extent, on large, sponge-dominated sites, but not at all on spongeless sites.

Methods

We applied methods and procedures used in previous experiments (details in Butler and Herrnkind 1997; Butler et al. 1997; Herrnkind et al. 1997b). As experimental comparisons to the 1-ha, 240-block treatment, we chose patches on spongeless substrate about 0.5 km from the block arrays and on sponge-rich sites that were relatively untouched by the 1991–1992 blooms (Butler et al. 1995; Herrnkind et al. 1997b).

In June 1995, study sites were established within widely separated about 0.5- to >1.0-km² patches of algal hard bottom. We marked 500-m² sampling plots

on the sponge-rich and spongeless sites and in the centers of 1-ha areas, which later received artificial shelters. Divers then surveyed each plot, using three parallel 25-m line (measuring tape) and belt transects (2 m wide) spaced about 5 m apart to characterize algal cover (percent cover) and potential den structures (sponges, corals, etc. >20 cm diameter). We also captured and measured all crevice-dwelling juvenile lobsters present there (<50 cm CL). During the following week, 240 artificial shelters (2 stacked, 3-slot partition blocks) were placed about 8 m apart throughout the 1-ha plots; the 12 blocks in the center plot were marked by numbered tags. The 500-m² plots on all sites were recensused for juvenile lobsters and resurveyed for algal cover in September 1995 and in February, May, and July 1996.

Results

Figure 6 shows the mean abundances (as per hectare density) of small postalgal juveniles (Figure 6a, <25 mm CL) and larger, more mobile juveniles (Figure 6b, 35–50 mm CL) for each site type through the project period. In June 1995, numbers of postalgal juveniles were similarly low on all the sites (20–30/ha), as is common in that season (Herrnkind et al. 1997b). Over the next 2 quarters, the abundances of new crevice dwellers (<25 mm CL) doubled or tripled on the shelter-supplemented and sponge sites but not on the spongeless plots (20/ha in September 1995; 0/ha in February 1996). Diver reconnaissance and supplemental censusing showed juveniles were also present throughout the sponge areas and among artificial shelters outside the sampled plots on all three sites. In May 1996, abundances of juveniles <25 mm CL were again seasonally low on all site categories (0–33/ha), but by July 1996 they increased to similarly high levels on sponge (100/ha) and block (93/ha) sites. Meanwhile, spongeless sites had 0/ha and 33/ha (i.e., no change from the previous year). Mean overall abundances of juveniles <25 mm CL were remarkably congruent on the natural sponge sites and on those on which we placed artificial shelters as substitutes for lost sponge crevices. These data affirm the hypothetical prediction that numbers of locally recruited, newly emerged postalgal juveniles on the shelter-supplemented as well as sponge sites should increase and exceed the numbers on spongeless sites.

The second prediction was also upheld, i.e., that larger, more nomadic juveniles from the surrounding low-shelter areas should quickly immigrate and

