ELSEVIER

Journal of Experimental Marine Biology and Ecology 334 (2006) 84 – 95

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

Density-dependent population dynamics in juvenile *Panulirus argus* (Latreille): The impact of artificial density enhancement

Donald C. Behringer, Mark J. Butler IV *

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

Received 22 October 2004; received in revised form 9 January 2006; accepted 10 January 2006

Abstract

The use of artificial structures to enhance marine animal populations, or as an aid to fishing, is widespread and increasing. While most investigators have studied the efficacy of artificial structure by measuring population abundance of the target species, or by comparison of the resulting community structure with that of natural communities, the effect of habitat enhancement on the processes creating such patterns is largely unknown. We enhanced density with the addition of artificial structures to examine the effect of local population density on the population dynamics (e.g., movement, mortality, and nutritional condition) of juvenile Caribbean spiny lobster (*Panulirus argus*) at natural and habitat-manipulated sites in the Florida Keys (USA). We artificially enhanced lobster density using small, scattered crevice-bearing structures that mimicked the natural shelters sought by juvenile lobsters. Enhanced density had no measurable effect on juvenile lobster mortality from predation or nutritional condition (as measured by hemolymph refractive index), but it increased the short-term residency of juvenile lobsters. The gregarious nature of spiny lobsters coupled with access to abundant prey may make them robust to high population density.

Keywords: Artificial habitat; Density dependence; Disease; Enhancement; Growth; Lobster; Movement; Nutrition

1. Introduction

Lobsters, both spiny and clawed, often rely on crevice shelters for refuge (Wahle and Steneck, 1991; Herrnkind and Butler, 1986; Smith and Herrnkind, 1992; Herrnkind et al., 1994; Polovina et al., 1995; Butler and Herrnkind, 1997a,b), a dependence demonstrated to limit juvenile spiny lobster populations (Butler and Herrnkind, 1997a, b; Herrnkind et al., 1997a,b). The availability of appropriately sized crevice shelters (Eggleston et al., 1990; Eggleston and Lipcius, 1992; Mintz et al., 1994) can be a “bottleneck” to future adult population size (Wahle and Steneck, 1991; Butler and Herrnkind, 1997a, b; Herrnkind et al., 1997a) and shelter-mediated recruitment bottlenecks are not unique to lobsters. Adult stone crab (*Menippe mercenaria* Say) abundance, individual size, and fecundity have all been linked to the availability of appropriately sized shelters (Beck, 1995, 1997), as has the abundance of gonodactylid stomatopods (Steger, 1987). These and other studies have demonstrated that augmentation of the natural habitat with appropriately placed and sized structures can increase the local abundance of shelter-limited species through greater survival (see Beck, 1997 for review).

Although enhancing natural habitat by artificial means may alleviate certain demographic bottlenecks

---

* Corresponding author. Tel.: +1 757 683 3595; fax: +1 757 683 5283.

E-mail address: mbutler@odu.edu (M.J. Butler).

0022-0981/$ - see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.jembe.2006.01.009

that limit local population abundance, it may also create conflicting bottlenecks. High local densities may result in density-dependent depression of growth, increased emigration, or more rapid spread of disease. Decapod crustaceans held in artificial laboratory conditions exhibit both positive (Jorstadt et al., 2001) and negative (Booth and Kittaka, 2000; James et al., 2001) density-dependent growth and survival. However, there are few experimental studies of density-dependent impacts among decapods in the field. Wahle et al. (2001) found that the growth of American clawed lobster (*Homarus americanus* H. Milne-Edwards) was depressed at high stocking densities in field enclosures, although the mechanism producing the result (including a possible caging artifact) was unknown. Dungeness crabs, *Cancer magister* Dana, emigrate at higher rates when at high experimental field densities (Iribarne et al., 1994). When densities of juvenile Western Australian rock lobster (*Panulirus cygnus* George) were experimentally decreased on several patch reefs, emigration declined compared to reefs where the social spiny lobsters dwelled at naturally high density (Ford et al., 1988).

The paucity of data regarding density-dependent growth, movement, and disease prevalence extends to situations where populations are enhanced via supplementation of habitat. This is particularly relevant to spiny lobsters that support highly valued fisheries in which artificial habitat enhancement is seeing increased use. Research on the artificial enhancement of habitat for marine fisheries typically focuses on habitat design (Briones-Fourzán et al., 2000; Cruz and Phillips, 2000; Sosa-Cordero et al., 1998; Nedimyer et al., 2001; Seaman, 2000; Losada-Torteson and Posada, 2001; Sherman et al., 2001a), the proper size and number of habitats (Seaman, 2000; Sherman et al., 2001a), the location of habitats (Sosa-Cordero et al., 1998; Sherman et al., 2001b) and the success of an artificial habitat in maintaining population abundance or improving exploitation efficiency (Cruz et al., 1986; Tangley, 1987; Coen and Luckenbach, 2000; Seaman, 2000; Losada-Torteson and Posada, 2001). In evaluating the usefulness of artificial structures, most investigators have studied the efficacy of artificial enhancement by measuring population abundance of the target species or by comparing species richness and diversity of communities recruiting to artificial structures in relation to unmanipulated natural regions, (e.g., Bohnsack et al., 1994; Lazano-Alvarez et al., 1994; Stanley and Wilson, 2000; Briones-Fourzán and Lozano-Alvarez, 2001). Appropriately controlled fields experiments examining the role of artificially enhanced local density on spiny lobster population processes (e.g., growth, movement, disease, etc.) have not been performed. This was our objective. We used artificial structures designed to mimic the shelter characteristics and spatial distribution of natural crevices to experimentally compare the effects of artificially enhanced and naturally varying differences in density on the population dynamics of Caribbean spiny lobster (*Panulirus argus*) in the Florida Keys (USA).

2. Materials and methods

2.1. Dietary intake influence on nutritional condition

We used the refractive index of raw hemolymph as an indication of serum protein level and thus the general nutritional condition of lobsters collected at field sites where lobster population density varied. This technique was initially described for *Jasus edwardsii* Hutton (Musgrove, 2001). Others (Stewart et al., 1967; Oliver and MacDairmid, 2001) have shown that blood serum protein is a reliable indicator of physiological condition in American lobster (*H. americanus*) and juvenile Rock Lobsters (*J. edwardsii*). Serum protein levels vary with molt stage (Smith and Dall, 1982; Depledge and Bjerregaard, 1989), so we assessed individual molt stage from microscopic examination of a pleopod (Aiken, 1973; Lyle and MacDonald, 1983) whenever we tested serum blood protein.

To determine if the serum protein and hemolymph refractive index technique was applicable for assessing nutritional condition in *P. argus*, we designed a laboratory study similar to that used by Oliver and MacDairmid (2001). In June of 1999, we captured 40 lobsters (35–50 mm carapace length; CL) from various locations in the Florida Keys and held them individually in floating baskets in a flow-through seawater system at ambient temperature (25–28 °C) and photoperiod (approximately 14-h light; 10-h dark) for 6 weeks. Lobsters were initially fed a pre-weighed diet of shrimp and squid ad libitum. Any food remaining after 4 h was re-weighed to determine their mean maximum daily consumption. For the remainder of the study, 20 lobsters were fed a diet at 25% of this empirically determined maximum and 20 were fed at 100% of the maximum. Hemolymph refractive index was measured for each lobster at the initiation and termination of the experiment. We used a 25-gauge tuberculin syringe to draw 0.1 to 0.2 ml of hemolymph from the pericardial sinus of the lobster and delivered this to a Leica hand-held industrial refractometer, read to within 0.5 units. The refractive index value was then compared to a standard curve developed using bovine albumin to determine the serum protein level (Musgrove, 2001). Hemolymph refractive index was converted to serum protein using the equation: $y = -0.139 + 1.203x$. To confirm that altering the feeding levels of the lobsters affected their condition, the carapace length and wet weight were also measured upon initiation and termination of the experiment. Whenever we sampled hemolymph, we also used microscopic examination of pleopod setal retraction to determine the molt stage of each lobster (Aiken, 1973; Lyle and MacDonald, 1983).

