Benthic Dispersal of Caribbean Spiny Lobsters among Insular Habitats: Implications for the Conservation of Exploited Marine Species

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Abstract: Understanding how populations of target species interact with their habitats is necessary for developing an effective conservation strategy. During its complex life bistory, the Caribbean spiny lobster (Panulirus argus) uses a variety of benthic marine babitats, but how habitat characteristics affect their dispersal is unclear. To assess how habitat insularity affects the benthic dispersal of spiny lobsters, I compared lobster abundance, size class structure, and migration among insular mangrove and coral reef babitats that were surrounded by bare rubble fields or by seagrass meadows. Lobsters were significantly more abundant on mangrove and coral islands surrounded by seagrass. The size-class distributions of lobsters in these habitats bad higher proportions of juveniles, whereas islands surrounded by sand and rubble had skewed distributions dominated by adult lobsters. Seagrass is known to serve as settlement babitat for larval recruits and is likely associated with the bigher abundances of lobsters found in seagrass-isolated babitats. Immigration and emigration rates were three to four times higher on seagrass-isolated islands than on rubble-isolated islands, reflected in the significantly greater number of juveniles moving into and from seagrass-isolated islands. Rubble fields appeared to function as a barrier to benthic dispersal for all lobsters except adults. Vegetated substrates may function as movement corridors for juvenile lobsters and may facilitate dispersal to areas containing new resources. The effects of insularity on a population may be lessened by the nature of the surrounding babitats if those habitats have important functional roles as larval settlement areas, foraging grounds, or movement corridors. Protection of insular habitats like coral reefs may be ineffective if related babitats like seagrass meadows are left unprotected. Conservation strategies for mobile bentbic species need to incorporate the protection of areas with heterogenous habitats that are important to meet the changing habitat requirements in complex life cycles.

Dispersión Béntica de la Langosta Espinosa del Caribe entre Hábitats Insulares: Implicaciones para la Conservación de Especies Marinas Explotadas

Resumen: El entendimiento de cómo las poblaciones de especies clave interactúan con sus bábitats es necesario para desarrollar una estrategia efectiva de conservación. Durante su compleja bistoria de vida, la langosta espinosa del Caribe (Panulirus argus) usa una gran variedad de bábitats bénticos marinos, pero es poco claro el cómo las características del bábitat afectan su dispersión. Para evaluar cómo el aislamiento del bábitat afecta la dispersión de las langostas comparé la abundancia, la estructura de clases de tallas y la migración entre manglares insulares y arrecífes de coral que estaban rodeados de campos de escombros desnudos o por vegas de pastos marinos. Las langostas fueron significativamentes más abundantes en manglares e islas coralinas rodeadas por pastos marinos. Las distribuciones de clases de talla de las langostas en estos bábitats tuvieron una mayor proporción de juveniles, mientras que las islas rodeadas de arena y escombros tuvieron distribuciones sesgadas dominadas por adultos. Los pastos marinos son conocidos por servir como

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un bábitat de asentamiento para las larvas reclutas y posiblemente están asociados con altas abundancias de langostas encontradas en bábitats de pastos marinos aislados. Las tasas de inmigración y emigración fueron 3 y 4 veces más altas en las islas de pastos marinos aislados que en las islas con pasto y escombros, esto se reflejó en un número significativamente mayor de juveniles moviéndose bacia y de las islas de pastos aislados. Los campos de escombros parencen funcionar como barreras de dispersión béntica para todas las langostas con excepción de los adultos. Los substratos vegetados pueden estar funcionando como corredores de movimiento de juveniles y podrían estar facilitando la dispersión bacia áreas conteniendo nuevos recursos. Los efectos del aislamiento de una población pueden ser aminorados por la naturaleza de los bábitats en los alrededores si estos bábitats tienen un papel funcional importante como áreas de asentamiento, terrenos de forrajeo o corredores de movimiento. La protección de bábitats insulares como los arrecífes coralinos puede ser poco efectiva si los bábitats relacionados como las vegas de pastos marinos no son protegidas. Las estrategias de conservación de especies bénticas móbiles necesitan incorporar la protección de áreas con babitats beterogéneos que son importantes para alcanzar los requerimientos cambiantes de bábitat de ciclos de vida complejos.