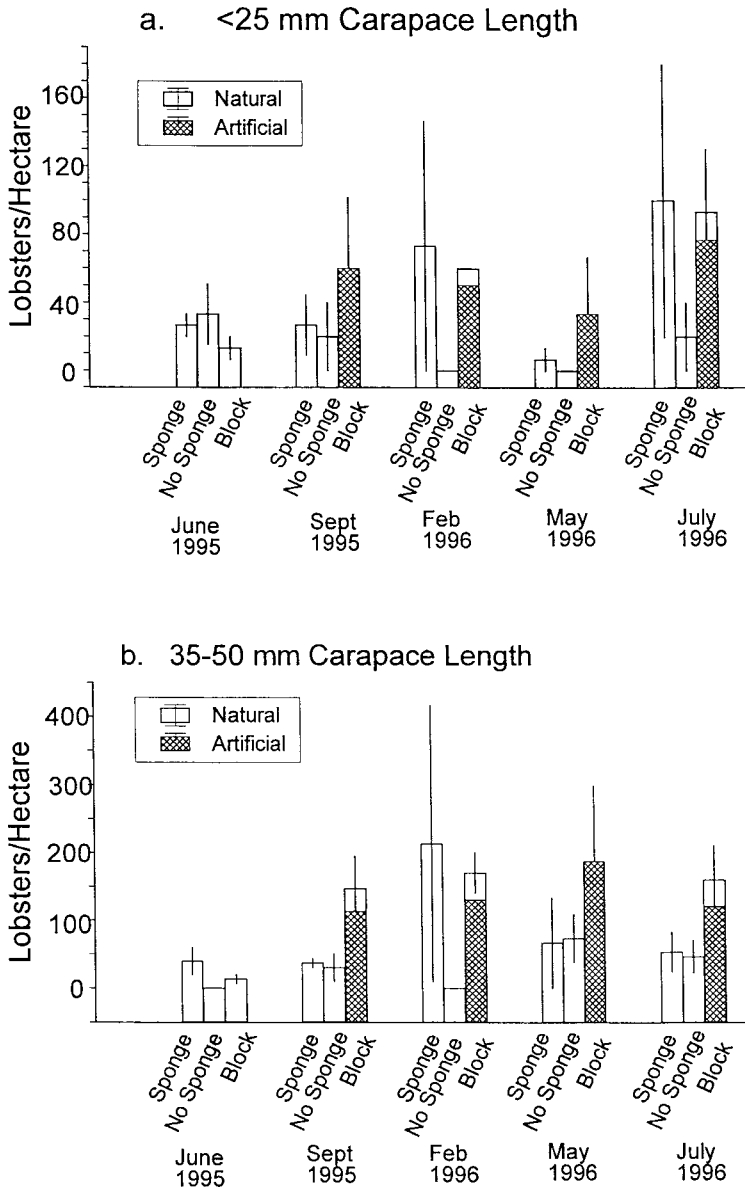


FIGURE 6.—Histogram comparison of abundances of small postalgal juvenile lobsters (a, <25 mm carapace length [CL]) and older, mobile juveniles (b, 35–50 mm CL) on sponge-dominated natural sites, natural sites with no sponges, and spongeless sites on which we arrayed 240 concrete shelter blocks. The initial lobster census (June 1995) was taken just before addition of the concrete blocks to the artificial shelter sites. There were 3 replicate sites in each category; means of census counts on 0.05-ha plots on the 3 sites in each category are scaled up to 1.00 ha. Bars represent 1 standard error. (6a, Feb 1996, includes only one Block site.)

markedly inflate numbers on the shelter-supplemented sites (Figure 6b). Between June and September 1995, the mean number of juveniles 35–50 mm CL increased from 20/ha in June 1995 to 146/ha in September 1995 on the shelter-supplemented sites. The intervening period (~2.5 months) was too

short for growth of sufficient numbers of algal juveniles to the larger size range (35–50 mm CL; Forcucci et al. 1994; W. Sharp, Florida Marine Research Institute, unpublished data), so the surge of older juveniles there had to be mostly immigrants. Shelter-supplemented sites had the highest abun-

dances of 35–50 mm CL juveniles for three of the four sampling periods after the shelters were added, suggesting continuous immigration and long residency.

Data from short-term antenna tagging of postalgal juveniles, done in conjunction with a separate study, are presently being analyzed and may establish the relative migration rates into and out of different kinds of sites (Butler, unpublished data). Although we set out microwire-tagged algal-phase juveniles, we recovered very few, possibly indicating movement out of the unbounded 0.05-ha plots or especially high mortality.

Discussion

The close match between recruitment patterns of young postalgal juveniles (<25 mm CL) observed on the 1-ha sites supplemented with cement-block shelters and their abundance and seasonal pattern on natural sponge sites resembles prior results from small, confined sites (Herrnkind et al. 1997a) and suggests that artificial shelters can effectively substitute for lost sponge refuge on a large scale. Because each shelter block has several crevices of appropriate size, relatively few are needed as compared to natural sponges, only a small fraction of which have suitable interstices; e.g., the mean density of sponges is >2,000 per ha in the undisturbed portion of the nursery (Herrnkind et al. 1997b). Large predatory fishes such as groupers and snappers are not strongly attracted to these small isolated structures, which are about the size of sponges. Spacing the blocks several meters apart yields juvenile spatial distributions typically observed in natural sponge habitat in the Florida nursery (Childress and Herrnkind 1997). Separation by at least 2 m additionally prevents close proximity of early postalgal juveniles (~15 mm CL), which potentially increases their vulnerability to predators (Butler et al. 1997).

