

Spatially explicit dispersal dynamics and equilibrium population sizes in marine harvest refuges

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For marine reserves to function as effective harvest refuges for exploited species, the reserve must protect a substantial proportion of the population for an indefinite period of time. Because most marine reserves are space-limited, the buildup and equilibrium population sizes of mobile species will be influenced by the size and boundary conditions of the refuge. A logistic rate model was used to predict equilibrium population sizes in a marine harvest refuge, based on species-specific dispersal dynamics and the spatial configuration of the refuge. The model parameters were derived for Caribbean spiny lobsters and queen conch in an isolated marine reserve at Glover's Reef, Belize, and were compared to observed population change over a 5-yr period. Spiny lobsters and queen conch, the two most heavily exploited species in the Caribbean, differ in larval recruitment rates (immigration) and mobility of adults (emigration). The expected increase in the population size of spiny lobsters in this refuge was 250% and queen conch was 420% over that of the initial fished population. The observed densities of lobsters and conch in the refuge approached the predicted estimates within three years. To further explore the impact of alternative spatial configurations on refuge populations, the model was run on the same populations in two hypothetical refuges. In a refuge of the same area but 50% less absorbing boundary (adjacent to intensively fished areas), the spiny lobster population was expected to be 30% larger than the equilibrium population size in the original refuge, whereas the queen conch population was not expected to change from that in the original refuge. In a refuge that was 50% larger and with 50% less absorbing boundary, the spiny lobster population was expected to increase 110% and the queen conch population was expected to increase 50% over the equilibrium population size in the original refuge. Relatively minor changes in refuge area and boundary conditions may thus result in major population-level responses by exploited species, depending on dispersal dynamics and habitat availability. This simple model may be applicable for rapid assessment of the potential efficacy of proposed harvest refuges.

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Introduction

Overfishing in the world's coastal ecosystems is a major challenge for marine resource management. Marine reserves are increasingly being viewed as a necessary tool for sustaining or even increasing coastal fisheries (Bohnsack, 1993; Davis and Dodrill, 1980). If a marine reserve functions as a harvest refuge for exploited species, increases are expected in the population size, mean individual size, and consequently, reproductive

output (Carr and Reed, 1993; Dugan and Davis, 1993). The local fishery is expected to benefit from an increase in larval production and from dispersal of mobile individuals from the refuge to adjacent fishing grounds. For these effects to be realized, however, the spatial characteristics of the refuge must allow for significant population increase in the refuge, while simultaneously limiting the net loss of animals to harvested areas. These dynamics may ultimately depend on the complex spatial interactions of target species with their habitats.

The primary feature of an effective nature reserve is a large areal size containing critical habitats to support the life history stages of target species (Diamond and May, 1976). However, the sizes of many reserves are most often constrained by economic and political limitations. Terrestrial studies have shown that spatial factors, particularly the geometrical shape and boundary conditions, play important roles in the efficacy of space-limited reserves by affecting the buildup and loss of mobile animals from the protected area (Blouin and Conner, 1985; Buechner, 1987; Game, 1980; Schonewald-Cox and Bayless, 1986; Stamps *et al.*, 1987). In space-limited reserves, the impact of dispersal (immigration and emigration) on population dynamics often occurs at an accelerated spatio-temporal scale than birth and death processes (Schonewald-Cox and Bayless, 1986). The buildup and persistence of a population within a reserve may thus be a complex function of the distribution of critical habitats (Acosta, 1999; McClanahan and Arthur, 2001; Paddock and Estes, 2000), the geometry of boundaries (Buechner, 1987; Stamps *et al.*, 1987), types of surrounding habitats (Janzen, 1983; Karieva, 1985), and species-specific dispersal dynamics (Turchin, 1986; With *et al.*, 1999).

An important consideration for marine reserves is that many species have "open" populations (*sensu* Caswell, 1978) in which the benthic population in coastal habitats may be decoupled from their larval output to the pelagic environment (Doherty, 1981; Hughes, 1990; Roughgarden *et al.*, 1985). Nevertheless, the magnitude of larval recruitment to a coastal population may be predictable with some inherent variability when a proportion of the common larval pool is regularly supplied to local coastal environments (Carr and Reed, 1993; Roughgarden *et al.*, 1985). Recruitment in many space-limited open populations then becomes analogous to births in closed populations (Bence and Nisbet, 1989; Caley *et al.*, 1996; Hughes, 1990).