A 1-factor MANOVA was performed on the data from the laboratory nutritional condition experiment to determine whether food treatment (25% and 100% daily ration) significantly influenced hemolymph refractive index values once molt stage (covariate) was included in the analysis. The after/before ratios for the dependent variables were used for analysis because there were only two sampling periods. We omitted molt stage as a possible covariate in this analysis because it did not explain a significant proportion of the variance in condition, in contrast to some previous studies (Musgrove, 2001). This presumably occurred because of little variation among individuals in molt stage when the refractive index measurements were taken. The raw after/before measurements of the hemolymph refractive index and weight/CL ratio data met the assumptions of the MANOVA test.

2.2. Impact of artificially enhanced density on juvenile lobster population dynamics

The effect of increased population density on juvenile *P. argus* population dynamics was investigated at a series of lobster nursery sites north of the Middle Keys, Florida (Fig. 1). A total of 4 mark-recapture surveys were conducted during June–August 1999, June–August 2000, January–March 2001, and June–August 2001. Hard-bottom is the preferred habitat of juvenile spiny lobsters in the Florida Keys. It is characterized by open patches of sediment-covered calcareous rock and stands of bushy, red macroalgaes (primarily *Laurencia* spp.). Sponges, octocorals, and scleractinian corals are the most conspicuous sessile fauna found in hard-bottom and, in conjunction with crevices in the substrate itself, these structures provide the majority of shelter for juvenile lobsters (Butler et al., 1995; Herrnkind et al., 1997a). This study focused on juvenile lobsters 18–60 mm CL that have ontogenetically shifted from an asocial macroalgal-dwelling settlement stage to a social crevice-dwelling stage (Childress and Herrnkind, 1996), but have not yet reached sexual maturity (~76 mm CL). Sites were selected haphazardly from areas of hard-bottom known to harbor juvenile lobsters. Prior to the assignment of treatments, all sites were surveyed to determine the natural abundance of lobsters. One of three types of treatments

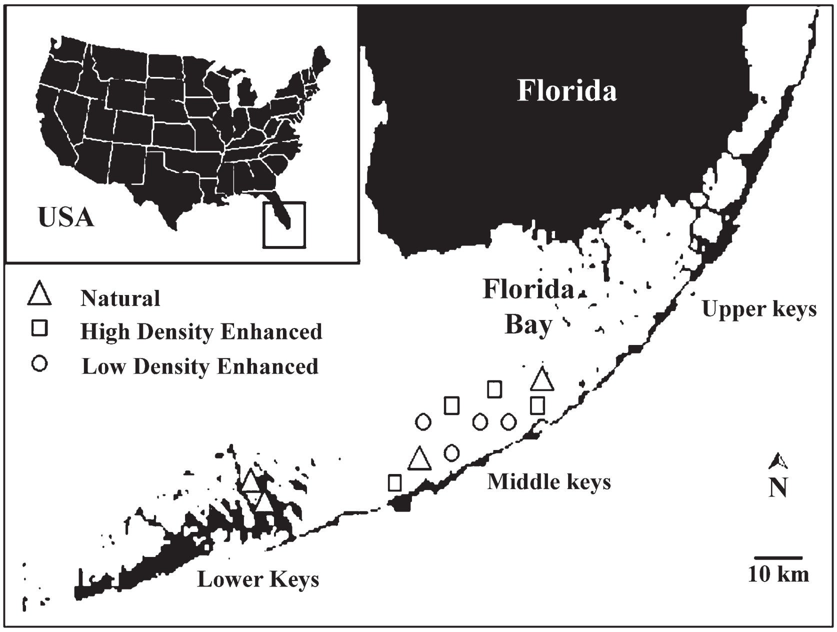

Fig. 1. Field site locations. Open shapes represent the three treatment types at field site locations north of the Middle Keys, Florida (USA).

were randomly applied and were based on the abundance and types of crevice-bearing structures that were present: (a) unmanipulated "natural" (NAT) sites, (b) "low density manipulated" (LOW) sites into which 12–18 artificial structures were added, and (c) "high density manipulated" (HIGH) sites to which 45–50 artificial shelters were added ($n = 4$ per treatment). The LOW and HIGH sites originally received 18 and 50 blocks, respectively, but due to storms, sediment deposition, or commercial fishing activities a few blocks at some sites were lost. Sites were 25 m × 25 m plots (0.0625 ha) of hard-bottom delineated with weighted polypropylene line. Each artificial structure that was placed on the manipulated sites consisted of a double-stacked concrete partition block (40 cm × 20 cm × 10 cm) with three oval holes (10 cm × 4 cm) that approximated the overall size and crevice dimensions of natural shelters. Previous studies (Butler and Herrnkind, 1997a,b) have shown that these structures attract similar sizes and numbers of juvenile lobsters as natural shelters.

Sites were all allowed 1 month for the concrete blocks to "condition" prior to the onset of the first survey. Sites were surveyed by divers who captured, measured (carapace length, CL), and marked with a uniquely coded antenna tag all lobsters encountered within the delineated site. These data were recorded underwater and the lobsters were then returned to their den. After the initial survey and marking episode, each site was re-surveyed 5 days later. During the second census all lobsters were collected and brought back to the laboratory, where we recorded their size, molt stage (as described in Lyle and MacDonald, 1983), wet weight, and hemolymph refractive index. Animals were later returned to the sites from which they were collected. The proportion of marked lobsters that remained on the site also provided an estimate of short-term residency.

On each site we also characterized the general structure of the natural habitat to account for potential among-site differences in natural shelter abundance and macroalgal bottom coverage on lobster density and movement. We established four non-overlapping haphazardly placed 2 m × 25 m belt transects within each site and divers recorded the number of structures found within each transect. Structures included any object >20 cm in diameter and judged to be capable of sheltering a juvenile lobster (e.g., sponges, corals, octocorals, holes, etc.). Macroalgal (*Laurencia* spp.) benthic cover was also estimated along each transect using a point-intercept method.