Until they attain substantially larger size, aggregated postalgal juveniles in a den probably gain little or no advantage in cooperative defense over solitary individuals (Childress 1995; Childress and Herrnkind 1997). Large objects like the “casitas” used by fishers to attract subadult and adult lobsters often attract large snappers and groupers that prey on smaller juveniles (Cruz and Phillips 1994; Mintz et al. 1994). For this reason, it seems unnecessary, or possibly counterproductive, to build large artificial structures for small postalgal juveniles (Cruz et al. 1986; Lozano-Alvarez

et al. 1994; Arce et al. 1997). There is evidence, however, that larger nomadic juveniles (>50 mm CL) and subadults benefit from group dens (Eggleston et al. 1992; Mintz et al. 1994; M. Butler, and A. McDiarmid, unpublished data). The great majority of older juveniles in the Florida nursery do not use sponges but instead occupy large rock crevices and undercuts (Butler and Herrnkind 1997). Although they sometimes den singly, 50–75-mm CL lobsters more commonly reside in groups; e.g., we have seen over 100 lobsters in a large natural crevice (Herrnkind, personal observation).

The comparison of abundances between our sites with artificial shelters and the sponge-dominated areas should be applied strictly to the newly emerged postalgal recruits and not to the largest juveniles. That is, the present data show that many mobile lobsters 35–50 mm CL immigrated to the 1-ha shelter-supplemented area from the large shelter-poor surrounding region. At first glance, mean total juvenile abundance (all juveniles <50 mm CL) for the study period appears substantially higher on sites with artificial shelter (387 per ha versus 211 per ha); that result is caused largely by the inflated numbers of older immigrants and is not a valid reflection of on-site recruitment. The present situation for 35–50-mm CL juveniles in spongeless areas seems analogous to the attraction and retention of large numbers of similar-aged juveniles to casitas set in sea grass and other crevice-poor habitat. Ontogenetic changes in mobility as well as sociality, vulnerability to predators, and other age-related features must be distinguished and separately evaluated for accurate assessment of the ecology of “juveniles” because effects differ markedly in the nursery depending on age and size (Childress and Herrnkind 1994, 1996).

The small-slot cement blocks we used may not be the most attractive or protective artificial shelter possible. Rather, they serve juveniles <50 mm CL analogously to the range of natural crevice-bearing structures in Florida nursery habitat. Small *P. argus* respond to the features of a crevice rather than to the structure bearing it (Herrnkind et al. 1997b). Our artificial shelters, like some natural crevices, allow for either solitary or communal denning. Across the nursery, about half of juveniles <50 mm CL shared a den with conspecifics, usually with one (45%) or two (27%) but up to nine (Childress and Herrnkind 1997). Space for several individuals to be close together, whether or not in the same den, may be an important attribute of both artificial shelters and large or closely spaced natural crevices because postalgal

juveniles are attracted to (or can find) other denned individuals from an as yet unspecified distance (probably exceeding several meters) away at night, presumably in response to chemical cues from conspecifics in the den (Zimmer-Faust and Spanier 1987; Childress 1995). Rapidly locating a den by homing to a resident individual shortens the exposure time of a shelter-seeking juvenile, thus reducing its probability of being intercepted by a predator (Childress 1995; Childress and Herrnkind 1997).

As a rehabilitation device, the small artificial shelters seem particularly appropriate because they match the sheltering qualities of the missing natural structures, even though other artificial objects may attract and hold more juveniles. The number of experimental blocks (240/ha) supported roughly the same juvenile recruitment rate as the sponge-rich habitat, although all shelters were not used simultaneously, and all slots were not filled to capacity. That is, an array of 240 shelters/ha may be sufficient to replace lost sponges in this region. Adding more seems unnecessary for rehabilitation, and adding many more would be unlikely to produce a corresponding increase in recruitment because of upper limits placed by episodically low settlement and crevice-independent mortality both during the algal phase and while postalgal juveniles forage in the open (Butler and Herrnkind 1997).

