

Is seagrass an important nursery habitat for the Caribbean spiny lobster, *Panulirus argus*, in Florida?

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Abstract Caribbean spiny lobster (*Panulirus argus*) settle preferentially in macroalgal-covered hard-bottom habitat, but seagrass is more prevalent in Florida (United States) and the Caribbean, so even low settlement of lobsters within seagrass could contribute substantially to recruitment if post-settlement survival and growth were high. We tested the role of seagrass and hard-bottom habitats

for *P. argus* recruitment in three ways. We first explored possible density-dependent regulation of early benthic juvenile lobster survival within cages deployed in seagrass and hard-bottom habitats. Second, we compared settlement and survival of *P. argus* in both habitats, by comparing the recovery of microwire-tagged early benthic juveniles from patches of seagrass and hard-bottom. Finally, we assessed the relative abundance of juvenile lobsters in each habitat by deploying artificial structures in seagrass sites and compared these data with data from similar deployments of artificial structures in hard-bottom habitat in other years. More early benthic juvenile lobsters were recovered from cages placed in hard-bottom than in seagrass, but mortality of the early benthic life stage was high in both habitats. In regional surveys, the mean number of lobsters recovered from artificial shelters deployed within seagrass was lower than in any year that we sampled hard-bottom, indicating that fewer lobsters reside naturally in seagrass, particularly large juveniles >40 mm carapace length. The greater abundance (and likely survival) of juvenile *P. argus* that we observed in hard-bottom habitat as opposed to seagrass, combined with previous studies demonstrating that postlarval *P. argus* are attracted to, settle in, and metamorphose more quickly in red macroalgae, confirm that macroalgae-dominated hard-bottom habitat appears to be the preferred and more optimal nursery for Caribbean spiny lobster.

Keywords hard-bottom; recruitment; *Thalassia*; *Laurencia*; postlarvae; survival; growth

INTRODUCTION

Hard-bottom habitat intersperses with seagrass meadows throughout much of south Florida and the Caribbean Sea, and together these habitats serve as nurseries and foraging grounds for numerous species of fish and shellfish, including the Caribbean spiny lobster (*Panulirus argus* Latrielle, 1804)—the target of one of the most economically valuable fisheries in

Florida (Hunt 2000) and the Caribbean (Baisre & Cruz 1994; Ehrhardt 1994; FAO 2000). Caribbean spiny lobster postlarvae settle preferentially within red macroalgae, especially *Laurencia* spp. (Marx & Herrnkind 1985; Herrnkind & Butler 1986), drawn there by the odour of the algae (Butler & Herrnkind 1991; Goldstein & Butler unpubl. data). Three to four months after settlement, the early benthic juvenile (EBJ) lobsters leave their vegetated settlement habitat to seek crevice shelters (Butler et al. 2006). Hard-bottom areas replete with red macroalgae are prime nurseries for *P. argus* because they provide both a settlement substrate and habitat for early benthic stage juveniles (i.e., macroalgae), as well as crevice shelters (e.g., sponges, solution holes, corals) used by later juvenile stages (Eggleston et al. 1990; Field & Butler 1994; Forcucci et al. 1994; Herrnkind & Butler 1994; Mintz et al. 1994). However, seagrass is more ubiquitous than macroalgae-covered hard-bottom in many regions of the Caribbean, and it may also provide habitat for settling postlarvae and EBJ lobsters (see Butler et al. 2006) as it does for many other animal species (Heck & Wetstone 1977; Heck & Thoman 1984; Lewis 1984; Stoner & Lewis 1985; Blaber et al. 1992; Adams et al. 2006).

Worldwide, there are about 50 species of seagrasses (den Hartog 1977). Turtle grass, *Thalassia testudinum*, is the most abundant seagrass in the Caribbean, overlapping in its broad distribution with *P. argus* (Littler & Littler 2000). Likewise, three species of seagrass are common in south Florida (turtle grass, *T. testudinum*; manatee grass, *Syringodium filiforme*; and shoal grass, *Halodule wrightii*), but turtle grass is the most abundant in the saline waters of southwestern Florida Bay and the Florida Keys (Fourqurean et al. 1992; Hall et al. 1999; Zieman et al. 1999). Macroalgal-covered hard-bottom is limited to this region of Florida Bay where it covers nearly 30% of the sea floor (Zieman et al. 1989; Herrnkind et al. 1997; Bertelsen et al. 2009, this issue), interspersing with seagrass meadows and carbonate sand and mud bottom. The primary nursery area for spiny lobster in Florida also occurs here (Herrnkind et al. 1997; Robles et al. 2005). Thus, there is a concomitant overlap in the distribution of turtle grass, macroalgae-covered hard-bottom, and juvenile spiny lobsters in this region of south Florida where we examined essential nursery habitat for spiny lobster.

