Marine reserves for Caribbean spiny lobster: empirical evaluation and theoretical metapopulation recruitment dynamics

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Abstract. Field data on spiny-lobster abundance, habitat quality, and hydrodynamic transport patterns for a reserve *(ECLSP)* and three exploited sites *(CI, EI, LSI)* were used to assess reserve success in reducing fishing mortality and increasing theoretical metapopulation recruitment. Fishing mortality was estimated empirically by quantification of lobster density at ECLSP and the three exploited sites before and after the start of the fishing season in two years. Fishing mortality was estimated to be 47–98% lower at the reserve. Using a circulation model, we theoretically assessed effectiveness of ECLSP and nominal reserves at the exploited sites in augmenting recruitment through redistribution of larvae to all sites. Larvae discharged from ECLSP and EI recruited throughout Exuma Sound, whereas those from LSI and CI recruited only to CI and LSI. Hence, only reserves at EI and ECLSP would be suitable for metapopulation recruitment. In selecting an optimal reserve for metapopulation recruitment, use of information on habitat quality or adult density did not yield a higher probability of success than did determining the reserve location by chance. The only successful strategy was one that used information on transport processes. Designation of effective marine reserves therefore requires careful attention to metapopulation dynamics and recruitment processes.

Extra keywords: marine protected areas, *Panulirus argus*, metapopulation dynamics, source-sink dynamics, larval transport, larval supply, marine conservation biology, no-take reserves

Introduction

Marine reserves may be particularly useful in the conservation of heavily exploited species (Roberts and Polunin 1993; Bohnsack 1994; Man *et al.* 1995; Guénette *et al.* 1998), including spiny lobsters (Davis and Dodrill 1980; Babcock *et al.* 1999; Edgar and Barrett 1999; Kelly *et al.* 2000), if spawning-stock biomass increases within reserves and subsequently increases larval production and recruitment to the metapopulation (*sensu* Hanski 1998, 1999). Reserve effectiveness in producing these effects will depend in part on the life history of target species (Allison *et al.* 1998; Guénette *et al.* 2000); on metapopulation source-sink dynamics (Lipcius *et al.* 1997; Crowder *et al.* 2000); on the management scheme (Gardner *et al.* in press); on spatial aspects such as reserve size, geometric configuration, and location (Dugan and Davis 1993; Stockhausen *et al.* 2000; Stockhausen and Lipcius 2001 this issue); and on hydrodynamic transport and recruitment processes (Carr and Reed 1992; Roberts 1997; Stockhausen *et al.* 2000; Botsford *et al.* 2001).

Various strategies are available for selecting the optimal site for a no-take marine reserve designed to augment metapopulation abundance and recruitment (Allison *et al.* 1998; Roberts 1998; Agardy 2000; Crowder *et al.* 2000). Selection can be somewhat random and opportunistic (Roberts 1998, 2000); can be based on societal needs (Agardy 2000); can result from empirical information on population density, habitat quality, migratory patterns, and exploitation rates (Bohnsack 1994; Mangel 2000; Walters 2000); and can be derived from an understanding of recruitment processes (Carr and Reed 1992; Crowder *et al.* 2000; Warner *et al.* 2000; Stockhausen *et al.* 2000; Botsford *et al.* 2001; Stockhausen and Lipcius 2001 this issue). We used two ecological criteria to appraise the success of an existing reserve and three proposed reserves for spiny lobster in increasing abundance and recruitment: empirical estimates of the rate of population loss due to fishing and theoretical estimates of the contribution of recruits to the metapopulation. Ultimately, the investigation provided insights into the utility of various ecological criteria in reserve selection.

Experimental approach and system

As a model system, we used the Caribbean spiny lobster (*Panulirus argus*) in Exuma Sound, Bahamas, where we have population, habitat, and larval-transport data for four widely separated sites (Lipcius *et al.* 1997). Specifically, we assessed the likelihood of success of a reserve at each of the four Exuma Sound sites (= populations) in increasing abundance, body size, and recruitment of *P. argus*, assuming that these sites comprise a semiclosed metapopulation (Lipcius *et al.* 1997; Stockhausen *et al.* 2000; Hickey in press; Stockhausen and Lipcius 2001 this issue). We did not assume that the populations comprise a classical metapopulation (*sensu* Levins 1969, 1970), which is characterized by frequent extinctions and dependent on recolonization for regional persistence. Rather, we assumed metapopulation dynamics in the broader sense (Harrison and Taylor 1997; Hanski 1998, 1999), which encompasses *fragmented* but *interconnected* populations (Hanski 1998) and which does not make detailed assumptions about the dynamics of the metapopulation.