We have concentrated research on processes specifically applying to the early juvenile phases because they suffer the highest natural mortality and consequently exert the greatest influence on recruitment to the fishable population (Smith and Herrnkind 1992; Butler and Herrnkind 1997). Nevertheless, older juveniles suffer predation and benefit from refuge in the habitats they traverse, including large areas of sea grass where prey can be plentiful but shelter is scarce. The ecology of late juvenile *P. argus* has been extensively studied in the Bahamas, Mexico, and Florida with respect to the impact of lobster-attracting casitas (or "pesqueros") by R. Lipcius, D. Eggleston, and their colleagues (Briones et al. 1994) and in Cuba by Cruz and others (Cruz and Phillips 1994). Although these devices can reduce predation and provide access to abundant food for large numbers of nomadic lobsters (Briones et al. 1994; Cruz and Phillips 1994), they have not been employed to replace lost natural shelters (but see Davis 1985), and there is not yet compelling evidence that the devices promote recruitment of juveniles making the transition to crevice-dwelling.

We refrain from advocating the large-scale deployment of artificial shelters for shelter rehabilitation (or for enhancement) in Florida although they seem suitable (innocuous, inexpensive, nonpolluting), and there is as yet no apparent sign of sponge recovery to pre-1991 levels. Such decisions need to be made by other agencies of the body politic. In addition, estimates of the lobster catch in the past several years have been about the same as those in years before the sponge loss, although this result may be attributable to several years of especially high postlarval supply to the unaffected portion of the nursery. Moreover, some important concerns about mass deployment of artificial structures remain worthy of further research. Because we expect that new sponges will eventually recruit, the artificial shelters would become redundant but remain a permanent part of the underwater landscape. Perhaps similar structures could be made of natural oolitic rock fragments and be weakly bonded so that they disintegrate into harmless substrate after 10–20 years. We do not know how long the structures will remain effective before silt and epibiota clog the crevices (some we set out in 1988 still house juveniles, but many slots have filled and become inaccessible). It is not certain how the massive presence of artificial structures would affect juvenile lobster-den competitors (stone crabs, small toadfish) and predators (octopus, portunid crabs). To this point, no one has performed an adequate cost-benefit economic projection. Also, much of the spongeless region lies within Everglades National Park and the rest within the Florida Keys National Marine Sanctuary, thus raising concerns about preservation and environmental impact. Irrespective of whether or where artificial shelters are deployed for shelter rehabilitation, we believe their performance as juvenile lobster refuge has been ecologically demonstrated at a relevant scale.

Basic Research for Applied Information Needs: A Retrospective

Both clawed and spiny lobsters have been the focus of long-term, intense efforts to enhance fished populations (see recent reviews by Conan 1986 [clawed]; Briones et al. 1994; Cruz and Phillips 1994; Nonaka and Fushimi 1994 [spiny]; Hunt and Scheibling 1997 [general]; Pickering and Whitmarsh 1997; Bannister and Addison 1998). The enhancement literature chronicles a long history of direct

attempts to stock or add habitat on a large scale to increase the catch or to improve harvesting efficiency, usually with good public support and sometimes initiated by the fishers. For example, once it became feasible to raise American clawed lobsters *Homarus americanus* through the egg and larval stage in the late 19th century, stocking efforts began and have continued since; restocking of *H. gammarus* (and *H. gammarus* × *H. americanus* hybrids) got underway in Europe around 1970 (Addison and Bannister 1994). Spiny lobsters have only recently been successfully cultured (see Kittaka 1994), but in the 1930s Japanese workers attempted to use artificial reefs to create new sites for lobster fishing, and in the 1970s they deployed arrays of large stone beds (5 m × 200 m) to improve recruitment of postlarval *Panulirus japonicus* (Nonaka and Fushimi 1994). Sometime around World War II, Cuban lobster fishers began to deploy shallow roofed structures of about 2 m² on shallow, open substrate to attract and concentrate *P. argus*, a fishing practice so effective that now at least 250,000 of these pesqueros account for half of the Cuban commercial catch—the largest for spiny lobster in the western hemisphere (Cruz and Phillips 1994). Analogous deployment of similar casitas has more recently taken place in eastern Mexico and in the Bahamas (Briones et al. 1994). Although the fishers argue that the structures are also refugia promoting survival of recruits, population-level evidence from which to make a valid determination has not yet been fully reported (Lipcius and Cobb 1994).