Establishing the contribution of seagrass to spiny lobster recruitment in the Florida Keys is important for several reasons. Seagrass is the most prevalent habitat north of the Florida Keys and in western

Florida Bay (Zieman et al. 1989; Herrnkind 1995), so even relatively low settlement of lobsters within seagrass compared with macroalgae, as predicted from laboratory studies (Herrnkind & Butler 1986), could potentially make a significant contribution to recruitment on a regional scale. Habitat structure in western Florida Bay has been dramatically altered by widespread die-offs of sponges and octocorals (Butler et al. 1995; Herrnkind et al. 1997; Peterson et al. 2006). Persistent cyanobacteria blooms (*Synecococcus* sp.) from 1991 to 1995 resulted in massive die-offs of the sponge community, local declines in macroalgae, and coincident shifts in the abundance and shelter use of juvenile spiny lobster (Butler et al. 1995). Cyanobacteria blooms may also negatively impact macroalgae through shading and competition for dissolved nutrients. Hard-bottom habitat may also be further impacted by the planned return of historical freshwater flow—an aim of the Comprehensive Everglades Restoration Project (United States Army Corp of Engineers & South Florida Water Management District 2002). The implications of these changes for lobster recruitment are not entirely known and are likely to be complex. Lastly, macroalgal abundance on hard-bottom sites, particularly the *Laurencia* spp. red algal complex, is also naturally ephemeral and at times may be insufficient for spiny lobster settlement (Butler et al. 1997). Seasonal abundance in the Middle Keys varies from <10% to over 30%, but does not correspond to postlarval supply, which might create local bottlenecks for lobster settlement (Butler et al. 1997). That is, large numbers of postlarvae may sometimes arrive when there is little algae for settlement. This variability adds a temporal dimension to nursery habitat dynamics wherein the importance of seagrass as a supplementary settlement habitat may vary with algal abundance in hard-bottom.

Understanding the relative value of seagrass and macroalgae-covered hard-bottom as nursery habitats for spiny lobster provides information essential to habitat-based management for this ecologically and economically important species. Designation and protection of “essential fish habitat” is a prominent component of the 1996 Sustainable Fisheries Act that is now law (Public Law 104–297) in United States. Therefore, we compared the relative value of seagrass and macroalgal habitats for recruitment of juvenile spiny lobster in south Florida in three ways. We tested density-dependent survival of newly settled lobsters within cages deployed in seagrass and hard-bottom habitats. We also examined settlement and survival of microwire-tagged EBJ *P. argus* released