A 3 × 2 (treatment × sampling date) repeated-measures MANOVA followed by post hoc Tukey's HSD multiple comparison tests of the univariate results was used to determine if nutritional condition, residency, or lobster density were affected by the shelter manipulation treatments. Habitat covariates (i.e., the density of natural structures and macroalgal percent cover) did

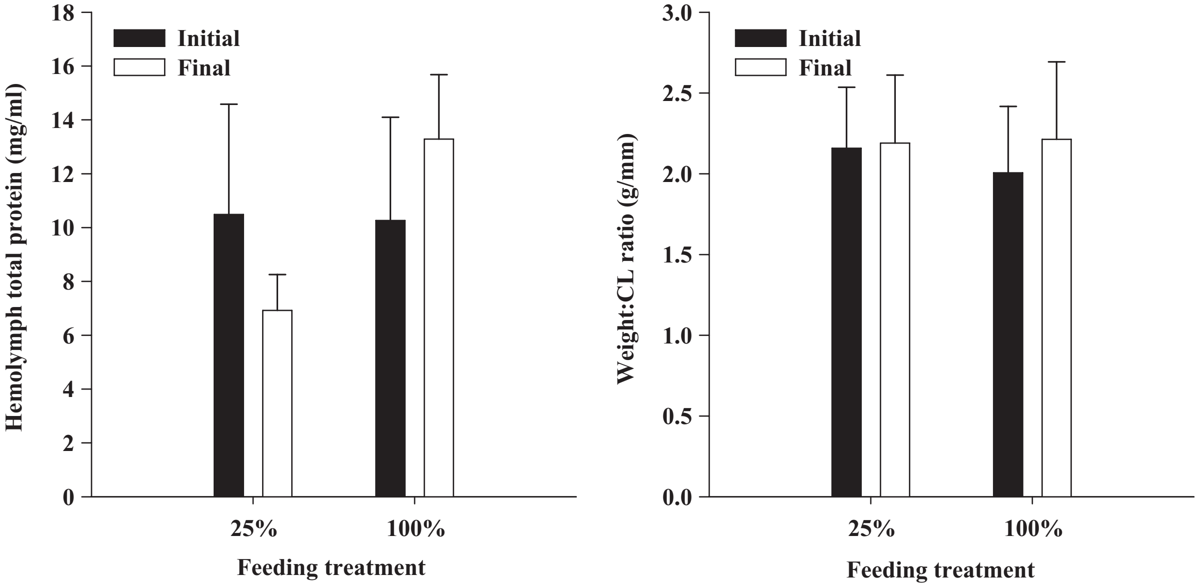

Fig. 2. Results of the dietary impact study comparing, on the left; hemolymph serum protein (mg/ml) and on the right; the weight/CL (g/mm) ratio for lobsters measured at the start of the study and after 6 weeks of feeding at 25% and 100% of their maximum daily consumption. Error bars represent 1 S.D.

not explain a significant amount of the variation in nutritional condition, residency, or juvenile lobster density, so they were therefore removed from the analysis. We were unable to use the summer 1999 and summer 2000 survey periods in the analysis because inclement weather precluded our sampling of all sites, resulting in unequal site replication during those two periods. Multivariate analyses do not handle unbalanced designs well, so we elected to narrow our analysis to the two sample periods with adequate replication of treatments so as to focus our evaluation on treatment effects rather than the effects of survey period.

Two multiple regression analyses were used to determine if nutritional condition (i.e., mean hemolymph refractive index) or short-term residency (i.e., proportion recaptured after 5 days) could be predicted by a combination of mean lobster density, habitat structure, or macroalgal coverage. The data from each survey were analyzed separately to avoid pseudoreplication (sensu Hurlbert, 1984). The data for large (>30 mm CL) and small (<30 mm CL) juveniles were also analyzed separately because of ontogenetic changes in juvenile behavior, habitat use, and morphology that may influence population dynamics (see Butler and Herrnkind, 2000 for review). All assumptions for multiple regression analysis were met using the raw data.

We also recognized that differences in predation intensity among sites could have affected our interpretation of the mark-recapture data, in particular, our use of residency on a site as a proxy for emigration/immigration dynamics. To account for potential differences in relative predation among sites, we collected 10 juvenile lobsters from a non-experimental location and then tagged, measured, and tethered them at each of our study sites. Lobsters were tethered to a concrete brick via a 20-cm-long strand of 4.6 kg test monofilament attached to their tail with a fishing swivel and a cable tie. Tethered lobsters were then distributed haphazardly around each site at least 2 m apart. After 2 days the number of surviving lobsters was recorded. The tethering procedure was repeated twice for each site for a total of 20 tethering observations per site. This method yields an estimate of relative predation pressure (Herrnkind and Butler, 1986; Eggleston et al., 1990, 1992; Pile et al., 1996) among sites. Tethering information (i.e., proportion of lobsters killed per site) was compared among sites to account for potential losses in the local lobster population that were due to predation, as compared to those that may have emigrated from the site. The lobster tethering data were analyzed with a three-way contingency table analysis (survey date × number surviving × site).

3. Results

3.1. Dietary intake influence on nutritional condition

Our laboratory experiments confirmed that serum protein, as reflected in the hemolymph refractive index, was a good general indicator of nutritional condition. Lobsters fed 100% of their daily intake had consistently higher serum protein values and weight/CL ratios after 6 weeks than those fed 25% of their daily intake (Fig. 2, Table 1). These results confirm that hemolymph refractive is a good indicator of nutritional condition in juvenile *P. argus*; hereafter we refer to this variable as “nutritional condition”.

3.2. Impact of artificially enhanced density on juvenile lobster population dynamics

The mean density of juvenile lobsters was higher at field sites where we enhanced shelter availability with

Table 1
A 1-factor MANOVA testing the effects of food abundance on hemolymph refractive index and weight/CL ratio

Multivariate tests

Effect	Wilks' Lambda	*F*	Hypothesis *df*	Error *df*	*P*
Intercept	0.005	3934.926	2	36	<0.01
Feeding trt	0.356	32.553	2	36	<0.01

Between-subjects tests

Source	*df*	Mean square	*F*	*P*
Refractive index				
Intercept	1	49.521	207.153	<0.01
Feeding trt	1	4.465	18.678	<0.01
Error	37	0.239		
Total	39			
Corrected total	38			
Weight/CL ratio				
Intercept	1	50.700	3408.385	<0.01
Feeding trt	1	0.0929	6.249	0.017
Error	37	0.0148		
Total	39			
Corrected total	38			

The “after/before” ratios were used in the MANOVA in lieu of a repeated-measures analysis. “Feeding trt” represents the two food abundance treatment levels: 25% and 100% of daily intake.

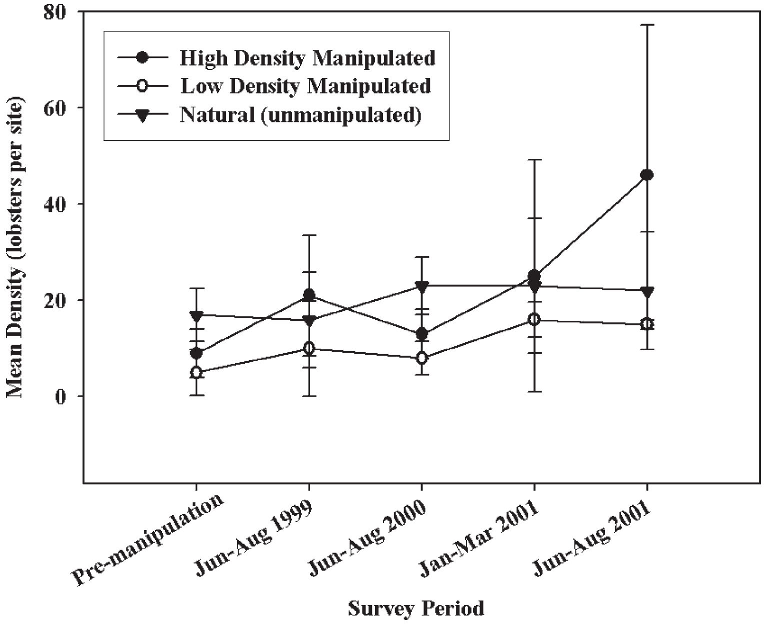

Fig. 3. Lobster density on 25 m × 25 m hard-bottom sites (0.0625 ha) as a function of shelter treatment (HIGH = high density manipulated, LOW = low density manipulated, and NAT = natural non-manipulated) for each survey. Error bars represent 1 S.D.

many artificial shelters (HIGH), as opposed to few (LOW) (Fig. 3), but the difference among treatments was not significant (Table 2). Shelter treatment also had no discernable affect on the mean nutritional condition of lobsters, nor did it significantly affect the short-term residency of lobsters (Table 2). Survey date and survey date * shelter treatment interaction had a significant impact on lobster density, but not nutritional condition or short-term residency (Table 2).