A number of population models have been developed to explore changes in exploited populations in a marine refuge (DeMartini, 1993; Guénette and Pitcher, 1999; Hastings and Botsford, 1999; Polacheck, 1990) or a network of two or more refuges (Crowder *et al.*, 2000; Man *et al.*, 1995; Quinn *et al.*, 1993; Sladek Nowlis and Roberts, 1999; Stockhausen *et al.*, 2000; Tuck and Possingham, 2000). Several models were based on the Beverton-Holt fisheries yield model, but as Beverton and Holt (1957) pointed out, this approach does not account for movement dynamics that may be especially critical in space-limited refuges. Some recent models explicitly ignored dispersal and spatial dynamics within a reserve while assuming population buildup will occur (Stockhausen *et al.*, 2000; Sladek Knowlis and Roberts, 1999). Other models indicated that movement across boundaries ("transfer rate") could substantially impact the size of refuge populations (DeMartini, 1993;

Guénette and Pitcher, 1999; Polacheck, 1990). Within a refuge, productivity in exploited populations is expected to increase as refuge size increases and as the transfer rate out of the refuge decreases. The mechanisms that impact this transfer rate and the resulting equilibrium population size in a refuge are not well known, and few empirical tests of refuge models have been done.

The goal of this study was to develop a simple model with a minimal number of parameters that may be applicable for conducting rapid ecological assessments of potential reserve sites for exploited marine populations. I used a dynamic rate model to define the spatial requirements for the buildup and persistence of exploited populations in a marine harvest refuge, based on spatially explicit, mechanistically defined terms for input and loss of animals. In this application, the model was used to estimate the potential equilibrium population sizes of mobile long-lived species protected within a given space. No assumptions of stock-recruit relationships or density-dependent effects were made. The predicted population sizes were compared to observed population trajectories of the two most heavily exploited species in the Caribbean, spiny lobsters and queen conch, in the Glover's Reef Marine Reserve, Belize. The model was then used to explore the population-level consequences of different spatial configurations of the harvest refuge.

Methods

The equilibrium population model

A logistic rate model was used to estimate the equilibrium density of exploited species in a given harvest refuge at the spatio-temporal scale of dispersal in open marine populations. Area and boundary conditions of the refuge are explicitly incorporated into estimates of immigration (recruitment by juveniles) and emigration (loss of mobile adults). Because the refuge carrying capacity is unknown, the upper bound of the equilibrium population size (N) in a harvest refuge is set by the magnitude of recruitment (r) and impacted by the instantaneous rate of loss (λ) of mobile adults in space and time:

$$\frac{dN}{dt} = r - \lambda N. \quad (1)$$

If the limit of N is the threshold between recruitment and loss of animals in the given area, then

$$\lim_{t \rightarrow \infty} N = \frac{r}{\lambda} \quad (2)$$

and the solution is:

$$N_t = \frac{r}{\lambda} + ce^{-\lambda t} \quad (3)$$

$$\text{where } c = N_0 - \frac{r}{\lambda}. \quad (4)$$

N_0 is the initial population size in the refuge and t is time in years. The parameters r and λ are based on several simplifying assumptions for mobile long-lived species but can be readily adjusted to specific conditions.

Assuming that intensive fishing mortality occurs in adjacent fishing areas, net immigration of adults into the refuge from the fishing area will be negligible. Therefore, the magnitude of input is solely by pelagic larval recruits, or alternatively, the density of post-settlement juveniles in nursery habitats. Recruitment (r) is defined as annual input into the refuge population over all available habitat and is the maximum population size in the absence of loss by emigration [Equation (2)]. Early post-settlement juveniles are often the most sedentary stage in the life history of many mobile benthic species (e.g., spiny lobsters: Acosta, 1999; queen conch: Hesse, 1979). Density estimates of the juveniles moving from nursery to adult habitats may thus represent annual recruitment to the mobile population.