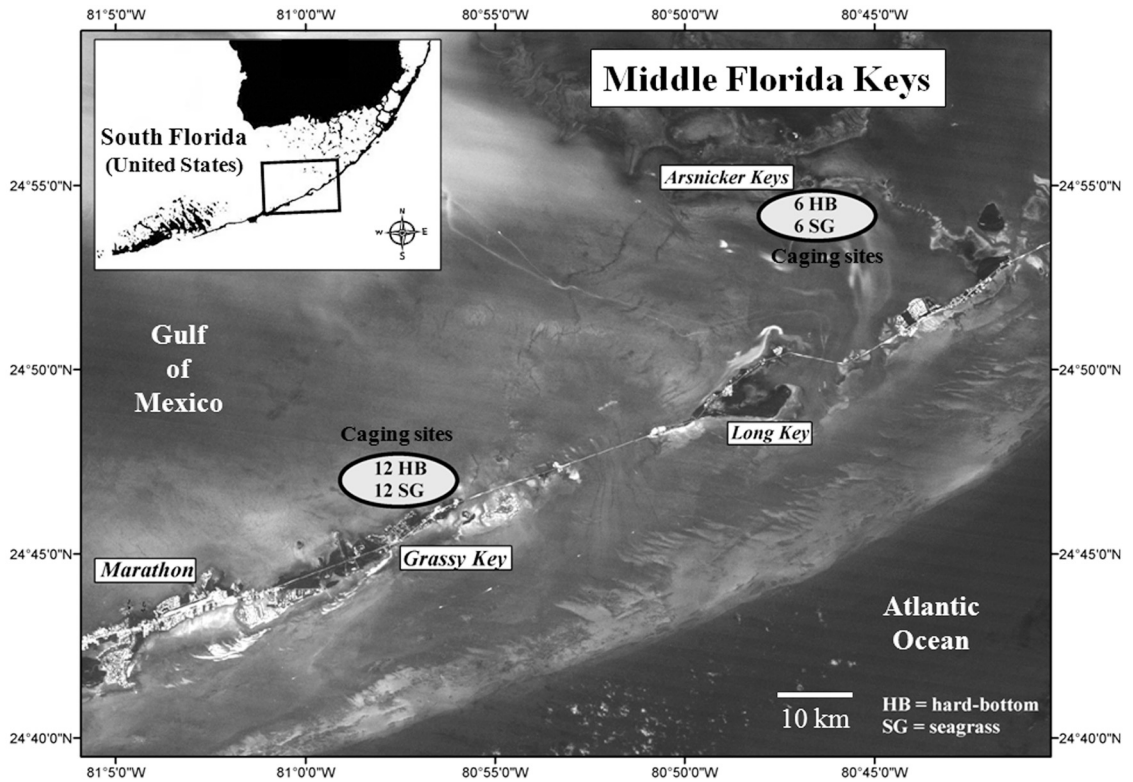


Fig. 1 Region within the Florida Keys (United States) (boxed area) where studies of *P. argus* recruitment into seagrass and hard-bottom habitats were conducted. Small-scale caging studies were conducted within the circled areas, large-scale mark-recapture and regional recruitment studies were conducted throughout the Middle Keys.

in both habitats. Finally, we compared the relative abundance of juvenile lobsters attracted to artificial structures that we deployed at seagrass sites and compared the results with similar data obtained in hard-bottom habitat.

MATERIALS AND METHODS

Small-scale mark-recapture study of recruitment

This part of the study took place north of the Middle Florida Keys in the Gulf of Mexico and western Florida Bay from May to July 1995 (Fig. 1). Sites were established at c. 1.5 m depth in representative seagrass and hard-bottom habitat. We placed one cage at each of six seagrass sites and six hard-bottom sites near Lower Arsnicker Key and 12 seagrass sites and 12 hard-bottom sites near Grassy Key. Cages were spaced at least 10 m apart. In related studies

of predation on tethered juvenile lobsters, Butler et al. (1997) and Acosta & Butler (1999) found that nocturnal predation events were independent for all tethered animals >1 m linear distance. Based on those studies, we believe that the separation of cages 10 times this distance assured their independence.

The cages covered a surface area of 1.0 m² (1.0 m long × 1.0 m wide) and were 40 cm in height. The cage frames were constructed of 2.5 cm diameter PVC with 0.5 cm × 0.5 cm plastic mesh strapped to the frame with cable ties. The tops of the cages were open (to permit access by predators), but 10 cm wide strips of plexiglass fixed at a 45° angle to the top of the PVC frame formed an overhang at the top of the cage that prevented escape of EBJ lobsters from the cage top. To prevent escape of lobsters from the bottom of the cages, the bottoms were sealed to the sea floor using strips of foam and a 10 cm wide plastic mesh skirt buried in the substrate. Predators could freely swim in and out of open-top cages

but it was considered improbable that newly-settled EBJ lobsters could climb the 40 cm mesh wall and then maneuver around the slick plexiglass overhang that capped each wall. Four concrete blocks were attached to the top corners of each cage, which firmly anchored the cages to the bottom. Great care was taken to ensure that the cages were well sealed in both habitats, eliminating any bias in retention. Cages introduce potential artifacts into experiments, but natural estimates of survivorship are difficult to obtain for mobile species that experience high mortality in open, natural systems (Peterson & Black 1994).

After placement of the cages, two different EBJ lobster density treatments (4 lobsters/cage and 14 lobsters/cage) were randomly assigned to the seagrass and hard-bottom cages with three replicates per habitat and treatment. The density of EBJ lobsters chosen was based on estimates of natural settlement obtained from microwire tag-recapture data from 0.1 ha sites (Butler et al. 1997). We estimated that the low-density treatment (4 lobsters/cage) mimicked a high natural settlement density, whereas the high-density treatment (14 lobsters/cage) may only be indicative of extremely high settlement periods, based on postlarval influx monitored on Witham-type collectors (Herrnkind & Butler 1994). Only first- and second-stage EBJ lobsters obtained from Witham-type collectors were used. Lobsters were measured (to the nearest 0.1 mm), weighed (to the nearest 0.01 g), tagged with microwire tags (1.00 mm × 0.25 mm diameter; Northwest Marine Technology, Inc., Washington, United States), and then held overnight to confirm post-tagging survival. We then transported them to the field where divers placed them into cages. Nine replicates of each of the four treatments (high-density hard-bottom, low-density hard-bottom, high density seagrass, and low-density seagrass) were left in the field for 20 days. For logistical reasons, the cages at one site (Grassy Key) were retrieved 30 days after deployment instead of the standard 20 days.