We assumed that the four sites in Exuma Sound harbour *fragmented* populations of *P. argus* because the sites are separated by either (i) approximately 100 km of shoreline, which is much greater than the average benthic dispersal distance of most juveniles and adults in populations of *P. argus* (Herrnkind 1980; Davis and Dodrill 1989); (ii) extensive shallow banks with little structural relief, food, or shelter, which limit intersite movements (Herrnkind 1980), or (iii) the deep, 2000-m basin of Exuma Sound (Fig. 1). Furthermore, the major coral reefs, where adults reside and reproduce, are fragmented similarly across the four sites in Exuma Sound (ReefBase: http://www.reefbase.org/database/Viewer.asp?PicFileName=bhs). The nominal

Fig. 1. Study sites in Exuma Sound, Bahamas: Exuma Cays Land and Sea Park (ECLSP), Eleuthera (EI), Cat Island (CI), and Lee Stocking Island (LSI).

populations are, however, *interconnected* by larval and postlarval interchange among breeding populations at the sites (Herrnkind and Lipcius 1989; Lipcius *et al.* 1997; Eggleston *et al.* 1998; Stockhausen *et al.* 2000). Thus, each of the four populations is characterized by reproductive and mortality rates within the populations and immigration and emigration rates of larvae and postlarvae among populations, which are the four basic demographic parameters of populations in a metapopulation (Hanski 1998).

We measured success of a reserve both empirically and hypothetically. First, we empirically assessed the effectiveness of an existing reserve (Exuma Cays Land and Sea Park [ECLSP]) by determining abundance and body size of *P. argus* in the spring reproductive period during the closed fishing season and again in the autumn after the chief activity of the fishing season. We considered the reserve at ECLSP to be effective if the decline in abundance and size of *P. argus* after intense fishing activity was less at ECLSP than at the three exploited sites. We assumed that the decrease in size-specific abundance of *P. argus* at each site was a function of total loss, which is composed of natural mortality, fishing mortality, and emigration. We further assumed that the range in variation of natural mortality and emigration rates was represented in the three exploited sites and that the rates at ECLSP did not differ from the mean of the rates in the exploited sites. Any discrepancy in total loss of *P. argus* between ECLSP and the three exploited sites would therefore be due to differential fishing mortality.

The use of a change in abundance across the fishing season in protected and exploited areas avoids much of the temporal and spatial confounding associated with comparisons of abundance in exploited and protected sites at single or different points in time (Allison *et al.* 1998). For example, comparisons of spiny lobster (Lipcius *et al.* 1997) and Nassau grouper (Chiappone and Sealey 2000) abundances in the ECLSP reserve with those at exploited sites in Exuma Sound suffered from spatial confounding and the lack of pre-reserve data. Similarly, a comparison of queen-conch abundances at ECLSP and an exploited site in Exuma Sound (Stoner and Ray 1996) was afflicted by spatial confounding, as well as by temporal confounding due to differences in the years of sampling at the protected and exploited sites. Spatial and temporal confounding are severe flaws in experimental designs for marine species (Underwood 1997), flaws that characterize retrospective analyses of abundance and size in protected and exploited areas (Roberts and Polunin 1993; Allison *et al.* 1998). We avoided much of the confounding by comparing abundances before and after the fishing season in the reserve and in replicated exploited areas. Nonetheless, our analysis of abundance and size remained spatially confounded because the reserve was not replicated.
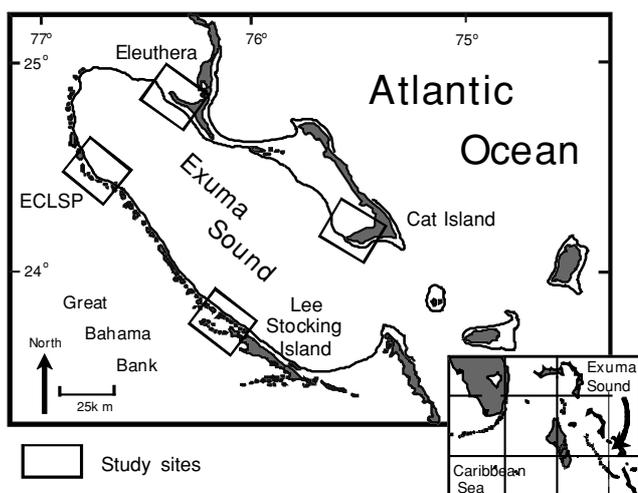
We assessed the effectiveness of the existing and proposed reserves theoretically by estimating the degree to which larvae produced at a reserve were redistributed as recruits among all the sites. An existing or proposed reserve was deemed to increase recruitment optimally when all four sites (*i.e.*, the metapopulation) received recruits from it. In essence, this criterion is a surrogate measure for a key postulated benefit of marine reserves—metapopulation enhancement (Roberts and Polunin 1993; Bohnsack 1994; Man *et al*. 1995). Each proposed reserve was large enough (~15% of coastal reefs) to meet the threshold requirement for enhancement of recruitment (Stockhausen *et al*. 2000). Source-sink dynamics (Lipcius *et al*. 1997; Crowder *et al*. 2000) and variation in habitat quality were considered only qualitatively (see below).