Loss of animals is assumed to occur primarily by emigration from the refuge, as would be the case for mobile long-lived species with low rates of natural (non-fishing) mortality. Emigration by mobile adults results in permanent loss from the population because animals that leave the refuge are assumed to experience total fishing mortality (i.e., source-sink dynamics; Pulliam, 1988). This rate of loss (λ) is based on dispersal dynamics (D) in space and the conditional permeability (ρ) of the refuge. Dispersal (D) is defined as the species-specific coefficient of diffusion (see below Methods – Species' Life Histories and Dispersal Dynamics). The conditional permeability (ρ) of the refuge for the case of nomadic species is simply the perimeter-to-area ratio, assuming that habitat is evenly distributed inside and outside the refuge (Stamps *et al.*, 1987; Okubo, 1980). There are two possible kinds of boundaries in this case: absorbing boundaries across which loss of animals occur, and reflecting boundaries (such as land or deep water) across which animals cannot cross. The conditional permeability of the refuge is:

$$\rho = \frac{\text{absorbing boundary}}{\text{refuge area}}. \quad (5)$$

Buechner (1987) and Stamps *et al.* (1987) present alternative formulations to account for the influence of other spatial factors on emigration, e.g., limited home ranges or varying degrees of boundary permeability.

The instantaneous rate of loss due to emigration from the refuge is (Figure 1):

$$\lambda = (D+1)^{\rho} \quad \rho > 0 \text{ and } D > 0. \quad (6)$$

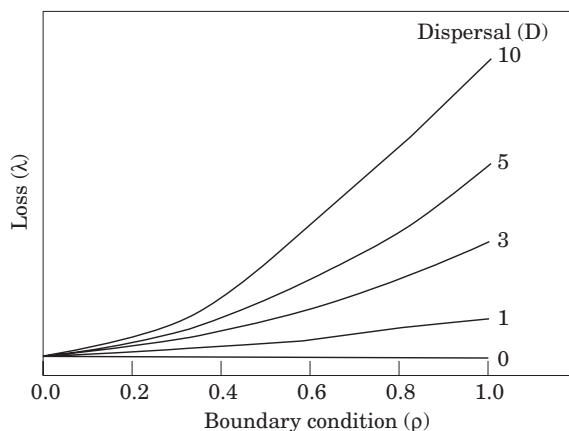


Figure 1. Loss of a mobile species (λ) across absorbing boundaries (ρ) in a marine reserve is dependent on species-specific diffusion rates (D), under the assumptions of a correlated random walk model.

If a portion or all of the boundary is absorbing, then loss will depend on the movement dynamics of the species and the size and shape of the refuge, in which case the loss of a low-mobility species will be minimal in a large round refuge. In the dispersal model, loss by emigration of any given species is thus related to the interaction of the mobile population with the refuge boundary, given the size of the refuge.

Species' life histories and dispersal dynamics

Spiny lobsters *Panulirus argus* Latreille and queen conch *Strombus gigas* Linné are the two most economically valuable and heavily exploited species in the Caribbean. Many coastal populations are in decline as indicated by decreasing catch per unit effort throughout the region. Queen conch appears to be particularly vulnerable to overfishing and was listed as a commercially threatened species on the IUCN Red List (Wells *et al.*, 1983). The current fishery regulations of many Caribbean countries appear to be inadequate to protect local populations, and marine reserves have been proposed as a conservation and management tool to sustain productive fisheries for species like spiny lobster and queen conch (Bohnsack, 1993).