After 20 (or 30) days, divers visually searched each cage for lobsters and removed all substrate material. Macroalgae and small sponge-encrusted rocks were removed from hard-bottom sites, whereas at seagrass sites, seagrass blades and calcareous green algae stalks were cut off at the sediment surface. The above-ground material from each cage was placed in mesh (0.1 cm × 0.1 cm mesh size) bags, and transported to a vessel where it was subsequently sorted to recover lobsters. We then returned to each cage, visually searched for lobsters again, and then swept each cage twice with small mesh (0.1 cm

× 0.1 cm mesh) hand nets. This method has been used successfully in the past to document habitat use by this same size class of juveniles (Marx & Herrnkind 1985). Lobsters that were recovered were measured, weighed, and evaluated for the presence of a microwire tag to distinguish natural settlers from those that were experimentally placed into the cages. Differences in the recovery (i.e., survival) of EBJs between habitats or stocking densities were analysed using a 2-way model I ANOVA (habitat × density) (Zar 1999). Before applying ANOVA, we evaluated the difference in the number of lobsters recovered between different durations using a *t* test (Zar 1999) and found no significant difference between cages left in the field for 20 or 30 days ($t = -0.569$, d.f. = 34, $P > 0.573$). Statistical tests were performed using JMP™ software v.5 and significance determined at $\alpha = 0.05$.

Large-scale mark-recapture study of recruitment

We selected four seagrass-covered sites and four macroalgae-covered hard-bottom sites within a 300 km² region immediately north of the Middle Keys for a large-scale mark-recapture study. The sites were each approximately 25 m in diameter (c. 491 m²) and isolated by open sand, and selected to represent a range of seagrass and macroalgal densities characteristic of the region.

Once each month for 7 months (beginning in March 1997), we introduced microwire-tagged first- and second-stage EBJ lobsters directly into vegetation within 10 m of the centre of all sites. Newly settled postlarvae were collected from arrays of Witham collectors placed near shore on the Atlantic Ocean side of Long Key, Florida and allowed to metamorphose to the juvenile phase in large continuous-flow seawater tables before we tagged them. We tagged 1335 juveniles, held them for 24 h (during which time nearly all handling mortality occurred), and then transported them to the field sites where they were released. We released between 149 and 188 tagged EBJ lobsters per site over the 7-month period.

Seven months after the last introduction of tagged lobsters (April 1998), allowing time for the juveniles to reach the postalgal, crevice-dwelling stage, we deployed 12 artificial juvenile lobster shelters (double-stacked three-hole concrete partition blocks 20 cm × 40 cm × 10 cm) haphazardly, 3–4 m apart throughout each site. This type of shelter attracts the full size range of postalgal juveniles (15–40 mm carapace length, CL) equally as well as natural

structures (Butler & Herrnkind 1997). The shelters were left for 3 weeks and then searched to recover juveniles. Because the shelters were only briefly at each site, they served as “passive collectors” of juvenile lobsters. We also sampled the seagrass and hard-bottom sites to recover any lobsters not dwelling in the artificial shelters. At hard-bottom sites, we searched for crevice-dwelling juveniles in natural shelters by searching all structures at each 500 m² site. At seagrass sites, pairs of divers repeatedly traversed the seagrass patch while holding the ends of 2 m PVC poles with which they gently bumped the substrate to frighten juvenile lobsters from the seagrass.

Upon capture, each juvenile lobster was scanned with a magnetic detector to distinguish those tagged and added by us from those of the same size (age) cohort that had settled naturally. The number of recaptured, tagged lobsters out of the total that had been added provided an estimate of post-settlement mortality, assuming no emigration from the site and recovery of all marked lobsters present. Only lobsters <35 mm CL were included in this evaluation because based on estimated growth rates from this region (Forcucci et al. 1994; Sharp et al. 2000), lobsters of this size probably settled within the previous 6–7 months and are likely to have remained nearby their site of settlement (Butler & Herrnkind 1997).