Relative predation (expressed by the number of lobsters that survived the 2-day tethering experiment) differed among sites (Table 3), but it did not differ among density treatments. Predation was much higher on two sites (one LOW site and one HIGH site) than on all the others. Survival of tethered lobsters on these sites was 30% whereas it ranged between 70% and 95% on all other sites. We also inspected the mean short-term residency at these sites in comparison to other sites in those treatments to determine if mortality may have lead to erroneous patterns of residency as predicted from our mark-recapture study. Lobsters on the LOW site actually had a higher mean short-term residency than those on other LOW sites and lobsters on the HIGH site had a mean short-term residency intermediate between the other HIGH sites. We therefore conclude that differences in relative predation among treatments did not confound our interpretation of site-specific residency patterns.

The density of small (<30 mm CL) lobsters was not correlated with mean nutritional condition in any of the surveys. Significant relationships were found in three of the four multiple regressions explaining the nutritional condition of large (>30 mm CL) lobsters during the three summer surveys (1999, 2000 and 2001) (Table 4). However, the independent variables (i.e., density, macroalgal cover or habitat structure) included in these models and their effects were inconsistent among regressions (Summer 1999: Refractive index = 4.786 + 0.108 (density) + 8.918 (cover) + 0.316 (structure); Summer 2000: Refractive index = 11.90 + 0.099 (density) − 0.283 (structure); Summer 2001: Refractive index = 4.786 + 8.918 (cover) + 0.316 (structure)). The only variable that was significant in all three equations, habitat structure, was positively correlated with lobster density in the June–August 1999 and 2001 surveys, but negatively correlated in the June–August 2000 survey. To explore whether a potential relationship was obscured by the low sample size of the separate survey data sets, we also plotted refractive index against density for the entire data set and re-analyzed the combined data set. There was still no significant relationship between nutritional condition and density, habitat structure, or macroalgal cover for either small or large juvenile lobsters.

The proportion of lobsters, either small (<30 mm CL) or large (>30 mm CL), recaptured on a site at the

Table 2

A 3 × 2 repeated-measures MANOVA examining the effect of habitat treatment (high, low, and natural shelter abundance: HIGH, LOW and NAT) on lobster density, nutritional condition (refractive index), and short-term residency

Within-subjects multivariate tests

Effect	Source	Wilks' Lambda	*F*	Hypothesis *df*	Error *df*	*P*
Between subjects	Intercept	0.006	360.080	3	7	<0.01
	Treatment	0.632	0.601	6	14	0.725
Within subjects	Survey date	0.271	6.265	3	7	0.022
	Survey date*Treatment	0.099	5.068	6	14	0.006

Within-subjects univariate tests

Source	Measure	*df*	Mean square	*F*	*P*
Survey date	Lobster density	1	234.375	8.527	0.017
	Refractive index	1	1.707	2.010	0.190
	Residency	1	0.0287	0.488	0.503
Survey date*Treatment	Lobster density	2	326.375	11.874	0.003
	Refractive index	2	2.295	2.703	0.120
	Residency	2	0.0646	1.098	0.374
Error (survey date)	Lobster density	9	27.486		
	Refractive index	9	0.849		
	Residency	9	0.0588		

Between-subjects tests

Source	Measure	*df*	Mean square	*F*	*P*
Intercept	Lobster density	1	14357.042	23.610	0.001
	Refractive index	1	3765.015	1351.486	<0.01
	Residency	1	6.710	70.298	<0.01
Treatment	Lobster density	2	840.292	1.382	0.300
	Refractive index	2	1.576	0.566	0.587
	Residency	2	0.00498	0.052	0.949
Error	Lobster density	9	608.097		
	Refractive index	9	2.786		
	Residency	9	0.0954		

end of a 5-day mark-recapture was also unrelated to density or the environmental characteristics of habitat structure or macroalgal cover during any survey period. The regression models developed for small lobsters for the summer 1999, summer 2000, and summer 2001 regressions were of borderline significance, but the variables were not consistent among models nor were the directions of the relationships. When the data for each survey period were combined, the proportion of both small and large lobsters recaptured increased with increasing lobster density (Fig. 4). The other independent variables of macroalgal

Table 3

A three-way contingency table analysis of the site-specific difference in number of lobsters surviving a 2-day tethering experiment

Interaction	*df*	Likelihood ratio χ^2	*P*
Survey × Site × No. surviving	11	13.706	0.25
Survey × No. surviving	1	0.545	0.46
Site × No. surviving	11	44.365	0.001

Table 4

Eight separate multiple regression analyses examining the relationship between the mean nutritional condition of small (<30 mm CL) and large (>30 mm CL) juvenile lobster over the 5-day mark-recapture period and three predictor variables: lobster density, habitat structure and macroalgal cover

Survey period	Adjusted R^2	Mean square	*df*	F	*P*
Small lobsters (<30 mm CL)					
June–August 1999	−0.178	2.015	3	0.698	0.61
June–August 2000	0.537	4.600	3	4.096	0.08
January–March 2001	−0.184	3.452	3	0.431	0.74
June–August 2001	−0.164	4.187	3	0.484	0.70
Large lobsters (>30 mm CL)					
June–August 1999	0.930	10.488	3	27.514	0.01
June–August 2000	0.648	5.917	3	5.910	0.04
January–March 2001	0.188	6.916	3	1.851	0.22
June–August 2001	0.766	7.734	3	12.975	<0.01

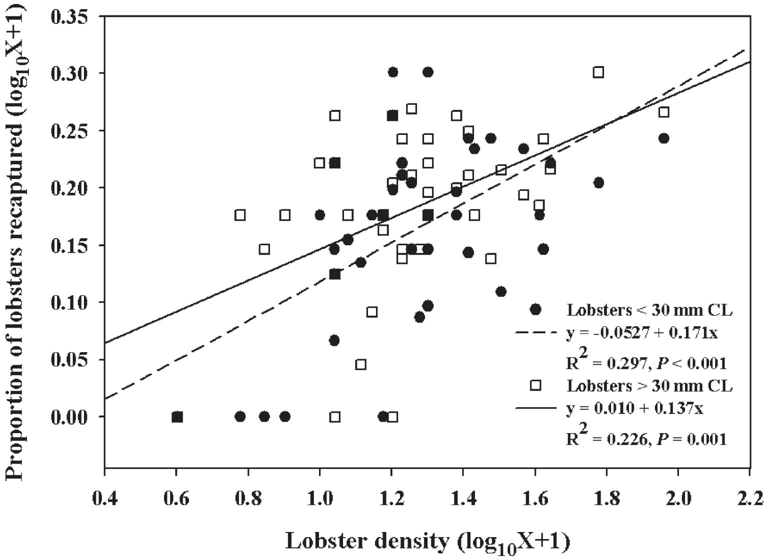

Fig. 4. Short-term residency of small and large juvenile lobsters over a 5-day mark-recapture as a function of lobster density per site for all surveys combined.

cover, habitat structure, and survey date did not significantly improve the relationship.