Methods

Exuma Sound sites

Exuma Sound is a large (200 × 65 km), deep (> 1 km), semienclosed (one major channel to the Atlantic Ocean) basin surrounded by the Exuma Cays, Great Bahama Bank, Eleuthera, Cat Island, and Long Island (Fig. 1). The sound is lined by a narrow shelf, by low islands, and by shallow carbonate banks. Circulation in the sound is dominated by an eddy field superimposed on a north-westward drift (Colin 1995; Hickey in press). The eddy field is composed of large, vigorous gyres (Fig. 2) extending to 200 m depth (Lipcius *et al*. 1997; Stockhausen *et al*. 2000; Hickey in press), above which most larvae and postlarvae of *Panulirus argus* occur (Yeung and McGowan 1991). Water in Exuma Sound is exchanged regularly with the Atlantic Ocean and with the shallow banks by means of dense, high-salinity intrusions. The Caribbean spiny lobster occurs commonly in reefs and inshore lagoons ringing Exuma Sound (Herrnkind and Lipcius 1989; Lipcius *et al*. 1997).

Sites other than the existing marine reserve in the north-western corner of the sound (ECLSP) were selected to provide broad spatial coverage of spiny-lobster habitats throughout Exuma Sound (Fig. 1): Cat Island (CI) to the south-east, Eleuthera (EI) to the north-east, and Lee Stocking Island (LSI) to the south-west. The sites are characterized by coral reefs, patch corals, sand-covered hard bottom, sea-grass meadows, and fields of gorgonians and sponges (Lipcius *et al*. 1997). Coral reefs occur commonly to 30 m depth before the bottom plunges to 2000 m. Most small islands (Exuma Cays) lie on the western edge of the sound; tidal inlets connect the sound to the shallow (3–5 m depth) Great Bahama Bank (Fig. 1).

The ECLSP reserve, which extends 35.4 km from Wax Cay Cut south-east to Conch Cut in the north-western quadrant of Exuma Sound, is a 456-km^2 no-take zone supervised by the Bahamas National Trust. The reserve, which was established in 1959 by the trust, is the world's oldest land and marine park. Most islands within ECLSP are uninhabited, but recreational boats are common. Although ECLSP has
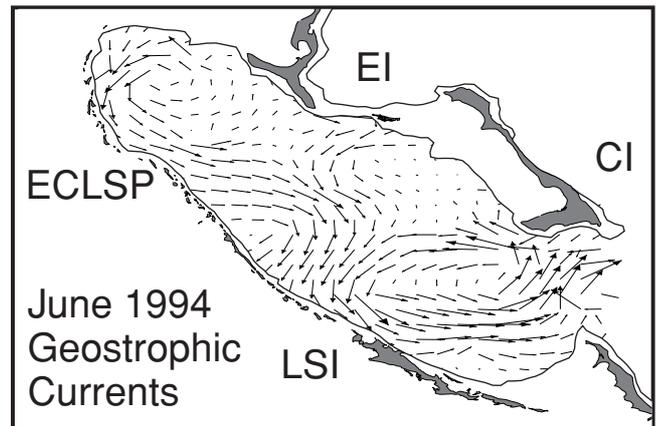

Fig. 2. Circulation in Exuma Sound: two-dimensional vector representation of near-surface flow field based on acoustic Doppler current profiler, conductivity-temperature-depth, and drifter measurements in Exuma Sound during the spring reproductive period (June, 1994; B. Hickey in press, unpubl. data).

been a no-take reserve since 1986, poaching by local fishers and visiting boaters is not uncommon (R. Darville, ECLSP Park Warden, pers. comm.).

Adult density and size

Adult spiny-lobster density was measured at each site during the reproductive period in the spring during the closed fishing season and again in the autumn after the principal active period of the fishing season. At each site, we surveyed haphazardly (1994) and randomly (1995) selected coral reefs (Table 1) drawn from a grid system superimposed over the total area at each site at depths shallower than 20 m; reefs were mapped with a Global Positioning System.

Reefs were surveyed visually by SCUBA. During a survey, divers examined crevices for lobsters until either the entire reef was surveyed or 30 min had elapsed. Carapace length, sex, reproductive condition, water depth, and shelter occupancy of each lobster were recorded. A subset of individuals was captured with a tail snare and measured with calipers to provide accurate size measurements. Otherwise, carapace length was estimated with a handheld ruler. Total reef area and the proportion of reef area searched were estimated after each survey. Density was calculated as the number of lobsters divided by area of reef surveyed.

Habitats were classified as (i) shelter habitat (live coral reefs, patch coral heads, relict spur and groove reefs, and ledges) (ii) gorgonians and sponges (iii) sea-grass meadows, or (iv) sand. Areal cover of each habitat type was estimated along the 7-m depth contour by means of replicate sets of six transects at each site. For each transect, the research vessel travelled along the contour at 6 knots for 12 min. An underwater viewing port permitted estimation of percent cover of each

Table 1. Number of coral reefs sampled for adult Caribbean spiny lobsters

Site	1994		1995	
	Spring	Autumn	Spring	Autumn
Eleuthera	6	10	9	11
Cat Island	3	15	8	10
Lee Stocking Island	17	7	10	9
Exuma Cays Land and Sea Park	13	7	8	7

habitat type every 30 s, while position (GPS) was recorded every 3 min. Site-specific availability of lobster shelters was calculated as the mean percentage cover from the replicated sets of six transects in each habitat type.