The complex life histories of the spiny lobster and queen conch are similar. The pelagic larval phases are extensive (6–11 mo for spiny lobsters and 0.5–1.5 mo for queen conch), and thus, larvae may not recruit to parent populations (Breen, 1994; Stoner *et al.*, 1992). Larval recruitment to coastal populations may occur through most of the year with defined seasonal peaks (Acosta *et al.*, 1997; Stoner *et al.*, 1992), but the survival of larval settlers in coastal habitats is often highly variable (Acosta and Butler, 1997, 1999). Seagrass and other shallow vegetated habitats function as primary nurseries

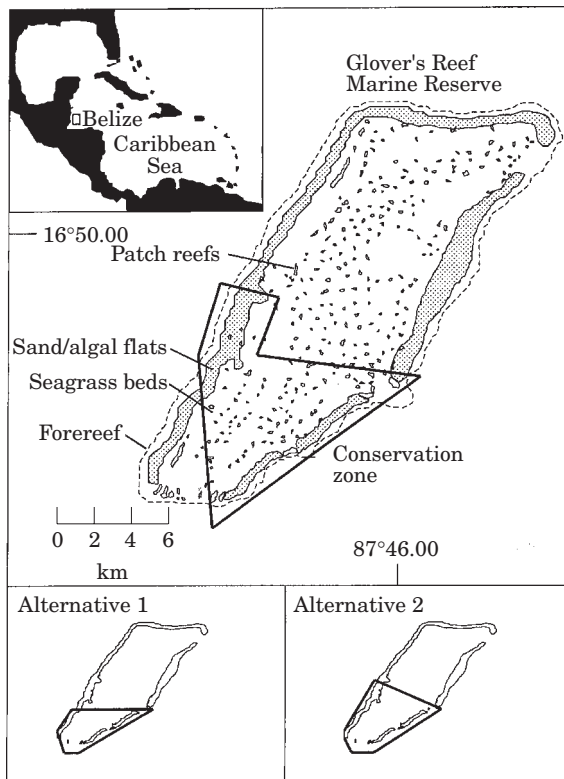


Figure 2. Habitat distribution at Glover's Reef, Belize, and its location in the western Caribbean (top inset). Shown outlined is the conservation (fishing prohibited) zone that encompasses all representative habitats for spiny lobsters and queen conch. Two alternative refuge designs considered in the model are shown (bottom insets).

for larval settlers, but older juveniles later colonize adult habitats (Butler and Herrnkind, 1997; Stoner and Ray, 1996). Lobsters undergo a size-structured ontogenetic habitat shift concordant with decreased predation and culminating with subadults moving to coral reef habitat (Acosta and Butler, 1997; Childress and Herrnkind, 1996; Smith and Herrnkind, 1992).

At the Glover's Reef Marine Reserve, Belize (Figure 2), the density and population size structure of lobsters and conch were monitored at quarterly intervals from 1997 through 2001. Standardized diver surveys were conducted on primary lobster habitat (eight coral patch reefs, mean size 0.5 ha) and on primary conch habitat (24 200-m² belt transects on sand-macroalgal flats) each inside and outside of the no-fishing conservation zone (Acosta, 2000). The magnitude of recruitment was defined as the density of juveniles colonizing adult habitat (spiny lobsters 30–45 mm carapace length, CL; queen conch 90–110 mm shell length, SL). Mean monthly recruitment during a particular year was calculated from quarterly sampling in the refuge and fishing

zone as 3-mo moving averages. The mean monthly number of recruits did not fluctuate widely over the five-year period, so the magnitude of annual recruitment in the model was extrapolated from monthly means by multiplying by 12 mo.

Mark-recapture experiments using various size classes showed that mobility increases significantly in subadult spiny lobsters (>45 mm CL; Acosta, 1999) and queen conch (>110 mm SL; Acosta, unpubl.). Adult spiny lobsters are known to undertake aperiodic mass migrations influenced by phenomenological events such as large storms (Herrnkind, 1969), but nomadic movement associated with habitat distribution is otherwise common (Herrnkind *et al.*, 1975). Juvenile queen conch may undertake aggregative movements, but large adults are nomadic (Hesse, 1979). Dispersal of each species at Glover's Reef was determined using tracking experiments to quantify the spatio-temporal spread of mobile adults. Ultrasonic telemetry was used to track daily movement of 12 lobsters and 15 conch for up 30 d or until the animal and its tag could not be relocated. Tracking was conducted during quarterly sampling (February, May, August, November) from 1997 to 2000. Adult lobsters and conch were fitted with small transmitters (Sonotronics Inc., Tucson, Arizona, USA), and the daily locations of individuals were recorded using global positioning satellite (GPS) coordinates.