Introduction

Nature reserves are often habitat "islands" surrounded by areas unsuitable for supporting populations of target species or maintaining community diversity due to habitat fragmentation, degradation, or loss (Terborgh & van Schaik 1997). Factors such as the size, shape, and number of reserves necessary to support maximum biodiversity have been the focus of much discussion (e.g., Diamond 1975; Simberloff & Abele 1976, 1982; Terborgh 1976; Schonewald-Cox & Bayless 1986), but ultimately the efficacy of reserves depends on how well the viability (Shaffer 1981) of populations of target species is preserved (Soulé & Simberloff 1986). This argument is based on the premise that, as the size of a population gets smaller, the probability of extinction increases due to genetic, demographic, and environmental stochasticity (MacArthur & Wilson 1967; Richter-Dyn & Goel 1972; Shaffer 1981). A proximal cause of the limitation on population viability is habitat fragmentation resulting in barriers to dispersal. For example, the detrimental effects of habitat fragmentation have been demonstrated for some terrestrial fauna (Bierregaard et al. 1992). Although corridors linking fragmented habitats may have a mitigating effect, few empirical data exist to demonstrate this (Simberloff et al. 1992). For effective conservation, the interaction between target species and their habitats in terms of habitat requirements and dispersal dynamics must be quantified and incorporated in the planning of nature reserves.

Marine reserves often function as harvest refuges for exploited species and so may have substantial benefits for coastal fisheries and marine resource management (Carr & Reed 1993; DeMartini 1993; Dugan & Davis 1993). A number of studies have demonstrated the potential of marine reserves to replenish stocks of exploited species by increasing biomass and abundance in protected areas (e.g., Alcala & Russ 1990; Cole et al. 1990; McClanahan & Shafir 1990; MacDiarmid & Breen 1993), increasing fishery yield in adjacent areas (Davis & Dodrill 1989; Cole et al. 1990), and protecting reproductive stock with a concomitant increase in larval production and subsequent recruitment to regional populations (Carr & Reed 1993). An additional function of marine reserves is the protection of juveniles from poaching or from injury due to handling, which affects growth and often increases incidental mortality (e.g., in spiny lobsters, Davis 1981; Hunt & Lyons 1986). MacDiarmid and Breen (1993) postulated that the lower abundance of juvenile lobsters (*Jasus edwardsii*) outside the Cape Rodney to Okakari Point marine reserve in New Zealand than in similar habitats inside the reserve boundaries could be due to capture and handling mortality.

The Caribbean spiny lobster (Panulirus argus) is heavily exploited throughout its range and constitutes the primary fishery in many Caribbean countries. With increasing fishing pressure, reduced population sizes denoted by decreasing catch per unit effort are becoming common despite regional fishery regulations (Ehrhardt 1994). Protection in harvest refuges is being touted as the new conservation strategy for such heavily exploited species, but few empirical studies have demonstrated how environmental factors optimize population viability (Davis & Dodrill 1980; Childress 1997). Spiny lobsters have complex life histories with an extensive pelagic larval phase (Herrnkind & Butler 1986; Acosta et al. 1997) and ontogenetic habitat shifts in benthic environments (Herrnkind & Butler 1986; Jernakoff et al. 1994; Childress & Herrnkind 1996). For example, young Caribbean spiny lobsters shelter cryptically in vegetation and other complex shelters, which provide them with adequate food and protection from predators, whereas older juveniles become increasingly social and shift to crevice dwelling in coral reefs or mangrove habitat (Herrnkind & Butler 1986; Childress & Herrnkind 1996). Vagility increases with age, and lobsters become nomadic

and highly mobile by the onset of sexual maturity (Herrnkind 1980; Cruz et al. 1986; Davis & Dodrill 1989).