Estimates of density per unit reef area may yield biased estimates of abundance (= density × reef area) at a site when sites differ significantly in areal cover of shelter (RNL and WTS unpubl. data) and lobsters do not disperse to distant sites. When lobsters distribute themselves across shelters at any given site, a high lobster density per unit of shelter area may derive from high lobster abundance at that site, concentration of a lower abundance of lobsters in only a few shelters (e.g., reefs) at that site, or both. Without measurement of the amount of shelter habitat available at a site, therefore, one cannot distinguish between high abundance and low shelter availability (RNL unpubl. data). Consequently, we standardized adult density by the amount of shelter per site. For each survey, we computed the standardized adult density as the product of adult density per shelter and mean percentage cover of shelters at that site, as described above. Size measurements from the adult surveys were calculated as the mean size per shelter for each site. Standardized densities and mean sizes per shelter were analysed as the dependent variables in ANOVA models with site (4 levels), season (2 levels), and year (2 levels) as fixed factors. To normalize the data and reduce heterogeneity of variance (Underwood 1997), we analysed density as the ln-transformed, standardized number of lobsters per shelter. In all cases, variances were not heterogeneous (Cochran's C statistic; $P > 0.05$) after transformation; size data did not require transformation to meet statistical assumptions of normality and homogeneity of variance. When necessary, Student-Newman-Keuls (SNK) tests were used in *a posteriori* multiple comparisons (Underwood 1997).

Simulated larval and postlarval transport

A two-dimensional (2-D) circulation model (Stockhausen *et al.* 2000) was used to simulate larval and postlarval transport in Exuma Sound. The model tracked changes in stage-specific density of planktonic larval stages within a 2-D (horizontal) oceanic region due to (a) hatching of larvae after adult reproduction along the coast (one-dimensional [1-D] boundary) (b) horizontal dispersal by 2-D advective currents and turbulent diffusion (c) age-specific mortality, and (d) settlement along the coast. The 2-D (horizontal) spatial grid for the model consisted of 1872 cells; each cell was 2.5 km × 2.5 km. The 1-D spatial grid for the coast consisted of the 254 linear segments (632.5 km total length) forming the coast and deep-water boundary to the model grid. In the coastal grid, the 21 segments (52.5 km) at the mouth of Exuma Sound were classified as a deepwater boundary, where larval and postlarval loss occurred. The remaining 580 km of coastline was classified as shallow coastal habitat, available for settlement by postlarvae.

Planktonic larvae were produced along the coast during the spring reproductive period at each of the four sites in equal numbers. Simulations with field adult abundance at each site and the corresponding estimates of larval output (Lipcius *et al.* 1997) yielded similar patterns. Because our goal was to examine the efficacy of marine reserves at each of the four sites, we have presented results of the simulations with equal adult abundances. In the simulations, larvae entered the offshore region, where they were subject to mortality and transport by hydrodynamic currents as passive particles. After 180 d in the plankton, surviving larvae metamorphosed to the postlarval stage, which actively migrated toward the nearest segment of the coast and settled. We believe that the circulation model yields a reasonable approximation of larval transport in Exuma Sound because spatial patterns in predicted settlement rates derived from the circulation model are significantly correlated with observed postlarval settlement rates at the four sites (RNL and WTS unpubl. data).

Results

Adult density

Adult density varied significantly by year (1995 > 1994), by season, and by site (Fig. 3, Table 2), although the season-×-site interaction effect was significant, precluding conclusions about the main effects of season and site. The effect of season was therefore analysed within each level of site and that of site within each level of season. Densities were significantly lower in the autumn, after the active fishing period, than in the spring at EI (SNK multiple
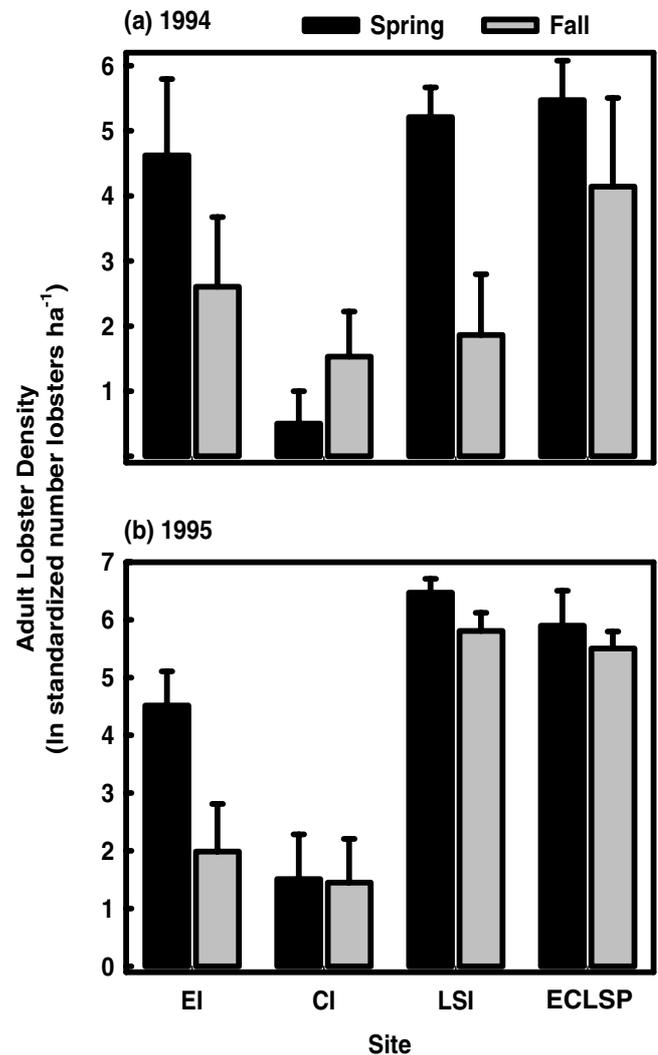