Data from the movement paths of individuals consisted of movement distance, movement direction, angular change in direction between movements, and duration of movement. Because adult movement appeared to be nomadic, a correlated random walk (CRW) model was used to compare population spread in space (Karieva and Shigesada, 1983). The data were first inspected to determine if they conformed to the assumptions of the CRW model using tests for autocorrelations in move lengths and frequency of turning angles (Turchin, 1998). The expected net squared displacement $E(R_n^2)$ for each n moves was calculated as (Karieva and Shigesada, 1983):

$$E(R_n^2) \cong n \left(m_2 + 2m_1 \frac{\psi}{1-\psi} \right) \quad (7)$$

where m_1 is the mean move length, m_2 is the mean move length squared, and ψ is the mean cosine of the turning angles. Squared displacement, rather than linear, was used because the expectation values can be calculated directly from turning angles and move lengths. Bootstrapping with replacement was used to simulate movement of a population of 1000 individuals for estimation of standard errors. Linear regression was then used to visually compare the spatial spread of the two populations. Turchin (1998) defined a number of other mechanistic models for movement under different biotic and abiotic conditions. For parameterizing loss rates in

the population model, the number of moves (n) was converted to a temporal component (τ in movement days per year) so that the species-specific diffusion coefficient (D) for this habitat was (Turchin, 1998):

$$D = \frac{m_2 - \psi m_2 + 2\psi m_1^2}{4\tau(1 - \psi)} \quad (8)$$

Study site

Glover's Reef is a coral atoll isolated by deep water (400–2000 m) 45 km off the coast of Belize, western Caribbean (Figure 2). The atoll is ringed by an emergent reef crest with few breaks, a narrow sloping forereef, and deep vertical walls. The lagoon contains extensive shallow habitats of sand-algal flats, seagrass beds, and coral patch reefs that collectively serve as habitats for the benthic life history stages of spiny lobsters and queen conch. Glover's Reef was designated as a marine reserve in 1993 with a general use zone (266 km²; 75% of the atoll) that is open to commercial fishing and a conservation zone (73 km²; 25%) where fishing is prohibited. The boundaries were designated by government agencies following negotiations with fishing, tourism, and conservation interests.

The boundary of the harvest refuge lies along the edge of the atoll and across the shallow lagoon where it delineates the fishing zone (Figure 2). Therefore, the boundary consists of two types: an impermeable (reflecting) boundary along the reef wall and a permeable (absorbing) boundary with the fishing zone in the lagoon. The area of primary habitats (coral reefs for lobsters and seagrass/sand-algal flats for conch) was estimated from field observations and satellite images and was standardized at a proportion of 0.3 of the total surface area of the refuge.

Model simulations

Although the reserve was designated in 1993, enforcement of the no-fishing zone has been relatively consistent only since 1998 (Acosta, 2000). Therefore, data from 1997 were used as the initial population size for the model (Table 1), and the observed population trajectories were plotted through 2001. Regression models were fitted to observed densities of recruits and the mobile population (large subadults and adults) in the refuge and fishing zone. Simple linear regressions were fit to data for all recruits and for the mobile population in the fishing zone; the non-linear equilibrium model equation was fit to the mobile population in the refuge. Data for these and further model regressions (below) were checked for normality (Shapiro-Wilkes statistic), homogeneity of variance (Bartlett's M -test), and auto-correlations (Durbin-Watson statistic).

Table 1. Parameter estimates for spiny lobsters and queen conch populations in the Glover's Reef Marine Reserve. Estimates are for 30% habitat coverage (coral reefs for lobster; macroalgal-seagrass flats for conch) of the total refuge area. N_0 is initial population size; r is total number of juvenile recruits to the refuge per year; D is the diffusion coefficient for each species in this habitat.

Parameter	Spiny lobster	Queen conch
N_0	61 800	553 000
r	220 000	3 010 000
D	3.620	0.057

Table 2. The spatial configuration of the actual marine harvest refuge and two alternative designs of the Glover's Reef Marine Reserve, Belize. The conditional permeability of the boundary (ρ) is the ratio of the length of the absorbing boundary to total area of the refuge.