I address the question of how the physical insularization of habitat by the surrounding substrate affects the benthic dispersal dynamics of the Caribbean spiny lobster. My objective was to compare lobster abundance, population size structure, and movement of spiny lobsters in insular habitats surrounded by bare rubble fields or by seagrass meadows. I tested the null hypotheses that (1) lobster abundances and size frequency distributions are similar among different habitat islands, (2) lobster dispersal (immigration and emigration) rates are equal among the habitat islands, and (3) the surrounding substrate does not influence lobster movement activity on a habitat island. I consider the implications of these findings on the design of coastal marine reserves for the protection of mobile benthic species.

Methods

Site Description

Experiments and censuses were conducted in discrete mangrove and coral reef habitats off the coast of Belize in the western Caribbean (Fig. 1). All habitats were in





shallow water (depth 1-3 m), and all islands were isolated from each other by at least 1 km of sand-rubble substrate or seagrass. Twelve sites (6 replicates in mangrove and 6 in coral habitats) were surrounded by bare sand and coral rubble fields, and 12 were surrounded by seagrass meadows. Thus, the experimental treatments were habitat type (mangrove or coral patches) and habitat isolation (by rubble or seagrass). Data on population size structure and movement for 8 of the 12 mangrove islands are taken from Acosta and Butler (1997) and reanalyzed as part of the larger data base.

The mangrove islands are located about 5 km west of the Belize Barrier Reef on an expansive back reef. Islands surrounded by shallow seagrass beds are located at Tobacco Range (two islands), Twin Cays, and Blue Ground Range (three islands) (lat 16°48.2'N, long 88°08.5'W; range refers to a group of nameless islands). The islands have margins 5-10 m wide covered by seagrass and macroalgae with interspersed corals and sponges. They are separated by homogenous seagrass (Thallasia testudinum) meadows at about 5 m maximum depth. Islands surrounded by fields of sand and coral rubble are located at the Pelican Cays (Bird Cay, Cat Cay, Cocat Cay, Elbow Cay, Fisherman Cay, Manatee Cay; lat 16° 40.0'N, long 88°11.5'W). These islands are part of an atoll-like faro formation in which the shelf drops abruptly 25-30 m. These mangrove islands have shallow margins 3-10 m wide with a high diversity of seagrasses, corals, and sponges (Acosta & Butler 1997). All islands support fringing and overwash red mangrove (Rhizophora mangle) forests with submerged mangrove prop roots about 0.5-1.5 m deep at mean low tide. Experimental sites were 1000 m² in area, consisting of 100 m of mangrove shoreline by 10 m (or edge) of the island margin.

Experiments in coral habitat were conducted at Glover's Reef, an atoll 25 km east of the barrier reef (Fig. 1). "Islands" were discrete, shallow coral patch reefs with an average 2–3 m vertical relief. More than 700 patch reefs occur in the lagoon of the atoll, so global positioning satellite (GPS) coordinates were used to locate coral island sites that averaged 1000 m² (range 800–1200 m²) in area. Coral islands surrounded by seagrass meadows were separated by waters 2–5 m deep (lat $87^{\circ}50.6'$ N, long $16^{\circ}43.0'$ W, to (lat $87^{\circ}46.0'$ N, long $16^{\circ}46.0'$ W), whereas islands surrounded by sand and rubble fields were separated by an average depth of 20 m (lat $87^{\circ}52.8'$ N, long $16^{\circ}44.0'$ W, to lat $87^{\circ}49.8'$ N, long $16^{\circ}48.0'$ W).

I minimized the potentially confounding effect of fishing on population size structure by locating sites in areas of light or no fishing activity. The coral reef sites were located in the conservation (fishing prohibited) zone of the Glover's Reef Marine Reserve. Although the mangrove island sites occur in an area open to fishing, fishermen seldom work near this habitat because of the low abundance of large, fishery-sized lobsters. Instead they generally concentrate their efforts on coral patch reefs and the barrier reef. Thus, lobsters in the mangrove sites are relatively undisturbed by fishing pressure.