Fig. 3. Standardized densities (ln-transformed number ha^{-1}) of adult spiny lobsters in coral reefs, patch coral heads, relict spur-and-groove reefs, and ledges during the spring reproductive period before the fishing season (dark bars) and during the autumn after 2–3 months of exploitation (light bars). Standardized densities of adult spiny lobsters were transformed by a factor representing the areal cover of adult habitat at each site. Vertical bars signify standard errors. Adult densities were significantly lower at CI than at the other sites, which did not differ (SNK multiple comparisons).

Table 2. Analysis of variance for adult density
Data were ln-transformed to equalize variances. Asterisks reflect degree of statistical significance

Source of Variation	SS	df	MS	F	P
Year	25.75	1	25.75	4.85	0.029*
Season	34.18	1	34.18	6.44	0.012*
Site	292.46	3	97.49	18.38	0.0005****
Year × Season	1.71	1	1.71	0.32	0.572
Year × Site	40.44	3	13.48	2.54	0.059
Season × Site	42.71	3	14.24	2.68	0.049*
Year × Season × Site	21.96	3	7.32	1.38	0.252
Error	705.13	133	5.31		

Table 3. Effectiveness of ECLSP reserve for Caribbean spiny lobster, as indicated by the decrease in total mortality (Z) during a portion of the fishing season
Densities are back-transformed means of the ln-transformed densities (number ha^{-1}) presented in Fig. 3. Proportional change is the ratio of autumn to spring density. Values of Z were calculated from the equation *proportional change* = e^{-Z}

Year	Site	Spring density	Autumn density	Proportional change	Z	Decrease in Z at ECLSP relative to LSI and EI	Mean Z reduction
1994	ECLSP	237.8	63.0	0.26	1.33		
	LSI	183.4	6.4	0.04	3.35	60.3%	
	EI	101.7	13.5	0.13	2.02	34.2%	
							47.3%
1995	ECLSP	251.2	245.3	0.98	0.02		
	LSI	646.4	332.5	0.51	0.66	97.0%	
	EI	91.5	7.3	0.08	2.53	99.2%	
							98.1%

comparisons; $P < 0.05$) and LSI ($P < 0.10$) but not at ECLSP ($P >> 0.10$) and CI ($P >> 0.10$). In these SNK multiple comparisons, we deemed $P < 0.10$ statistically significant to provide a risk-averse test of the fishing effect. In spring, density was significantly lower at CI than at the remaining three sites ($P < 0.05$), which did not differ significantly ($P > 0.10$). In autumn, density at ECLSP was higher than that at CI ($P < 0.05$), but none of the other intersite comparisons was significant ($P > 0.10$). Adult density and depth showed no significant relationship over the range of 3–30 m ($F = 1.32$; df = 5, 184; $P = 0.26$).

In the analysis of the decrease in adult density during the fishing season, which serves as an approximation of fishing mortality (F), we estimated that the ECLSP reserve lowered fishing mortality markedly but differently in the two years (Table 3). In 1994, the estimated average reduction in fishing mortality at ECLSP from that at EI and LSI was 47% (range 34–60%); in 1995 it was 98% (range 97–99%). We did not contrast ECLSP and CI because the low densities at CI precluded an accurate estimate of fishing mortality (Table 3).

Size structure

Mean size of both males and females differed significantly by site but not by season or gender in a consistent fashion (Figs 4 and 5, Table 4). Males were significantly smaller at EI and LSI than at ECLSP and CI (SNK multiple comparisons; $P < 0.05$); females were significantly smaller at LSI than at all other sites ($P < 0.05$), which did not differ significantly ($P > 0.10$). Given the significant site × gender interaction effect (Table 4), we also analysed the effect of site within each level of gender. We found no detectable pattern in the effect of gender within each level of site (Fig. 5). Like density, adult size showed no significant relationship with depth ($F = 0.42$; df = 5, 483; $P = 0.84$).