4. Discussion

Juvenile *P. argus* are robust to the effects of high population density. The density of lobsters varied considerably among sites and survey dates regardless of treatment, which points to the complex interactions between environmental (e.g., settlement habitat, hydrodynamic regimes) and life history characteristics (e.g., larval supply, gregarious behavior, home range) that lead to observed densities. However, high lobster density, whether accomplished by habitat enhancement or due to natural differences among sites, had little effect on the nutritional condition, mortality, or local residency patterns of juvenile lobsters. This study also demonstrates that the use of artificial structures targeted to this critical life-stage remains a viable means of augmenting natural habitat, although other considerations regarding the possible indirect impacts of habitat enhancement have yet to be addressed.

4.1. Dietary intake influence on nutritional condition

Hemolymph refractive index has been used as a proxy for serum protein, and thus, nutritional condition in *J. edwardsii* (Stewart et al., 1967; Oliver and MacDairmid, 2001; Musgrove, 2001), and we have confirmed its efficacy for use with *P. argus*. Our laboratory experiments show that the mean refractive index and weight/CL ratio of lobsters fed 25% and 100% of their maximum daily consumption reflected the differences in growth observed between the treatments. Juvenile *P. argus* that we captured in the field, regardless of size, acquired adequate nutrition relative to lobsters in our dietary impact study, as reflected in their moderate serum protein values. The mean hemolymph serum protein for lobsters in the field surveys (10.3±3.8) was similar to the mean serum protein for all lobsters at the initiation of the dietary impact study (10.3±4.0), but intermediate to those we measured in the final serum protein for the 100% (13.3±2.5) and 25% food ration treatments (6.9±1.5) (1-way ANOVA; $F_{3,684}=9.678$, $P<0.001$). The exceptionally high final value for the 100% food ration laboratory group probably reflects the high quality food administered during the experiment.

4.2. Impact of artificially enhanced density on juvenile lobster population dynamics

It has been suggested that several species of lobster are subject to density-dependent growth or survival, with varying degrees of supporting evidence (*H. americanus*, Wahle et al., 2001; *J. edwardsii* in New Zealand, Breen and Booth, 1989 and in South Australia, McGarvey et al., 1999; *Jasus lalandii* H. Milne-Edwards in South Africa, Newman and Pollock, 1974; Pollock, 1979; Griffiths and Seiderer, 1980; *Nephrops norvegicus* Linnaeus in Scotland, Tuck et al., 1997; *P. cygnus* in Western Australia, Chittleborough, 1976; Ford et al., 1988; Jernakoff et al., 1994; *Panulirus* *marginatus* Quoy and Gaimard in the Hawaiian Islands, Polovina, 1989; and *Panulirus ornatus* Fabricius in the Torres Strait, Australia, Skewes et al., 1997). For *P. cygnus*, localized juvenile density can reach exceptional levels (9374±1442 lobsters/ha, Chittleborough, 1974) and density-dependent competition for resources may depress the growth rate and increase juvenile mortality in comparison to less-dense locations (Chittleborough, 1970, 1976; Jernakoff et al., 1994). For *J. lalandii*, a specialist predator, growth appears limited by competition for a single limited prey item, the mussel *Aulacomya ater* Molina, although the possibility that differences in water temperature among regions could yield the same disparity in growth between populations remains open for investigation (Newman and Pollock, 1974; Pollock, 1979; Griffiths and Seiderer, 1980). Evidence for density-dependent growth in *J. edwardsii*, *N. norvegicus*, and *P. ornatus*, is drawn primarily from comparative population size- and length-frequency analysis between regions or cohorts (Breen and Booth, 1989; Polovina, 1989; Skewes et al., 1997; Tuck et al., 1997; McGarvey et al., 1999), but experimental evidence is lacking. Experimental evidence for density-dependent growth is often difficult to obtain due to the inability to accurately measure growth, inaccessible habitat, or logistical difficulties in designing manipulation experiments in the field—limitations we did not encounter.

Predators can have substantial impacts on local prey populations, evidence which, in turn, is also often used to support a hypothesis of density-dependent food limitation. For example, *J. lalandii* (Griffiths and Seiderer, 1980) and *Panulirus interruptus* J.W. Randall (Robles, 1987; Robles et al., 1990) both alter the abundance and size structure of their target prey, mussels (*A. ater* and *Mytilus califonianus* Conrad, respectively), but no density-dependent growth has been observed for *P. interruptus*. At natural density levels, *P. argus* do not appear to impact the abundance of benthic prey items, although they may alter gastropod size structure near dens used by lobsters (Nizinski, 1998).

Juvenile *P. cygnus* dwelling on uncrowded reefs off Western Australia, are estimated to move no more than 15 m over the course of a year, but some evidence suggests possibly >50 m on crowded reefs (Chittleborough, 1974; Phillips et al., 1984). Similarly, *Panulirus guttatus* Latreille, an obligate inhabitant of shallow Caribbean coral reefs, are restricted to the reef and move little over their lifetime (Sharp et al., 1997; Robertson, 2001). In contrast, adult *J. edwardsii* off New Zealand move an estimated 29–41 m per night, although this varies with reproductive season (MacDiarmid et al., 1991; Kelly, 2001). Movement of juvenile *P. argus* is size-dependent; the smallest juveniles (<20 mm CL) generally forage <1 m from their daytime shelter, whereas those approaching 40 mm CL can move tens of meters overnight (Butler and Herrnkind, 2000). The greater foraging ranges of large juveniles combined with a diverse and scattered prey assemblage in tropical hard-bottom habitat may be sufficient to negate any localized effect of high lobster density on their prey (Nizinski, 1998). The nonspecific diet of *P. argus,* abundance of available prey items (e.g., small bivalve and gastropod mollusks) found in hard-bottom habitat (Andree, 1981; Marx and Herrnkind, 1985; Herrnkind et al., 1988), and rapid recolonization of prey following local depletion (Butler et al., 1997) may combine to present small juvenile lobsters with nearly unlimited food. Evidence from measures of nutritional condition also suggests that even with artificially enhanced density, juvenile *P. argus* are not food limited.

We had initially hypothesized that local food resources might be depressed at high lobster density, and therefore theorized that lobsters might forage further from their dens in search of food when at high local densities. Adult *P. argus* that shelter in crevices on coral reefs by day, do indeed forage at night in seagrass beds and coral rubble hundreds of meters from the reef (Herrnkind et al., 1975; Cox et al., 1997). However, small juveniles probably do not engage in the same nightly long-distance foraging as adults because juvenile lobsters do not depress prey resources beyond a few meters from their den (Nizinski, 1998). Moreover, stable isotope data from juvenile lobsters confirms that the isotopic signature for juvenile lobsters shows a hard-bottom algal-based rather than a seagrass-based ultimate carbon source (Behringer and Butler, in press), which indicates that they forage within hard-bottom habitat. In fact, the gregarious nature of *P. argus* is most likely the cause of the positive link between population density and short-term residency. Lobsters are attracted to the odor of conspecifics (Ratchford and Eggleston, 1998, 2000; Childress and Herrnkind, 1996, 1997; Butler et al., 1997), so higher lobster density could equate to a stronger odor plume and thus increase the attractiveness of high-density areas, regardless of shelter density.