Population Stucture and Dispersal

To determine lobster abundance and dispersal patterns, replicated short-term individual mark-recapture experiments were conducted on the mangrove and coral islands at quarterly intervals from 1995 to 1997. Experiments were conducted over 5- to 7-day periods with four markings and five censuses of each site. This time period allowed for the measurement of instantaneous immigration and emigration rates by the highly mobile adult lobsters, while minimizing the loss of external tags by molting. Jolly-Seber parameter estimates were derived for lobster abundance on islands, loss of animals by emigration of benthic lobsters (Krebs 1989). Recruitment of postlarval settlers was not measured during the short experimental time periods.

All structures (vegetation, coral crevices, mangrove prop roots, etc.) on sites were visually searched by divers using SCUBA or snorkel. While underwater, lobsters were captured, measured (carapace length [CL] to the nearest 0.1 mm), sexed (by external dimorphic characters), and tagged with color-coded, plastic antennal tags. They were then returned to their original dens, which were also marked with numbered tags. Despite meticulous searching of habitats, it is likely that small lobsters (1-2 months post-settlement or 7-12 mm CL) were undercensused due to their cryptic nature. During subsequent surveys, unmarked lobsters were tagged, and the distance moved from one den to another on the site by each resighted lobster was measured. Except for the initial handling during marking with this noninvasive tag, lobsters were not further disturbed.

Data Analysis

Parameter estimates of abundance, loss by emigration and mortality, and addition by immigration from a Jolly-Seber model were used as response variables in a multivariate analysis of variance (MANOVA) with habitat type (mangrove or coral) and island isolation (rubble or seagrass) as factors. Data for the proportion of animals lost were arcsine-square-root-transformed to conform to the assumption of normality; the other two variables had normal distributions. The Bartlett-Box homogeneity test was used to check for equality of variance-covariance matrices, and pairs of response variables were plotted to check for linearity. To check the assumption of multicollinearity, within-cell correlation analyses were conducted on all combinations of response variables. Roy's greatest characteristic root (GCR) was used as the factorial test statistic in the MANOVA (Harris 1985), and the mean square (MS) was used for the response variables. The within-cell correlation-covariance matrix formed by averaging across all group matrices was used to analyze the covariances and the correlations among variables.

Because the effect of habitat type (mangrove or coral) was not significantly different in the MANOVA, these data were pooled by habitat isolation (rubble or seagrass) for further analysis. For a more detailed analysis of population size structure, I plotted the mean proportions of lobster size classes on habitat islands. Lobsters were divided into four size classes based on ontogenetic changes in behavior and habitat use (Herrnkind & Butler 1986; Childress & Herrnkind 1996): (1) under 26 mm CL including new settlers to post-cryptic juveniles, (2) active juveniles 26-50 mm CL, (3) subadults 51-76 mm CL, and (4) mature adults over 76 mm CL. Skewness (g_1) and kurtosis (g_2) values were then calculated for the lobster size distributions on islands surrounded by bare rubble or seagrass, and a two-sample Kolmogorov-Smirnoff test for differences in distributions was run using the $D_{\rm mn}$ statistic. For a closer inspection of dispersal, movement into or from each island was calculated as N =I - E, where N is the net number of migrants, I is the number of immigrants, and E is the number of emigrants. The resulting sign indicates direction of movement to or from an island, and the absolute value is the magnitude of migration. Emigration was determined by multiplying loss of animals by the probability of predation mortality for a given size class in a particular type of habitat (Acosta & Butler 1997) and subtracting that amount from the total number of animals in that size class lost from the site each day. Predation mortality was estimated in tethering experiments, which most likely reveal the upper bounds of predation and so give the most conservative estimate. Proportions of each size class lost by emigration and gained by immigration were then plotted to compare dispersal into or from the rubble field or seagrass meadow.

To study the dynamics of movement within a site, movement activity (mean daily distance moved by a lobster on a site for more than 2 days) and den fidelity (time spent in a particular den by an individual on a site for more than 2 days) were analyzed on habitat islands. Because larger lobsters may be more vagile than smaller ones, an analysis of covariance (ANCOVA) was conducted on the response variables with lobster size as the covariate and island isolation as the factor. The Kolmogorov-Smirnov statistic was used to test for normality, and the maximum variance ratio (F_{max}) test was used to test for homogeneity of variances (Sokal & Rohlf 1981). All slopes were inspected for linearity and tested for equality among slopes.