Simulated larval and postlarval transport

The patterns in simulated larval transport and postlarval settlement showed four major features (Fig. 6). First, retention rates of larvae and postlarvae produced at each of the four sites were spatially variable, ranging from nearly 80% retention of larvae produced at CI to an average of less than 20% retention at the other three sites. Second, larvae
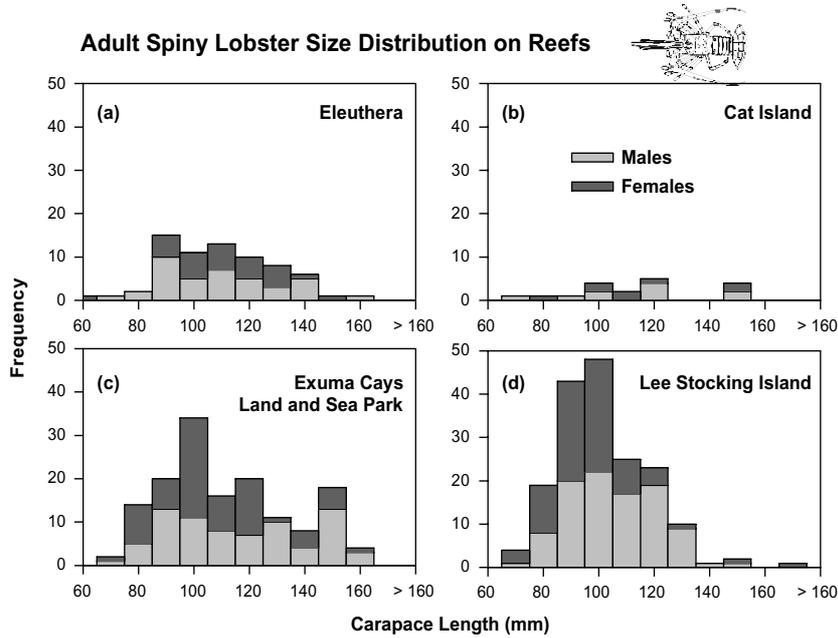
Adult Spiny Lobster Size Distribution on Reefs

Fig. 4. Size-frequency distribution of male and female adult spiny lobsters on coral reefs at Eleuthera (*a*), Cat Island (*b*), Exuma Cays Land and Sea Park (*c*), and Lee Stocking Island (*d*) in 1994 and 1995. The data are aggregated over all sampling periods in 1994 and 1995 when lobster size was measured.

Table 4. Analysis of variance for adult size in 1995

Asterisks mark *P* values deemed statistically significant. The Season-×-Gender interaction effect was deemed significant to provide a conservative analysis, but the lower-level analysis (SNK multiple comparisons) revealed no consistent patterns. Because the Site-×-Gender interaction effect was significant, the effect of Site was analysed within each level of Gender. Males were significantly smaller at EI and LSI than at ECLSP and CI; females were significantly smaller at LSI than at all other sites (SNK multiple comparisons; *P* < 0.05)

Source of variation	SS	df	MS	*F*	*P*
Season	431.6	1	431.6	1.2	0.271
Site	4726.4	3	1575.5	4.5	0.005*
Gender	60.6	1	60.6	0.2	0.679
Season × Site	1720.9	3	573.6	1.6	0.186
Season × Gender	1108.9	1	1108.9	3.1	0.078
Site × Gender	3202.9	3	1067.6	3	0.031*
Season × Site × Gender	809.8	3	269.9	0.8	0.516
Error	59743.4	169	353.5		

discharged from southern Exuma Sound sites (*i.e.*, LSI and CI) settled mostly in southern Exuma Sound; virtually no larvae were transported from LSI and CI to ECLSP and EI. Third, larvae produced in northern Exuma Sound (*i.e.*, ECLSP and EI) were advected to all four sites; the most equitable advection of larvae was from EI to the other sites. Fourth, most larvae retained in the sound were advected to CI, resulting in a spatially inequitable redistribution of larvae and settling postlarvae in Exuma Sound.

Additional simulations were conducted with larvae released at the mouth of Exuma Sound to mimic advection of larvae from sites outside. Few of these larvae invaded the sound; their retention rate was less than 0.1%, and their pattern of simulated settlement mimicked that of larvae released in southern Exuma Sound. We therefore did not pursue these simulations further because the conclusions about these spatial patterns were similar to those derived from the analysis of larvae released within Exuma Sound.
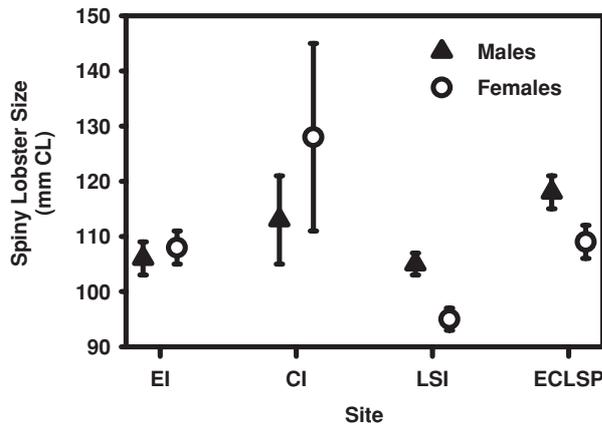
Fig. 5. Mean size of male and female adult spiny lobsters on coral reefs at Eleuthera (EI), Cat Island (CI), Exuma Cays Land and Sea Park (ECLSP), and Lee Stocking Island (LSI) in 1994 and 1995. The data are collapsed over the seasons (spring and autumn) because seasons did not differ consistently in lobster size (Table 4). Vertical bars signify standard errors. For females, mean size was significantly lower at LSI than at the other locations, whereas for males, mean size at EI and LSI was lower than that at ECLSP but not CI (SNK multiple comparisons, $P < 0.05$).
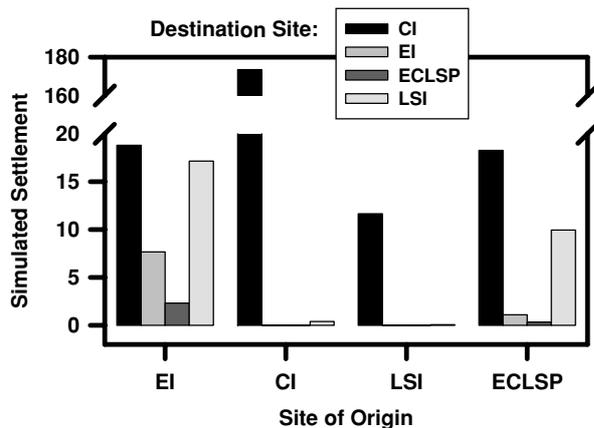