Alternatively, greater site fidelity could also be a consequence of the fact that artificially augmented sites often had the highest lobster density and probably had more functional shelters per unit area, thus more crevices per unit area in which to hide (50 double-stacked blocks with 3 holes/block=300 potential shelters). This may also be the case for natural sites with high density, but it is difficult to quantify which structures are functional shelters if they are not inhabited or could harbor multiple lobsters. Therefore, the higher retention of lobsters on sites with high densities may be an artifact of greater shelter availability rather than a lobster density effect per se.

The benefits to recruitment of enhancing the availability of appropriately sized shelters as refuges from predators has been extensively tested in lobsters (Wahle and Steneck, 1991; Mintz et al., 1994; Herrnkind et al., 1997b; Butler and Herrnkind, 1997a,b; Eggleston et al., 1990, 1992, 1997). Much of the empirical work on the utility of artificial structures in relieving the recruitment bottlenecks in *P. argus* have been positive (e.g., Butler and Herrnkind, 1997a,b; Herrnkind et al., 1997b; Briones-Fourzán and Lozano-Alvarez, 2001). In this study, hard-bottom habitat sites harbored vastly different densities of lobster, with the highest occurring on sites augmented with artificial shelters (48–1440 lobsters/ha, S.D. = 256). The high-end of this range is similar to those observed by others investigating enhancement with artificial "casitas" (1200 lobsters/ha, Lipcius and Eggleston, personal communication), and it well exceeds the density reported for natural habitat in the Florida Keys (454 lobsters/ha, Forcucci et al., 1994; 160 lobsters/ha, Butler and Herrnkind, 1997a,b).

In our studies we used small, scattered concrete blocks that mimic the natural shelter requirements of small juvenile lobsters. Other types of structures, most notably "casitas", are typically used to enhance lobster stocks. Casitas are large (1–2 m wide) open-sided, roofed structures of variable height, and have long been used by fishermen in the Caribbean to concentrate lobsters for ease of capture (Cruz and Phillips, 2000). Yet, because casitas are scaled in size to attract and concentrate large lobsters, they are ineffective in enhancing recruitment of small juvenile lobsters, the size at which they are most vulnerable and thus the potential for population enhancement greatest.

Even though the results of this investigation imply that artificially enhanced density is not detrimental to juvenile spiny lobster populations, we do not advocate large-scale deployment of artificial structures for this purpose. Nursery ecosystems throughout the Caribbean can be markedly different in structure and important ecological dynamics (i.e., larval supply dynamics, settlement habitat and community composition) and thus the effectiveness of artificial structures in enhancing density and their impact on the surrounding environment may be different (Acosta and Butler, 1997; Butler and Herrnkind, 1997a,b). Artificial shelters have the potential to enhance lobster populations in shelter-limited areas because they provide shelter to vulnerable life-stages and do not aggregate them unnaturally. However, there is still much that is unknown, such as the density at which such structures alter local environmental conditions (e.g., sedimentation, flow, or species compositions) or what factors might alter the suitability of artificial structures to the target organism (e.g., colonization by predators, competitors or fouling organisms).

Acknowledgements

We would like to thank Old Dominion University, the Keys Marine Laboratory and the Florida Fish and Wildlife Conservation Commission for logistics and facility support. Many thanks to Richard Musgrove for his advice regarding refractive index measurement. Numerous people assisted with field and laboratory experiments including: Eugene Beal, Dianne Behringer, Rodney Bertelsen, Scott Donahue, Jason Goldstein, Jamie Heisig-Mitchell, Jennifer Lear, Emmanuel Riclet, Denice Robertson, and Jason Schratweiser. This project was funded in part by NOAA National Undersea Program (UNCW 9817) and National Science Foundation (OCE-9730195) grants to M. Butler. **[AU]**

References

Acosta, C.A., Butler IV, M.J., 1997. Role of mangrove habitat as a nursery for juvenile spiny lobster, *Panulirus argus*, in Belize. Mar. Freshw. Res. 48, 721–727.

Aiken, D.E., 1973. Proecdysis, setal development, and molt prediction in the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 30, 1337–1344.

Andree, S.W., 1981. Locomotory activity patterns and food items of benthic postlarval spiny lobsters, *Panulirus argus*. M.S. thesis, Florida State University, Tallahassee. 50 pp.

Beck, M.W., 1995. Size-specific shelter limitation in stone crabs: a test of the demographic bottleneck hypothesis. Ecology 76, 968–980.

Beck, M.W., 1997. A test of the generality of the effects of shelter bottlenecks in four stone crab populations. Ecology 78, 2487–2504.

Behringer, D.C., Butler IV, M.J., in press. Stable isotope analysis of production and trophic relationships in a tropical marine hard-bottom community. Oecologia.

Bohnsack, J.A., Harper, D.E., McClellan, D.B., Hulsbeck, M., 1994. Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off southeastern Florida, U.S.A. Bull. Mar. Sci. 55, 796–823.

Booth, J.D., Kittaka, J., 2000. Growout of juvenile spiny lobsters, In: Phillips, B.F., Cobb, J.S., Kittaka, J. (Eds.), Spiny Lobster Management, 2nd edition. Blackwell Scientific Press, Oxford, pp. 556–585.

Breen, P.A., Booth, J.D., 1989. Puerulus and juvenile abundance in the rock lobster *Jasus edwardsii* at Stewart Island, New Zealand (Note). N.Z.J. Mar. Freshw. Res. 23, 519–523.

Briones-Fourzán, P., Lozano-Alvarez, E., 2001. Effects of artificial shelters (casitas) on the abundance and biomass of juvenile spiny lobsters *Panulirus argus* in a habitat-limited tropical reef lagoon. Mar. Ecol., Prog. Ser. 221, 221–232.

Briones-Fourzán, P., Lozano, E., Eggleston, D.B., 2000. The use of artificial shelters ("casitas") in research and harvesting of Caribbean spiny lobsters in Mexico, In: Phillips, B.F., Cobb, J.S., Kittaka, J. (Eds.), Spiny Lobster Management, 2nd edition. Blackwell Scientific Press, Oxford, pp. 420–446.

Butler IV, M.J., Herrnkind, W.F., 1997a. Factors affecting the recruitment of juvenile Caribbean spiny lobsters dwelling in macroalgae. Bull. Mar. Sci. 61, 3–19.

Butler, M.J., Herrnkind, W.F., 1997b. A test of recruitment limitation and the potential for artificial enhancement of spiny lobster (*Panulirus argus*) populations in Florida. Can. J. Fish. Aquat. Sci. 54, 452–463.

Butler IV, M.J., Herrnkind, W.F., 2000. Puerulus and juvenile ecology, In: Phillips, B.F., Cobb, J.S., Kittaka, J. (Eds.), Spiny Lobster Management, 2nd edition. Blackwell Scientific Press, Oxford, pp. 276–301.