Results

In total, 467 lobsters was tagged, ranging in size from recently settled juveniles 10 mm CL to mature adults 110 mm CL (mean \pm SE: 45.9 \pm 2.0; mode: 65 mm CL on rubble-isolated islands, 28 mm CL on seagrass-isolated islands). The male-to-female ratio was 1.4:1. In the Jolly-Seber model, an estimated 85% of the greater population of lobsters on all islands were tagged. An average 78% of tagged lobsters on rubble-isolated islands were recaptured at least once, and a 75% recapture rate occurred on seagrass-isolated islands.

The MANOVA on Jolly-Seber estimates of abundance, loss by emigration and mortality, and addition by immigration showed no differences among mangrove and coral habitats (Table 1). But, significant differences in all three response variables occurred between rubble- and seagrass-isolated islands. The daily abundance of lobsters on seagrass-isolated islands (mean \pm SE: 14.1 \pm 2.5) was more than double that of rubble-isolated islands (mean \pm SE: 6.2 \pm 0.8). The rate of immigration to seagrassisolated islands was higher (mean \pm SE: 4.11 \pm 0.28) than to rubble-isolated islands (mean \pm SE: 1.01 \pm 0.11). The overall correlation-covariance matrix showed a positive relationship between abundance and additions, suggesting that immigration of benthic lobsters is associated with higher lobster abundance, especially on islands surrounded by shallow seagrass meadows (Table 2). Addition of lobsters had a negative but nonsignificant correlation to loss by emigration and mortality, suggesting that migration to or from an island is not densitydependent in these habitats.

Table 1. Results of the multivariate analysis of variance (MANOVA) on lobster abundance, loss by emigration and mortality, and addition by immigration (response variables) in mangrove or coral habitats that were isolated by bare rubble or seagrass (factors).*

Source	Test value	F	Numerator df	Denominator df	р
Habitat	0.08	0.48	3	18	ns
Island isolation	460.89	0	3	1	0.05
abundance	358.05	627.71	1	1	0.02
loss	0.12	261.06	1	1	0.03
addition	52.96	195.45	1	1	0.04
Habitat \times isolation	0.03	0.21	3	18	ns

*Shown are MANOVA results using Roy's greatest characteristic root as the test statistic for the factors and the mean square for the response variables (ns, not significant at $\alpha = 0.05$).

Table 2. Within-cells correlations-covariance matrix showing covariation within (on the diagonal and upper right corner) and correlations between (lower left corner) the variables from the Jolly-Seber model.

	Abundance	Loss	Addition
Abundance	3.73	0.04	0.59
Loss	0.23	0.01	-0.02
Addition	0.39	-0.33	0.61

The analysis of size-class structure clarifies the relationships among the variables. The size-class structure on rubble-isolated islands had a negatively skewed ($g_1 =$ -1.41) and leptokurtic ($g_2 = 5.12$) distribution and was significantly different from that on seagrass-isolated islands ($D_{mn} = 0.31, p < 0.01$; Fig. 2). The size-class structure on rubble-isolated islands was dominated by large subadult lobsters, whereas a more even distribution of sizes occurred on islands surrounded by seagrass. Net movement of lobsters was similar on seagrass-isolated islands (+39 lobsters) and on rubble-isolated islands (+24 lobsters). There was, however, a three- to four-fold increase in both the number of immigrants and emigrants on seagrass-isolated islands (199 immigrants, 160 emigrants) compared to those on rubble-isolated islands (65 immigrants, 41 emigrants). The sizes of lobsters entering or leaving islands reflected the patterns of the size-class structure (Fig. 3). The emigrants and immigrants on seagrassisolated islands ranged in size from juveniles to mature adults. Emigration and immigration on rubble-isolated islands, however, were almost exclusively by large subadults and mature adults. A total of 185 juveniles were identified as immigrants and emigrants on seagrassisolated islands, versus 4 on rubble-isolated islands.