Fig. 6. Simulated larval transport and postlarval settlement in Exuma Sound. Release sites are on the abscissa; settlement sites are on the ordinate. Planktonic larvae were produced along the coast during the spring reproductive period at each of the four sites in equal numbers. In the simulations, larvae entered the offshore region and were transported by advection and diffusion as passive particles. After 180 days in the plankton, larvae metamorphosed to the postlarval stage, which actively migrated toward the nearest coast and settled.

Discussion

In the study reported here, we did not address the relative merit of a single reserve and several small reserves (Stockhausen and Lipcius 2001 this issue) but instead emphasized the effect of spatial position on reserve success. Our major findings were that mature lobster density and size were not the most reliable measures of reserve effectiveness; that, in contrast, estimating fishing mortality

at the reserve and exploited sites demonstrated that ECLSP does have a substantially positive effect on local population abundance; and that the likelihood that a reserve would effectively replenish recruitment at the metapopulation level depended significantly on its location.

Exuma Cays Land and Sea Park

Our results indicate that the existing marine reserve at ECLSP is situated effectively. Reductions in adult density due to fishing were substantially less at ECLSP than at EI and LSI. Lobsters there were at least as large as, and sometimes markedly larger than, those at the other sites. Similar patterns in density and size occurred in the queen conch, *Strombus gigas* (Stoner and Ray 1996), and in Nassau grouper, *Epinephelus striatus* (Chiappone and Sealey 2000), in comparisons of ECLSP and other sites in Exuma Sound. Because larval output depends on adult biomass, and because the sites do not differ in fecundity (Lipcius *et al*. 1997), the high density and large size of adult spiny lobster at ECLSP also yields a high larval output.

In the hydrodynamic transport simulations, larvae released at ECLSP settled as postlarvae throughout Exuma Sound, so the high abundance of adults at ECLSP increased recruitment of postlarvae for the metapopulation in Exuma Sound. The level of observed postlarval settlement at ECLSP (Lipcius *et al*. 1997), although low, was comparable to those at EI and LSI, so recruits are available to regenerate spawning stocks at ECLSP and potentially at the exploited sites.

Conversely, because adult lobster density at ECLSP was not significantly higher than that at EI and LSI, despite its protected status, recruitment or habitat quality at ECLSP may be inferior to those of LSI and EI. In fact, we found higher cover of coral reefs, gorgonians, and sponges and more preferred settlement and juvenile habitat such as the structurally complex red alga *Laurencia* (Herrnkind *et al*. 1994; Lipcius *et al*. 1997; Lipcius and Eggleston 2000) at sites other than ECLSP. Therefore, the reserve at ECLSP appears effective for increasing recruitment, though it may not be at the optimal site for a reserve.

Cat Island

Establishment of a marine reserve at CI would not be prudent if the prime consideration is protection of a spiny lobster spawning stock and enhancement of metapopulation recruitment. Larvae produced at CI are highly unlikely to settle as postlarvae at sites other than at LSI, so CI would contribute little to metapopulation enhancement. Moreover, it provides few nursery grounds of high quality (Lipcius *et al*. 1997), so postlarval and juvenile mortality are probably high, as reflected in the low adult density at CI despite high postlarval influx (Lipcius *et al*. 1997). The population at CI very probably acts as a metapopulation sink (Lipcius *et al*. 1997), so establishment of a marine reserve there would

redirect fishing effort to other sites and potentially lead to metapopulation decline as a result of source-sink dynamics (Crowder *et al.* 2000).