Nearly all recent reviewers and researchers have pointed out that most of these projects have yielded no discernable, documented increase in population recruitment. What is scientifically discordant is that the actual implementation of these practices each constituted a large-scale, expensive trial-and-error exercise, not a valid experiment. Researchers typically have had to try to evaluate impacts after the fact rather than initially evaluating important ecological processes or performing feasibility experiments. Instead, what researchers learn about ecological regulating processes emerges from their attempt to understand the effects that an extensive practice has already caused (Addison and Bannister 1994; Briones et al. 1994). It seems unreasonable to criticize the lack of appropriate science in past enhancement attempts before the relatively recent advent (since ~1960) of certain powerful technologies (scuba, microwire tags, telemetry, molecular-genetic identification) and sophisticated field experimental

designs and quantitative statistical methods for ecology. In addition, neither the strong theoretical framework nor the rigorous hypothesis-testing approach of contemporary ecology existed then, but those tools are available now, so we should integrate them into scientifically and economically sound research programs (Cobb 1995).

Our own experience, in retrospect, and lessons learned from other recent workers make a strong case for immediately beginning extensive, rigorous basic research leading to field experiments at an appropriate scale, even if doing so means deferring an important project with a large potential payoff. The answers needed for either a proposed new application or to assess the impact of an ongoing one (shelter rehabilitation, restocking, etc.) must ultimately come from an understanding of the natural mechanisms and processes operating on the focal population and region.

An apparent criticism of the basic-research-first approach is the unknown duration of studies, during which the stock or habitat is not being enhanced, and uncertainty that the knowledge gained will be sufficient. However, historical information shows that years of full-scale, direct applications without solid understanding of natural processes have rarely been successful. Our recruitment research reported here took over a decade to accomplish largely because large-scale experiments necessary for population-level inferences required years to perform and replicate. Our work to understand the dynamics of postlarval delivery and integrate a decade of research findings to develop a predictive individual-based model continues today. In addition, our recognition of the need to scale up each subsequent step was partly serendipitous, so the rate of progress varied. That is, we did not conceive a structured research track from the outset, but others to follow can do better. The important nursery and recruitment studies on western Australian *P. cygnus* took about two decades (1970–1990), but the knowledge gained has served as the framework for what is widely recognized as a model of spiny-lobster fishery management. Yet the time invested in the above projects is not particularly long compared to that for other approaches. For example, Norwegian scientists recently carried out an eight-year program to restock *Homarus gammarus*, involving release of >130,000 small tagged juveniles (van der Meeren 1994) with the aim of eventually replenishing a severely depleted population. However, because postrelease mortality was so extreme and so few were recov-

ered, a three-year intensive ecological study is now underway to assess predation, habitat requirements, and settlement density (Phillips and Evans 1997)—basic questions that emerged early as the focus of the Florida juvenile-recruitment study. Answers about ecological processes will be needed sooner or later, and we recommend seeking that information sooner.

That more intensive and thorough basic research presently is not being done, particularly in the United States, seems to be the result of a production-oriented economic mind-set of the public, commerce, and politicians and the granting agencies they control. Our research has been sponsored largely by the Florida Sea Grant College Program and the Florida Department of Environmental Protection (FDEP), primarily through personnel and logistical support by the Florida Marine Research Institute (FMRI). We view the dynamic cross-linkage between the applied goals and information needs of management and the tenets and research protocols of basic ecology as a central reason for our successes. The collaboration and logistical contributions by the FDEP and FMRI have been essential both to the conduct of the study and, more pragmatically, to meeting granting-agency matching requirements. Although research for fisheries management has been a priority of Sea Grant and some other agencies, such research usually has no immediately specifiable monetary benefit. It is both little valued by fishers or related private enterprise (i.e., “users”) and poorly understood by the general public, so it is difficult to gain popular or special-interest backing and to meet fund-matching requirements. As is the case with most government granting agencies intended to support university-based and other nonagency researchers, funds must be obtained competitively every two years. The short term of such grants and frequent priority shifts to new areas of emphasis create a situation nearly irreconcilable with conducting ecological research on fisheries species. To achieve effective research in fisheries ecology, fishery agencies, as well as granting entities, must put in place programs that promote, foster, and better support closely linked basic and applied collaborative research among scientists in academia and government.

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