Field surveys of regional recruitment

To provide a broader geographical component to our assessment of seagrass as a nursery habitat for *P. argus* in Florida Keys, we surveyed juvenile lobster abundance in artificial structures (as described above) that we deployed in seagrass meadows in June–July 1997 at 16 sites spread over an area of approximately 500 km² in Middle Florida Keys. Seagrass sampling sites were selected by stratified random sampling to ensure regional coverage of the area north of the Middle Keys from the western end of Marathon to the eastern end of Long Key (Fig. 1). We assessed lobster population structure (i.e., abundance and size structure) at each seagrass site once, 3 weeks after deploying 12 artificial shelters at each site using the same methods as above. Captured juveniles <40 mm CL provided a relative indication of successful settlement and survival over the past c. 8 months. That is, juveniles up to 40 mm CL (approximately 8 months post-settlement) typically do not wander far from their settling location, probably less than 100 m (Butler & Herrnkind 1997).

Data on lobster recruitment in seagrass habitat were compared with similar data obtained from 18

hard-bottom sites (6 sites in 1996, 12 sites in 1998) studied in the same season (June–July) and same region. As at the seagrass sites, artificial shelters were added to the hard-bottom sites and lobster population structure determined approximately 3 weeks later. The number of shelters used per hard-bottom site varied slightly, therefore lobster abundance was scaled per shelter (i.e., number of lobsters/shelter). For logistical reasons, the data for the regional comparison of lobster recruitment in seagrass and hard-bottom were not collected at the same time; seagrass data were collected in 1997, whereas hard-bottom data were collected in 1996 and 1998. We chose to bracket the seagrass data collection year to minimise the effect of recruitment variability on the intra-year comparison. For this reason and because macroalgae-covered hard-bottom is considered the preferred nursery habitat for *P. argus*, we analysed these data using one-sample *t* tests (Zar 1999) to determine whether the number of lobsters/structure or the CL of lobsters collected on seagrass sites differed from expected values obtained from the hard-bottom sites ($\alpha = 0.05$).

RESULTS

Small-scale mark-recapture study of recruitment

Of the 162 microwire-tagged EBJ lobsters released in cages in both hard-bottom and seagrass habitats (total released = 324), 28 were recaptured from the hard-bottom cages compared with 14 in the seagrass cages; no unmarked lobsters or carcasses were recovered. The mean number of surviving EBJ lobsters within hard-bottom habitat (1.6 ± 1.4 SD) was double that within seagrass (0.78 ± 0.94 SD); but the 2-way model I ANOVA had low power ($1 - \beta < 0.40$) to detect differences of this magnitude. There was no significant effect of lobster density or any of the interactions on EBJ survival (Table 1; Fig. 2A). Owing to logistical constraints, not all lobsters recovered could be weighed and measured. As a result, insufficient numbers of lobster were recovered from the treatments for which weight and length were recorded to permit a reliable statistical analysis. However, lobsters seeded into hard-bottom habitat at either low or high density gained more weight than those in seagrass habitat (Fig. 2B). Changes in length were not as great, probably because of the short duration of the study and the incremental nature of arthropod growth through moulting.

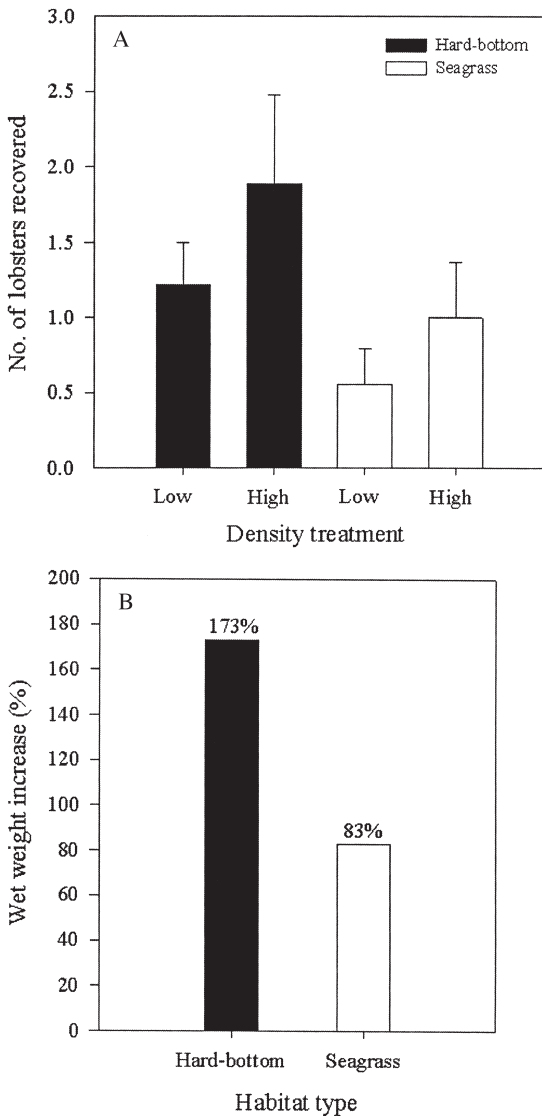


Fig. 2 Comparison of **A**, survival (mean number of post-larval lobsters recovered, \pm SD) and **B**, growth (wet weight increase) of first- and second-stage early benthic juvenile lobsters caged in hard-bottom and seagrass habitats. (Error bars not included in B because of insufficient replication.)