Figure 2. Mean proportions of spiny lobsters in four size classes found on 12 babitat islands isolated by rubble fields (n = 132) and 12 islands isolated by seagrass meadows (n = 335). Note the skewed distribution of mostly large lobsters on rubble-isolated islands. Error bars are +1 SE.



Figure 3. The mean proportions of spiny lobster immigrants and emigrants from each size class on 12 habitat islands isolated by rubble fields (immigrants = 65, emigrants = 41) and 12 islands isolated by seagrass meadows (immigrants = 199, emigrants = 160). Similar net movement (N) of lobsters occurred into habitat islands (i.e., immigrations). Dark circles represent seagrass-isolated islands and open circles represent rubble-isolated islands. Error bars are ± 1 SE.

The evidence for the size-specific dispersal patterns is supported by movement activity patterns in which isolation of habitat island had no effect on daily movement within an island. The ANCOVA showed no significant difference in island isolation, but the covariate-lobster size-was significantly associated with distance moved (Table 3). Mean daily movement rates were not significantly different within habitats, (mean ± SE: rubbleisolated habitats, 10.0 ± 1.0 m; seagrass-isolated habitats; 7.1 ± 0.7 m) but increased significantly with increased lobster size (Fig. 4). There was a marked increase in movement activity in lobsters 25-30 mm CL. Den fidelity data did not conform to the statistical assumption of homogeneity of slopes, and therefore the ANCOVA was not run. Plots of the average residence time spent in a particular den by various sizes of lobsters showed no trends on islands.

Table 3. Results of the analysis of covariance on the effects ofisland isolation on daily movement activity, with individual lobstersize as the covariate.

Source	df	MS	F	р
Island isolation	1	0.04	0.56	ns*
Lobster size (covariate)	1	51.05	825.8	< 0.0001
Error	178	0.06		
TOTAL	180			

*Not significant at $\alpha = 0.05$.



Figure 4. Daily movement of spiny lobsters on 12 babitat islands isolated by rubble fields and 12 islands isolated by seagrass meadows. There were no significant differences in mean distance moved on babitat islands. Significant increases in movement activity occurred in lobsters over 25 mm CL. Solid lines are 95% confidence intervals, and dasbed lines are 95% prediction intervals.

Discussion

Effects of Habitat Insularity on Dispersal

The availability of critical habitat for all life-history stages of mobile benthic species may result in population bottlenecks if those habitats are limited in areal extent or are degraded (Wahle & Steneck 1991; Butler & Herrnkind 1997). Butler and Herrnkind (1997) show that the size of the P. argus population in Florida Bay, U.S.A., increases when crevice shelters are added to shallow vegetated habitats. They postulate that the immediate availability of crevice habitat relieves the demographic restriction that young juveniles face when they leave vegetation settlement habitat to dwell in crevice shelters. The reverse scenario may also be true, in which the absence of vegetated substrate around crevice habitats may have a similar regulatory effect on populations. In insular mangrove and coral habitats in Belize, greater abundances of spiny lobsters with a corresponding higher proportion of juveniles occurred on habitat islands surrounded by seagrass meadows. This probably reflects an increase in the settlement of postlarval recruits in the surrounding seagrass habitat, as well as the use of seagrass cover by juveniles for dispersal to coral or mangrove patches. The probability of colonization by pelagic spiny lobster postlarvae may decrease with smaller patch sizes due to the stochastic and patchy nature of larval supply and the variability in physical transport to patches (e.g., P. argus, Herrnkind & Butler 1994; Acosta et al. 1997; Butler et al. 1997). Seagrass is an important settlement habitat for postlarvae settling from the plankton, and the availability of seagrass meadows

increases the primary settlement area around insular mangrove islands and coral reefs. Although larval recruitment was not directly measured in this study, the contrasting lobster abundances and size-class distributions on rubble-isolated versus seagrass-isolated islands were as expected with the availability of seagrass meadows. Smaller populations dominated by large lobsters were found on islands isolated by rubble fields, whereas higher abundances with a greater proportion of small juveniles occurred on seagrass-surrounded islands.