Butler IV, M.J., Hunt, J.H., Herrnkind, W.F., Matthews, T., Childress, M., Bertelsen, R., Sharp, W., Field, J.M., Marshall, H., 1995. Cascading disturbances in Florida Bay, USA: cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobster *Panulirus argus*. Mar. Ecol., Prog. Ser. 129, 119–125.

Butler IV, M.J., Herrnkind, W.F., Hunt, J.H., 1997. Factors affecting the recruitment of juvenile Caribbean spiny lobsters dwelling in macroalgae. Bull. Mar. Sci. 61, 3–19.

Childress, M., Herrnkind, W.F., 1996. The ontogeny of social behavior among juvenile Caribbean spiny lobsters. Anim. Behav. 51, 1–13.

Childress, M., Herrnkind, W.F., 1997. Den sharing by juvenile Caribbean spiny lobsters (*Panulirus argus*) in nursery habitat: cooperation or coincidence? Mar. Freshw. Res. 48, 751–758.

Chittleborough, R.G., 1970. Home range, homing and dominance in juvenile western rock lobsters. Aust. J. Mar. Freshw. Res. 21, 131–148.

Chittleborough, R.G., 1974. Home range, homing and dominance in juvenile western rock lobsters. Aust. J. Mar. Freshw. Res. 25, 227–234.

Chittleborough, R.G., 1976. Growth of juvenile *Panulirus longipes cygnus* George on Coastal reefs compared with those reared under optimal environmental conditions. Aust. J. Mar. Freshw. Res. 27, 279–295.

Coen, L.D., Luckenbach, M.W., 2000. Developing success criteria and goals for evaluating oyster reef restoration: ecological function or resource exploitation? Ecol. Eng. 15, 323–343.

Cox, C., Hunt, J.H., Lyons, W.G., Davis, G.E., 1997. Nocturnal foraging of the Caribbean spiny lobster (*Panulirus argus*) on offshore reefs of Florida, USA. Mar. Freshw. Res. 48, 671–679.

Cruz, R., Phillips, B.F., 2000. The artificial shelters (pesqueros) used for spiny lobster (*Panulirus argus*) fisheries in Cuba, In: Phillips, B.F., Cobb, J.S., Kittaka, J. (Eds.), Spiny Lobster Management, 2nd edition. Blackwell Scientific Press, Oxford, pp. 400–419.

Cruz, R., Brito, R., Diaz, E., Lalana, R., 1986. Ecologia de la langosta (*Panulirus argus*) al SE de la Isla de la Juventud: I. Colonizacion de arrecifes artificiales. Rev. Investig. Mar. (Cuba) 7, 3–17.

Depledge, M.H., Bjerregaard, P., 1989. Haemolymph protein composition and copper levels in decapod crustaceans. Helgol. Meeresunters. 3, 207–223.

Eggleston, D.B., Lipcius, R.N., 1992. Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. Ecology 73, 992–1011.

Eggleston, D.B., Lipcius, R.N., Miller, D.L., Coba-Cetina, L., 1990. Shelter scaling regulates survival of juvenile Caribbean spiny lobster *Panulirus argus*. Mar. Ecol., Prog. Ser. 62, 70–88.

Eggleston, D.B., Lipcius, R.N., Miller, D.L., 1992. Artificial shelters and survival of juvenile Caribbean spiny lobster *Panulirus argus*: spatial, habitat, and lobster size effects. Fish. Bull. 90, 691–702.

Eggleston, D.B., Lipcius, R.N., Grover, J.J., 1997. Predator and shelter-size effects on coral reef fish and spiny lobster prey. Mar. Ecol., Prog. Ser. 149, 43–59.

Forcucci, D., Butler IV, M.J., Hunt, J.H., 1994. Population dynamics of juvenile Caribbean spiny lobster, *Panulirus argus*, in Florida Bay, Florida. Bull. Mar. Sci. 54, 805–818.

Ford, R.F., Phillips, B.F., Joll, L.M., 1988. Experimental manipulation of population density and its effects on growth and mortality of juvenile western rock lobsters, *Panulirus cygnus* George. Fish. Bull. 86, 773–787.

Griffiths, C.L., Seiderer, J.L., 1980. Rock-lobsters and mussels—limitations and preferences in a predator–prey interaction. J. Exp. Mar. Biol. Ecol. 44, 95–109.

Herrnkind, W.F., Butler IV, M.J., 1986. Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters, *Panulirus argus*. Mar. Ecol., Prog. Ser. 34, 23–30.

Herrnkind, W.F., Vanderwalker, J., Barr, L., 1975. Population dynamics, ecology and behaviour of spiny lobster, *Panulirus argus* of St. John, U.S. Virgin Islands: habitation and pattern of movements. Sci. Bull. Nat. Hist. Mus. Los Angelos Cty 20, 31–45.

Herrnkind, W.F., Butler IV, M.J., Tankersley, R.A., 1988. The effects of siltation on recruitment of spiny lobsters, *Panulirus argus*. Fish. Bull. 86, 331–338.

Herrnkind, W.F., Jernakoff, P., Butler IV, M.J., 1994. Puerulus and post-puerulus ecology, In: Phillips, B.F., Cobb, J.S., Kittaka, J. (Eds.), Spiny Lobster Management, 2nd edition. Blackwell Scientific Press, Oxford, pp. 213–229.

Herrnkind, W.F., Butler IV, M.J., Hunt, J.H., 1997a. Can artificial habitats that mimic natural structures enhance recruitment of Caribbean spiny lobster? Fisheries 22, 24–27.

Herrnkind, W.F., Butler IV, M.J., Hunt, J.H., Childress, M., 1997b. Role of physical refugia: implications from a mass sponge die-off in a lobster nursery in Florida. Mar. Freshw. Res. 48, 759–769.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.

Iribarne, O., Fernandez, M., Armstrong, D., 1994. Does space competition regulate density of juvenile Dungeness crab *Cancer magister* Dana in sheltered habitats? J. Exp. Mar. Biol. Ecol. 183, 259–271.

James, P.J., Tong, L.J., Paewai, M.P., 2001. Effect of stocking density and shelter on growth and mortality of early juvenile *Jasus edwardsii* held in captivity. Mar. Freshw. Res. 52, 1413–1418.

Jernakoff, P., Fitzpatrick, J., Phillips, B.F., De Boer, E., 1994. Density and growth in populations of juvenile western rock lobsters, *Panulirus cygnus* (George). Aust. J. Mar. Freshw. Res. 45, 69–81.

Jorstadt, K.E., Agnalt, A., Kristiansen, T.S., Nostvold, E., 2001. High survival and growth of European lobster juveniles (*Homarus gammarus*) reared communally on a natural-bottom substrate. Mar. Freshw. Res. 52, 1431–1438.

Kelly, S., 2001. Temporal variation in the movement of the spiny lobster *Jasus edwardsii*. Mar. Freshw. Res. 52, 323–331.

Lazano-Alvarez, E., Briones-Fourzán, P., Negrete-Soto, F., 1994. An evaluation of concrete block structures as shelter for juvenile Caribbean spiny lobsters, *Panulirus argus*. Bull. Mar. Sci. 55, 351–362.

Losada-Torteson, V., Posada, J.M., 2001. Using tyres as shelters for the protection of juvenile spiny lobsters, *Panulirus argus*, or as a fishing gear for adults. Mar. Freshw. Res. 52, 1445–1450.