Table 1 Results of 2-way model ANOVA examining the effects of habitat type and postlarval lobster density on lobster survival/recovery.

Source	d.f.	SS	F	P
Habitat	1	5.44	3.909	0.057
Density	1	2.78	1.990	0.168
Habitat \times Density	1	0.11	0.080	0.778
Error	32	44.67		
Corrected total	35	53.00		

Large-scale mark-recapture study of recruitment

Only 1 of 668 tagged lobsters was recovered from the hard-bottom sites, compared with 4 of 667 recovered from seagrass sites. This extremely low recapture success (<1%), reflecting the high mortality experienced by recently settled, non-migratory juveniles, precluded any formal mark-recapture analysis or reliable comparison of survival between the habitats. However, comparing the mean number of similar-sized, tagged and untagged juvenile lobsters captured with the number of tagged numbers released at the sites provided an estimate of natural settlement of 2.2 postlarvae/m² settling per month. This estimate is based on the assumption that lobsters settling naturally on the sites survive and grow at rates similar to tagged lobsters (Sharp et al. 2000).

Field surveys of regional recruitment

No lobsters were found within artificial shelters at nine of the 16 seagrass sites that we sampled 3 weeks after deploying the structures. Moreover, juvenile lobsters were significantly less abundant ($t = 5.50$, d.f. = 15, $P < 0.0005$) and smaller ($t = 3.63$, d.f. = 6, $P < 0.012$) at seagrass than at hard-bottom sites (Fig. 3). More than 90% of lobsters collected in seagrass habitat were <40 mm CL (Fig. 4), whereas those collected at hard-bottom sites represented a broader range of sizes (Fig. 4).

DISCUSSION

Seagrass appeared to be an inferior settlement habitat for *P. argus* in Florida compared with macroalgal-dominated hard-bottom. The caging study showed that survival of EBJ lobsters was probably greater in hard-bottom than in seagrass, as it may have been for growth. However, this study demonstrated that mortality was extremely high for lobsters in the initial months following settlement regardless of habitat type, and the poor recovery of EBJ lobsters diminished the power of statistical tests. The regional surveys of recruitment also revealed that lobsters were larger and more abundant in hard-bottom than those found in seagrass habitat, and were distributed across a broader range of size classes. The capacity for hard-bottom to support more and larger lobsters suggests that it remains a superior habitat after lobsters grow from the asocial, vegetation-dwelling stage to the larger social crevice-dwelling stage. These results support the conclusion that macroalgae-

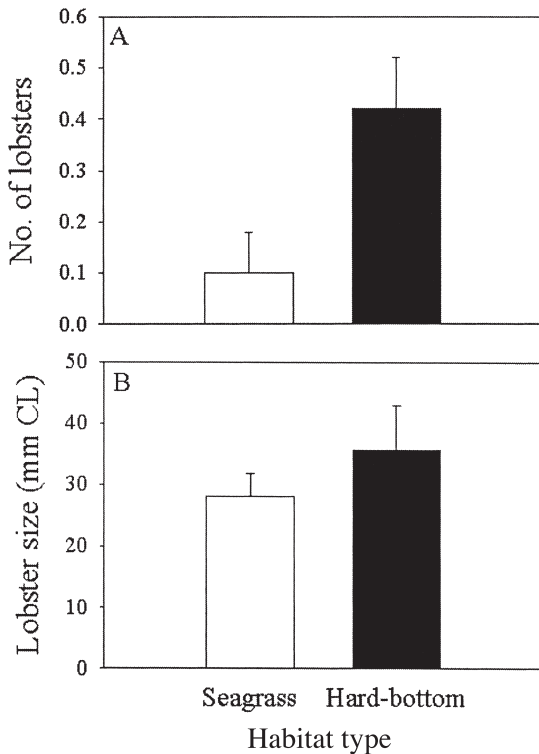


Fig. 3 Comparison of regional recruitment of juvenile lobsters captured in June–July from artificial structures placed in seagrass (1997) and hard-bottom habitat (1996 and 1998). **A**, number of lobsters (mean + 1 SD) captured per artificial structure, **B**, size (carapace length; mean + SD) of lobsters captured in each habitat.

covered hard-bottom is superior to seagrass as a nursery habitat for *P. argus*. Yet, settlement of lobsters in seagrass probably supplements that in hard-bottom habitat and may be especially important in areas where hard-bottom is unavailable or of poor quality for lobster settlement (i.e., low red macroalgal cover).