Lee Stocking Island

Various attributes of LSI render it attractive as a marine reserve. Adult density there was among the highest we measured and never differed statistically from the highest density at ECLSP. Habitat quality of adult reefs and the nursery grounds at LSI was unsurpassed in Exuma Sound, both in the areal cover of coral reefs used by the spawning stock (Lipcius *et al.* 1997) and in the extent of *Laurencia* meadows and other structured microhabitats (*e.g.*, *Porites* coral clumps) that are inhabited by postlarval and juvenile Caribbean spiny lobster and Nassau grouper (Herrnkind and Lipcius 1989; Eggleston 1995; Lipcius *et al.* 1997; Dahlgren and Eggleston 2000). Observed postlarval settlement at LSI was moderate and consistent from year to year (Lipcius *et al.* 1997; Eggleston *et al.* 1998), resulting in relatively stable replenishment of recruits to renew future spawning potential.

The greatest defect of LSI as a potential reserve is that larvae produced there would be highly unlikely to settle as postlarvae at sites other than CI and LSI and would therefore contribute little to enhancement of recruitment in the metapopulation. Moreover, lobsters were generally smaller at LSI than at other sites, so larval output would not be as high as the relatively high adult densities might suggest. Despite its many favourable attributes, therefore, LSI would not be a wise choice as a marine reserve intended to augment metapopulation recruitment.

Eleuthera

Eleuthera was moderate in most of its characteristics and would not necessarily be identified as a potentially optimal site for a marine reserve. Adult density was lower, though not significantly, than that at ECLSP and LSI. Similarly, lobster size was intermediate at EI between the larger sizes of ECLSP and CI and the small sizes measured at LSI. Habitat quality was lower than that at other sites but was not inadequate (Lipcius *et al.* 1997).

Nonetheless, our results show that larvae released at EI settle as postlarvae throughout Exuma Sound. Increased abundance of adults at EI would therefore be most likely to boost recruitment at all sites in the metapopulation. Given that EI harbours moderate densities of reasonably sized adults, that it supports ample coral reef and nursery habitats, that it experiences sufficient postlarval settlement for replenishment of the spawning stock, and that it is superior in providing larvae to the remainder of the metapopulation, we conclude that a marine reserve situated at EI would best serve the purpose of increasing metapopulation recruitment of the Caribbean spiny lobster in Exuma Sound. Fishing pressure there is apparently high, as indicated by the sharp (87–92%) reductions in adult density during the fishing season, but given effective enforcement, a no-take reserve at EI would be optimal.

Selection of marine reserves

Our results show that random selection of a reserve site from among the four studied here would yield only a 50% chance of increasing metapopulation recruitment (Table 5). They further show that selection based on habitat quality,

Table 5. Strategies for selection of an optimal no-take marine reserve designed to enhance metapopulation recruitment of the Caribbean spiny lobster and their estimated likelihood of success in Exuma Sound

We assumed that only one of the four sites could be established as a reserve and that the optimal sites were EI and ECLSP because of their redistribution of larvae and postlarvae to the metapopulation. ECLSP = Exuma Cays Land and Sea Park (existing reserve), EI = Eleuthera, LSI = Lee Stocking Island, CI = Cat Island

Basis for selection	Probable choice(s)	Estimated success probability
Random choice	ECLSP, EI, LSI, or CI	0.5
Habitat quality[A]	LSI or ECLSP	0.5
Adult (or juvenile) density	ECLSP or LSI	0.5 (or 0.0[B])
Habitat quality and adult density	ECLSP or LSI	0.5
Transport and recruitment	EI or ECLSP	1

[A]Habitat quality was defined as the areal cover of coral reefs and the extent of nursery grounds, which were highest at LSI (Lipcius *et al.* 1997). Although the sites in Exuma Sound are relatively free of development, the most nearly 'pristine' of the sites was ECLSP, as it is farthest from developing townships.

[B]On the assumptions that ECLSP would have lower adult density were it not a no-take marine reserve and that the resulting density at ECLSP under exploitation would be significantly lower than that at LSI, then LSI would be selected, yielding a success probability of 0.0.

the 'pristine' nature of the site, or adult density would, in this case, provide no greater likelihood of success than would random selection—50% in each case. The ecological basis for this counterintuitive outcome stems from the decoupling of adult abundance and recruitment in Exuma Sound for the Caribbean spiny lobster—postlarval recruitment, habitat quality, and adult abundance are not positively correlated, probably because of larval and postlarval transport by gyral circulation and source-sink dynamics (Lipcius et al. 1997). The only strategy that increases the likelihood of selecting a marine reserve effective in increasing metapopulation recruitment is one that incorporates transport processes. We show that selection of either EI or ECLSP by such a method yields an estimated probability of success of 1.0 given sufficient absolute levels of recruitment and constant fishing and natural mortality rates (Table 5). A reserve at EI, which was characterized by the most equitable distribution of larvae and postlarvae to the metapopulation, would in fact be more effective than one at ECLSP, although ECLSP functions effectively in metapopulation recruitment enhancement. Similarly, selection of a network of reserves (Roberts 1997), rather than a single reserve, would profit from a comparable analysis of metapopulation processes. The designation of a reserve location cannot be random and indiscriminate; rather, it requires attention to metapopulation dynamics and recruitment processes when the opportunity to use such information presents itself.

Acknowledgments

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