Postlarval recruitment patterns and habitat use by juvenile lobsters are under significant control by habitatspecific predation. Postlarval recruits have significantly higher survival in seagrass (Thallasia testudinum) and macroalgae (Laurencia spp.) than on rubble substrate (Acosta & Butler, unpublished data). Similarly, predation on small juveniles <20 mm CL is lowest in vegetation, but predation on larger juveniles >25 mm CL is lower in coral and other crevice shelters than in vegetation (Herrnkind & Butler 1986; Acosta & Butler 1997). Although crevice shelter is the primary habitat for larger lobsters, Thallasia meadows are important for maximizing the survival of young juvenile P. argus. Other vegetated habitats may play similar roles for small juveniles of other species of lobsters (e.g., Phyllospadix seagrass beds for P. interruptus off California [Serfling & Ford 1975]; small algal-covered holes in boulder fields for P. japonicus off Japan [Yoshimura & Yamakawa 1988], and P. cygnus off western Australia [Jernakoff et al. 1994]). Also, the predation risk associated with crossing extensive areas of bare substrate may be prohibitively high for all but large adult lobsters that are under threat from fewer kinds of predators (Smith & Herrnkind 1992).

The nature of the surrounding habitat is important for benthic dispersal as well. By reducing exposure to predators, seagrass linkages may facilitate the dispersal of juvenile lobsters. Movement of all sizes of lobsters into or from islands surrounded by seagrass was up to four times higher than on rubble-isolated islands, especially in the movement of large juveniles to and from seagrassisolated islands. On habitat islands isolated by rubble fields, there was little or no immigration or emigration of juveniles, so it is possible that most of the juveniles present on those islands may have settled there as postlarvae and become restricted to those habitats. The net direction of movement was into habitat islands. Therefore, the population size structure on seagrass-isolated islands may be associated with increased immigration of juveniles from the surrounding seagrass beds and nearby habitat islands.

The effect of the surrounding substrate on juvenile dispersal is further supported by other lines of evidence. Whereas young juveniles (<25 mm CL) are fairly sedentary in nursery habitats, older juveniles become increasingly vagile with size (Childress & Herrnkind 1996; this study). This increase in movement activity occurred

within islands surrounded by seagrass meadows or rubble fields, but immigration and emigration of juveniles occurred mainly on seagrass-isolated sites. Disturbance of animals by handling could result in a significant number of those animals leaving the area. For example, Mac-Diarmid et al. (1991) evaluated the effects of capture and tagging on site fidelity for Jasus edwardsii on New Zealand reefs and found that up to 50% of handled animals left the area 1 day later. In the present study, a greater proportion of lobsters remained on site more than 1 day, but this was not compared to a no-handling control treatment. The differences between the two studies may be due to the larger sizes of adult J. edwardsii used in trials by MacDiarmid et al. (1991), compared with this study in which juvenile *P. argus* dominated the population. The residence time spent in a particular den appeared to have no relationship to surrounding habitat and may be associated with some other factor, such as the availability of food nearby.

These results, coupled with evidence from differences in population size structure in insular habitats, suggest that dispersal of juveniles is restricted to habitats surrounded by bare sand and rubble fields. The effects of demographic bottlenecks due to habitat isolation may be mitigated in areas with extensive shallow vegetated habitats that have multifunctional roles in the life history of mobile benthic species. This indicates the need to quantify and understand how the different life-history stages of mobile animals like spiny lobsters interact with heterogenous habitats.