Regardless of the methods used to compare juvenile lobster mortality among habitats (e.g., caging, mark-recapture, tethering), previous studies have revealed the same result, that survival of benthic juvenile lobsters is exceedingly rare (reviewed in Butler et al. 2006). Intense predation on early benthic stages of many fish and invertebrates is commonly viewed as a bottleneck to recruitment (Menge & Sutherland 1987; Moksnes et al. 1998; Heck et al. 2001; Lee et al. 2006), which can obscure the potential impact of episodic larval supply by

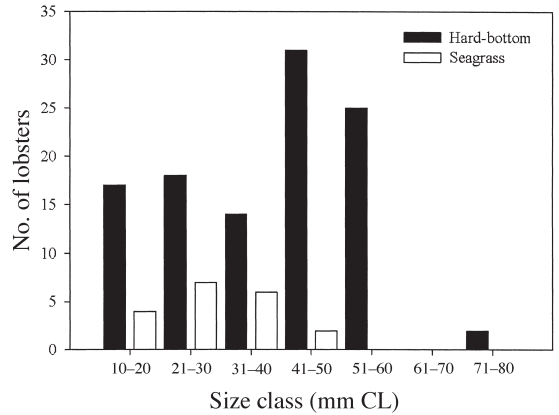


Fig. 4 Size (carapace length, CL) frequency distribution of lobsters captured within seagrass ($n = 19$) and hard-bottom habitats ($n = 107$) during the surveys of regional recruitment.

rapidly eliminating additional individuals (Wahle & Steneck 1991; Eggleston & Armstrong 1995; Pile et al. 1996; Butler & Herrnkind 1997; Heck et al. 2001). Density-dependent predation can act rapidly in decapod crustaceans, typically within 2–14 days (Eggleston & Armstrong 1995; Heck et al. 2001). Thus, the duration of the caging experiment (20–30 days), afforded sufficient time for predators to eliminate the influence of the high-density treatment on recruitment.

Despite high mortality, EBJ lobsters seeded into macroalgae within cages placed in hard-bottom habitat appeared to have a greater chance of survival compared with those added to cages placed in seagrass. Past studies have documented not only the preference of EBJ *P. argus* for macroalgae, but also a survival advantage conferred on those settling in macroalgae (Herrnkind & Butler 1986; Butler et al. 1997; Acosta & Butler 1999). Although the poor recovery of tagged lobsters in the large-scale mark-recapture study prevented reliable estimation of natural mortality in seagrass and hard-bottom habitats, the observed magnitude of EBJ loss is not unprecedented. Previous mark-recapture studies of microwire tagged EBJ *P. argus* in the Florida Keys produced estimates of natural mortality from settlement to 3–4 months post-settlement at 94–98% (Butler et al. 1997; Sharp et al. 2000). Mortality of the subsequent crevice-dwelling postlarval stage may be as high as 20% per month based on mark-recapture studies (Forcucci et al. 1994). Daily estimates of mortality from tethering studies of juvenile lobsters range from 20 to 30% in hard-bottom and 80 to

100% in unvegetated open substratum (Smith & Herrnkind 1992; Childress & Herrnkind 1994; Mintz et al. 1994). The poor natural survival of young lobsters, especially in seagrass, is of concern for stock-enhancement efforts, which have been and continue to be explored given the high market value of this species.

Predation has long been assumed to be the primary source of the rapid post-settlement mortality of EBJ lobsters; however, disease may also play a role in this species. A lethal virus (PaV1) infects juvenile *P. argus* in the Florida Keys and elsewhere in the Caribbean (Shields & Behringer 2004; Huchin-Mian et al. 2008) with a mean prevalence among EBJ lobsters in Florida of 16% and local hot spots of prevalence exceeding 35% (Shields & Behringer 2004). Among larger juveniles, the prevalence of PaV1 diminishes and is unrelated to population density (Butler et al. 2008), so mortality owing to this pathogen centres on the asocial EBJs where its relationship to population density—thus its role as a source of density-dependent mortality—is unknown.