Parameter	Actual refuge	Alternative refuge 1	Alternative refuge 2
Area (km ²)	73	73	106
Absorbing boundary (km)	28.9	14.5	13.7
ρ	0.400	0.201	0.129

The population trajectories and the equilibrium population sizes were then calculated for the current refuge and two alternative refuge designs. To assess how changes in boundary conditions and size of the refuge might impact equilibrium population size, two hypothetical refuges were constructed: Alternative 1: the absorbing boundary was reduced by 50%, but the area was the same as the actual refuge; Alternative 2: the absorbing boundary was reduced by 50%, and the area was increased by 50% (Figure 2; Table 2). Reduction of the absorbing boundary served to make the refuge more compact in shape. In effect, altering refuge geometry served to compare the sensitivity of the populations to the spatial configurations. Comparing differential mobility of the two species also functioned as a sensitivity analysis on the impact of movement dynamics on the refuge population. Additional sensitivity analysis was conducted by varying the magnitude of recruitment by ± 10 and 20% in the refuge.

Results

From 1997 through 2001, the densities of spiny lobsters and queen conch in the refuge increased significantly from the initial sizes of the fished populations. The population sizes of mobile spiny lobsters (>45 mm CL; Figure 3) increased by a factor of 3 and queen conch (>110 mm CL; Figure 4) increased by a factor of 4.5 in

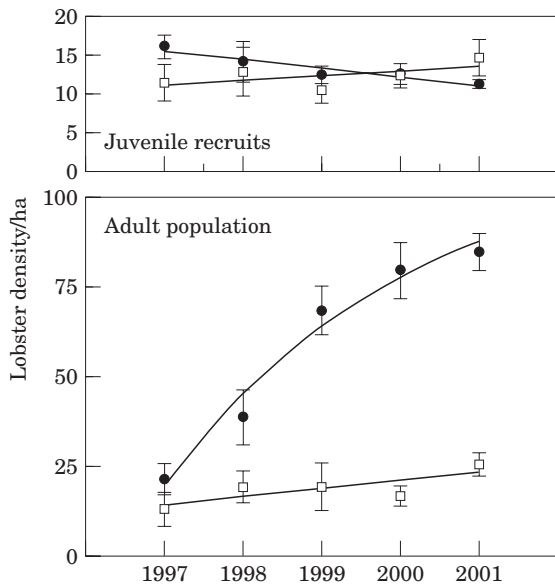


Figure 3. Fluctuation in the mean monthly density of juvenile recruits (top panel) and adult spiny lobsters *Panulirus argus* (bottom panel) in the refuge (filled circles) and fishing zone (open squares) of the Glover's Reef Marine Reserve, 1997–2001; bars represent ± 1 standard error calculated from quarterly surveys. Linear least-squares regressions were fitted to data for fished adults ($R^2=0.59$), recruits in the fished zone ($R^2=0.80$), and recruits in the refuge ($R^2=0.91$); trends did not significantly fluctuate from 0. The logistic model equation provided a significant fit to data for mean density of adults protected in the refuge ($R^2=0.97$).

the refuge. The equilibrium equation provided a significant fit to the observed population trajectories for both species. In contrast, the density of subadult and adult spiny lobsters (18.5/ha/mo) and queen conch (202.5/ha/mo) in the fishing zone did not fluctuate significantly over the five-year period. Recruitment of lobster juveniles to adult habitat remained relatively stable at 13.1/ha/mo in the refuge and 12.1 in the fishing zone (cf. Figure 3). The density of conch recruits was slightly higher in the fished zone at 131/ha/mo than density in the refuge 109/ha/mo (cf. Figure 4). However, trend analysis showed that mean densities of lobster and conch recruits did not vary significantly throughout the period in both the refuge and the fishing zone.