Lyle, W.G., MacDonald, C.D., 1983. Molt stage determination in the Hawaiian spiny lobster *Panulirus marginatus*. J. Crustac. Biol. 3, 208–216.

MacDiarmid, A.B., Hickey, B., Maller, R.A., 1991. Daily movement patterns of the spiny lobster *Jasus edwardsii* (Hutton) on a shallow reef in northern New Zealand. J. Exp. Mar. Biol. Ecol. 147, 185–205.

Marx, J., Herrnkind, W., 1985. Factors regulating microhabitat use by young juvenile spiny lobsters, *Panulirus argus*: food and shelter. J. Crustac. Biol. 5, 650–657.

McGarvey, R., Ferguson, G.J., Prescott, J.H., 1999. Spatial variation in mean growth rates at size of southern rock lobster, *Jasus edwardsii*, in South Australian waters. Mar. Freshw. Res. 50, 333–342.

Mintz, J.D., Lipcius, R.N., Eggleston, D.B., Seebo, M.S., 1994. Survival of juvenile Caribbean spiny lobster: effects of shelter size, geographic location, and conspecific abundance. Mar. Ecol., Prog. Ser. 112, 255–266.

Musgrove, R.J.B., 2001. Interactions between haemolymph chemistry and condition in the southern rock lobster, *Jasus edwardsii*. Mar. Biol. 139, 891–899.

Nedimyer, K., Osenberg, C.W., St. Mary, C.M., 2001. Species Composition and Collection Efficiency Associated with Artificial and Natural Substrates. Florida Sea Grant College Program, Gainesville.

Newman, G.G., Pollock, D.E., 1974. Growth of the rock lobster *Jasus lalandii* and its relationship to benthos. Mar. Biol. 24, 339–346.

Nizinski, M., 1998. Caribbean spiny lobster and their molluscan prey: are top-down forces key in structuring prey assemblages in a Florida Bay seagrass system? Ph.D. dissertation, College of William and Mary, Williamsburg. 292 pp.

Oliver, M.D., MacDairmid, A.B., 2001. Blood refractive index and ratio of weight to carapace length as indices of nutritional condition in juvenile rock lobsters (*Jasus edwardsii*). Mar. Freshw. Res. 52, 1395–1400.

Phillips, B.F., Joll, L.M., Ramm, D.C., 1984. An electromagnetic tracking system for studying the movements of rock (spiny) lobsters. J. Exp. Mar. Biol. Ecol. 79, 9–18.

Pile, A.J., Lipcius, R.N., van Montfrans, J., Orth, R.J., 1996. Density-dependent settler–recruit–juvenile relationships in blue crabs. Ecol. Monogr. 66, 277–300.

Pollock, D.E., 1979. Predator–prey relationships between the rock lobster *Jasus lalandii* and the mussel *Aulacomya ater* at Robben Island on the Cape West Coast of Africa. Mar. Biol. 52, 347–356.

Polovina, J.J., 1989. Density dependence in spiny lobster, *Panulirus marginatus*, in the northwestern Hawaiian Islands. Can. J. Fish. Aquat. Sci. 46, 660–665.

Polovina, J.J., Haight, W.R., Moffitt, R.B., Parrish, F.A., 1995. The role of benthic habitat, oceanography, and fishing on the population dynamics of the spiny lobster, *Panulirus marginatus* (Decapoda, Palinuridae), in the Hawaiian archipelago. Crustaceana 68, 203–212.

Ratchford, S.G., Eggleston, D.B., 1998. Size- and scale-dependent chemical attraction contribute to ontogenetic shift in sociality. Anim. Behav. 56, 1027–1034.

Ratchford, S.G., Eggleston, D.B., 2000. Temporal shift in the presence of a chemical cue contributes to a diel shift in sociality. Anim. Behav. 59, 793–799.

Robertson, D.N., 2001. The implications of the Target Area hypothesis on the population dynamics of the spotted spiny lobster, *Panulirus guttatus*. Ph.D. dissertation, Old Dominion University, Norfolk. 103 pp.

Robles, C., 1987. Predator foraging characteristics and prey population structure on a sheltered shore. Ecology 68, 1502–1514.

Robles, C., Sweetnam, D., Eminike, J., 1990. Lobster predation on mussels: shore-level differences in prey vulnerability and predator preference. Ecology 71, 1564–1577.

Seaman Jr., W.C., 2000. Artificial Reef Evaluation—With Application to Natural Marine Habitats. CRC Press, Boca Raton.

Sharp, W.C., Hunt, J.H., Lyons, W.G., 1997. Life history of the spotted spiny lobster, *Panulirus guttatus* (Latreille, 1804) (Palinuridae). Mar. Freshw. Res. 48, 687–698.

Sherman, R.L., Gilliam, D.S., Spieler, R.E., 2001a. Effects of refuge size and complexity on recruitment and fish assemblage formation on small artificial reefs. Proc. Gulf Caribb. Fish. Inst. 52, 455–467.

Sherman, R.L., Gilliam, D.S., Spieler, R.E., 2001b. Site-dependent differences in artificial reef function: implications for coral reef restoration. Bull. Mar. Sci. 69, 1053–1056.

Skewes, T.D., Pitcher, C.R., Dennis, D.M., 1997. Growth of ornate rock lobsters, *Panulirus ornatus*, in Torres Strait. Aust. Mar. Freshw. Res. 48, 497–501.

Smith, D.M., Dall, W., 1982. Blood protein, blood volume and extracellular space relationships in two *Penaeus* spp. (Decapoda: Crustacea). J. Exp. Biol. Ecol. 63, 1–15.

Smith, K.N., Herrnkind, W.F., 1992. Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): influence of size and shelter. J. Exp. Mar. Biol. Ecol. 157, 3–18.

Sosa-Cordero, E., Arce, E., Aquilar-Dávila, A.M., Ramírez-González, A., 1998. Artificial shelters for spiny lobster *Panulirus argus* (Latreille): an evaluation of occupancy in different benthic habitats. J. Exp. Mar. Biol. Ecol. 229, 1–18.

Stanley, D.R., Wilson, C.A., 2000. Variation in the density and species composition of fishes associated with three petroleum platforms using dual beam hydroacoustics. Fish. Res. 47, 161–172.

Steger, R., 1987. Effects of refuges and recruitment on gonodactylid stomatopods, a guild of mobile prey. Ecology 68, 1520–1533.

Stewart, J.E., Corrick, J.W., Foley, D.M., Li, M.F., Bishop, C.M., 1967. Muscle weight relationship to serum proteins, haemocytes, and hepatopancreas in lobster, *Homarus americanus*. J. Fish. Res. Board Can. 24, 2339–2354.

Tangley, L., 1987. Enhancing coastal production: do artificial shelters help or hurt Mexico's valuable spiny lobster fishery? Bioscience 37, 309–312.

Tuck, I.D., Chapman, C.J., Atkinson, R.J.A., 1997. Population biology of the Norway lobster, *Nephrops norvegicus* (L.) in the Firth of Clyde, Scotland: I. Growth and density. ICES J. Mar. Sci. 54, 125–135.

Wahle, R., Steneck, R.S., 1991. Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck? Mar. Ecol., Prog. Ser. 69, 231–243.

Wahle, R.A., Tully, O., O'Donovan, V., 2001. Environmentally mediated crowding effects on growth, survival and metabolic rate of juvenile American lobsters (*Homarus americanus*). Mar. Freshw. Res. 52, 1157–1166.