In addition to survival, the growth of juvenile *P. argus* may also be compromised in seagrass habitat. Although too few to provide conclusive results, the tagged lobsters that survived and were recaptured in hard-bottom habitat gained more than twice the weight of those we recovered in seagrass. It appears that small prey such as crustaceans, gastropods, and echinoderms that inhabit bushy macroalgae (e.g., *Laurencia* spp.) and upon which EBJ lobsters prey, provide a nearly limitless food supply for EBJ (Marx & Herrnkind 1985; Herrnkind et al. 1988). Similarly, food for larger juveniles dwelling in hard-bottom appears plentiful because the growth and nutritional condition of larger crevice-dwelling lobsters are unaffected by lobster density (Behringer & Butler 2006a), and lobsters have little measurable impact on infaunal prey abundance (Nizinski 2007). Stable-isotope analysis of juvenile lobster tissue relative to potential sources of energy in Florida Bay also indicates an association between lobsters and macroalgae, not seagrass (Behringer & Butler 2006b).

Seagrass also did not appear to support the full size-range of juvenile lobsters nor did it provide shelter to lobsters >40 mm CL. Only one lobster >40 mm CL was captured within seagrass habitat during our study. Lobsters that settle within seagrass probably relocate to adjacent crevice-bearing habitats (e.g., hard-bottom areas, mangrove prop roots, rubble zones, coral reefs, edges of seagrass “blow-outs”) once they grow large and become social. Dispersal of

small, solitary juveniles among habitats is hazardous, but once in adjacent shelter-rich habitats, the risk of predation is ameliorated not only by shelter, but also by the presence of conspecifics that provide odour cues for locating shelter (Childress & Herrnkind 1997, 2001; Ratchford & Eggleston 1998, 2000; Butler et al. 1999) and enhance survival through group defense (Butler et al. 1999; Dolan & Butler 2006). However, the degree to which juvenile lobsters disperse from seagrass relative to other habitats is unknown.

Combined, these studies provide evidence of the importance of macroalgae-covered hard-bottom habitat as essential nursery habitat for lobsters in Florida. However, our results also show that seagrass habitat is used by some *P. argus* (<40 mm CL), and thus, can augment hard-bottom habitat when the latter is unavailable. Juvenile *P. argus* have been found in seagrass meadows, mangrove prop roots, in artificial structures, and even among the spines of sea urchins (Davis 1971; Herrnkind & Butler 1986; Holmquist et al. 1989; Acosta & Butler 1997), but these habitats are not their preferred settlement habitat. The estimate of natural settlement from this study (2.2 postlarvae/m²) is comparable to previous counts of postlarvae settling into clumps of macroalgae deployed in arrays on the seafloor (Herrnkind & Butler 1994), but much higher than estimates of settlement derived from counts of postlarvae recovered from macroalgae collected directly from the seafloor (Marx & Herrnkind 1985). Laboratory experiments confirm the attraction of *P. argus* pueruli and EBJs to red macroalgae (Herrnkind & Butler 1986; Herrnkind et al. 1988; Butler & Herrnkind 1991; Butler et al. 1997; Goldstein 2006), whereas this study and others indicate that survival and perhaps growth of juvenile *P. argus* is higher in hard-bottom habitat.

However, the abundance of seagrass meadows with the absence of macroalgae dominated hard-bottom habitat in many areas of the Caribbean, suggests that seagrass nurtures considerable numbers of new recruits in these areas where it is an important nursery habitat for *P. argus* (Acosta & Butler 1997; Acosta 1999) and other species that preferentially recruit into macroalgae such as the Nassau grouper, *Epinephelus striatus* (Dahlgren & Eggleston 2001). At these locations, seagrass may be critical in sustaining juvenile populations and recruitment to adult lobster fisheries. Yet, wherever shallow hard-bottom habitat is reasonably abundant and replete with bushy red macroalgae and crevice-bearing shelters, its contribution to the local recruitment of

P. argus may be substantially higher than seagrass habitat.

ACKNOWLEDGMENTS

This research was supported by Florida Sea Grant award R/LR-B44 (W.F. Herrnkind & M.J. Butler) and Florida Department of Environmental Protection Florida Marine Research Institute contract MR-068 (W.F. Herrnkind) and 37202010006EOD1 (M.J. Butler). The authors thank the following people for their assistance during this project: Dianne Behringer, Rodney Bertelsen, Carolyn Cox, Thomas Matthews, Denice Robertson, Jason Schratwieser, and the entire staff of the Keys Marine Laboratory.

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