The results from the tracking studies indicated that adult spiny lobsters ranged widely between coral patches in the lagoon, the shallow reef crest, and the fore reef. The mean linear distance per movement step for lobsters was 60.7 m (range 25.7–110 m) among coral patch reefs (Table 3). Adult conch ranged between the sand-algal flats and lagoon patch reefs. Individuals moved an average daily linear distance of 8.5 m (range 6.11–14.0 m) during foraging activity on the sand-macroalgal and seagrass flats. Duration of movement for queen conch was measured as one day per move as the animals

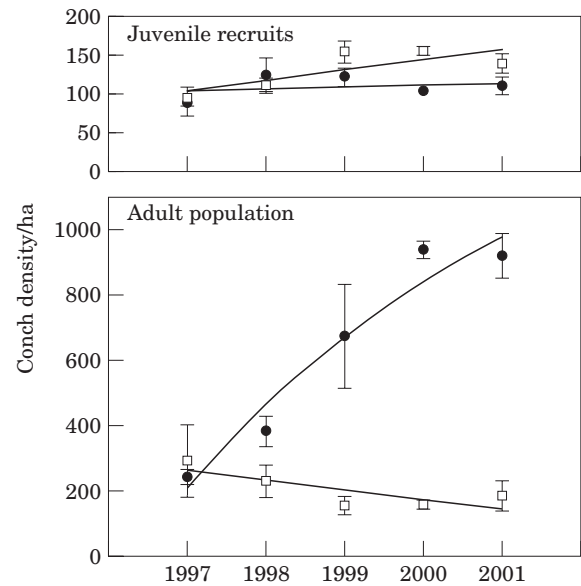


Figure 4. Fluctuation in the mean monthly density of juvenile recruits (top panel) and adult queen conch *Strombus gigas* (bottom panel) in the refuge (filled circles) and fishing zone (open squares) of the Glover's Reef Marine Reserve, 1997–2001; bars represent ± 1 standard error calculated from quarterly surveys. Linear least-squares regressions were fitted to data for fished adults ($R^2=0.63$), recruits in the fished zone ($R^2=0.59$), and recruits in the refuge ($R^2=0.66$); trends did not significantly fluctuate from 0. The logistic model equation provided a significant fit to data for mean density of adults protected in the refuge ($R^2=0.89$).

foraged continuously, whereas duration of lobster movement varied from one to several days (mean \pm SE: 3.9 ± 2.8 d; range 1–12 d) between movement from one coral reef to another (see also Herrnkind *et al.*, 1975).

Adults of both species did not exhibit strongly directional movement throughout the study. There were no serial correlations in movement distances and turning angles, and the correlated random walk model adequately represented the benthic dispersal patterns. The plot of expected net squared displacement indicated that the spread of the lobster population occurred at a rate 16 times greater than queen conch dispersal during normal movement activity (Figure 5). However, lobsters often remained in shelters on a single patch reef for several days, and consequently, the disparity between the spatial area covered by a lobster or conch was reduced over a given period of time (Table 3).

The model predicted that the density of both lobsters and conch may reach an asymptote in the refuge within three years (Figure 6). Under current recruitment and emigration rates (Table 1), the population size of spiny lobsters was expected to increase 350% in the refuge, from the initial population size of 61 800 individuals to an equilibrium population of 220 000 lobsters. The

Table 3. Movement of adult spiny lobsters and queen conch in the Glover's Reef Marine Reserve, Belize, determined from tracking studies. Captured individuals were randomly chosen for tracking during February, May, August, and November from 1997 to 2000. The frequency of turns of lobster represents the average number of turning angles measured during the mean tracking duration of each sex, but turning angles of conch was determined each day for the 30-d periods.

	n	Size range (mm)	Mean tracking duration (d)	Frequency of turns (mean \pm s.e.)	E(R ²) in ha (mean \pm s.e.)	Linear distance moved in m (mean \pm s.e.)
Lobster, male	5	95–130	27	9.11 (0.901)	1.49 (0.203)	268.1 (6.701)
Lobster, female	7	85–110	24	7.40 (0.311)	1.38 (0.083)	235.2 (8.31)
Conch*	15	190–225	30	30	0.730 (0.851)	87.3 (1.42)

*The sex of individual conch was undetermined.