Implications for the Conservation of Exploited Benthic Species

Soulé and Simberloff (1986) outlined three stages in the design of nature reserves: identify target or key species, determine the minimum number of individuals necessary to maintain a viable population, and estimate the minimum critical area needed to sustain the population. The design of many marine reserves is generally based on incorporation of "representative" habitats for the conservation of species diversity rather than the requirements of threatened or "target" species (Inglis 1993). For marine reserves and harvest refuges in particular, to effectively protect exploited species, the interaction of the organisms with their physical habitats must be understood, including larval supply to key nursery habitats, ontogenetic habitat requirements, and dispersal and migration patterns (Carr & Reed 1993; Dugan & Davis 1993). Conservation efforts in marine harvest refuges have been directed largely at protecting a breeding stock or increasing the fishery yield of target species (DeMartini 1993). These limited goals must be expanded to the protection of all important habitats that will support an intact life history. The role of habitats that serve as shelter, foraging grounds, or movement corridors for exploited species must be quantified and incorporated into the design of protected areas.

The physical characteristics of nature reserves necessary to support minimum viable populations have been the focus of much discussion, but few empirical studies have investigated the mechanisms by which these factors affect habitat use and dispersal. For example, the size and shape of reserves and the nature of the surrounding habitat may influence the dispersal of terrestrial fauna into or out of insular patches (Hooper 1971; Wegner & Merriam 1979; Janzen 1983; Schonewald-Cox & Bayless 1986; Stamps et al. 1987). Dispersal may be more restricted on habitat islands with "hard edges," which animals will not cross, than on patches with "permeable" or "soft-edged" boundaries, which animals utilize to some extent (Buechner 1987; Stamps et al. 1987). In coastal marine environments, seagrass, macroalgae, or other vegetation may make insular habitats more permeable, allowing for an increase in foraging range or making insular patches more accessible to vulnerable size classes of mobile animals. If these habitats are not protected along with important insular habitats, protection of target species that use such habitats may be negated (Hooper 1971; Janzen 1983). The work of Hunt et al. (1991, cited in Childress 1997) suggests that the small core protected area at Looe Key reef of Florida, U.S.A., is inadequate for protecting spiny lobsters that may be removed by the fishery during the lobsters' nightly foraging in adjacent seagrass beds.

The function of habitat as movement corridors has been the focus of much discussion (Simberloff et al. 1992 and references therein). If corridors are shown to aid dispersal and, in particular, increase immigration rates, the effects of demographic stochasticity may be lessened. Natural barriers to the immigration of wideranging species may limit the size of a population, its size structure, and the ability of individuals to exploit new resources. Simberloff et al. (1992) point out that such effects depend on the dispersal of target species in specific refuge systems and on the characteristics of the corridor that facilitate such movement. Understanding the migration patterns of spiny lobsters and the habitats used to facilitate movement are important to the effective planning of conservation strategies for protecting such heavily exploited animals (MacDiarmid et al. 1991). Vegetated habitats may indirectly affect lobster populations in primary habitats like coral reefs and mangroves by facilitating the dispersal of juveniles that might otherwise be confined. If juvenile "nursery" habitats are physically separated from adult breeding grounds, then movement corridors need to be identified and protected to prevent poaching of dispersing subadults or degradation of the habitat by the destructive practices associated with fishing. Young adults migrating to breeding grounds may become the focus of intensive fishing if migratory routes are left unprotected.

Restrictions on emigration may also have destabilizing effects on insular populations that may reach critical densities (Rolf 1975; Okubo 1980; Stamps et al. 1987). For "open" populations of marine species with widely dispersing larvae, larval supply and the availability of suitable benthic habitat often interact to produce observed distribution and abundance (see review by Caley et al. 1996). In limited-area marine habitats where larval supply is high, the limitation on emigration may lead to elevated population densities and density-dependent regulation of the population. For example, such densitydependent effects on population size and dynamics have been postulated for limiting demersal flatfish (Beverton 1995) and rock lobster populations (Phillips 1990) in which juveniles become over-crowded on insular habitats of limited size. If larval supply to an area is low, however, an increase in settlement habitat may increase recruitment levels. In this context, seagrass constitutes an important habitat that warrants protection. Seagrass habitat appears to play multiple roles for Caribbean spiny lobster populations, including that of settlement habitat and dispersal corridors between habitat islands. Much work still needs to be done to elucidate the dispersal dynamics of larvae and adults of open populations in heterogenous habitats.

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