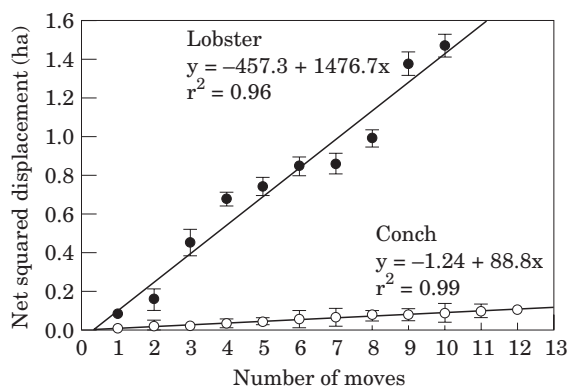


Figure 5. Expected net squared displacement of spiny lobster and queen conch populations over n consecutive moves. Standard errors were calculated from bootstrapped estimates for simulated populations of 1000 individuals, and linear least-squares regressions were fitted for comparisons between the species.

queen conch population was expected to increase 480% from an initial population size of 0.55 million to 2.92 million conch in the refuge. The observed population trajectories in the refuge initially lagged predicted estimates but appeared to reach an asymptote near the predicted equilibrium population sizes within three years.

In the first alternative refuge design, the area was the same as that of the actual refuge (73 km²), but the absorbing boundary was simplified and reduced by 50% (Table 2; Figure 2). In this refuge, the equilibrium population size predicted for spiny lobster was 30% larger (285 000 lobsters) than that predicted for the actual refuge (Figure 6), or a 5 \times increase over the initial density of the fished population. However, the equilibrium population size of queen conch was not expected to substantially increase over that in the actual refuge. The rates of increase were again rapid with the populations approaching asymptotic densities within three years.

In the second alternative refuge design, the area was increased by 50% to 107 km², and the absorbing bound-

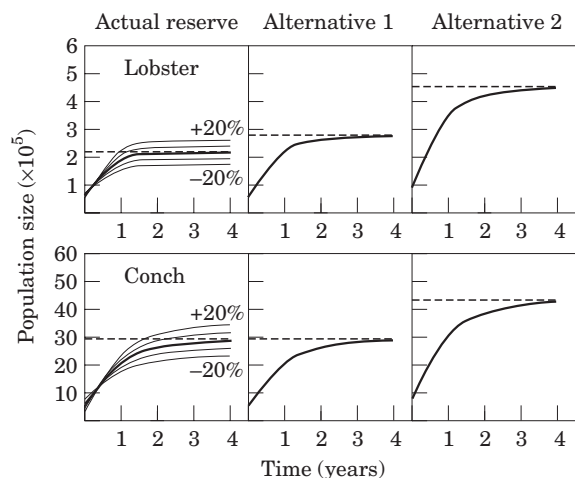


Figure 6. Predicted population trajectories (dark solid lines) and equilibrium population sizes (dashed lines) for spiny lobsters and queen conch over a five-year period. Shown are comparisons between the actual harvest refuge and two alternative designs of the Glover's Reef Marine Reserve. Results of sensitivity analyses (light solid lines) on recruitment variability (± 10 and 20%) are shown for the actual refuge.

ary was again simplified and reduced by 50% (Table 2; Figure 2). Both populations were predicted to respond to this spatial arrangement (Figure 6). The predicted size of the spiny lobster population was expected to increase 110% (462 000 lobsters) over that of the actual refuge, or 7 \times greater than the initial density of lobsters. The queen conch equilibrium population was expected to increase 50% (4.42 million conch) over the actual refuge, representing an 8 \times increase over the initial fished population.

Discussion

Performance of the model

The model evaluated here used a logistic function to describe population change based on spatially explicit

recruitment and loss that impact the buildup and persistence of refuge populations. For open populations of mobile, long-lived species, boundary type and geometrical configuration of a refuge play an increasingly crucial role in determining the potential equilibrium population size as the areal size of the refuge becomes limited (Schonewald-Cox and Bayless, 1986). The rate of emigration of mobile species from a refuge scales with refuge area and boundary conditions in predictable ways (Buechner, 1987; Stamps *et al.*, 1987). Interactions with boundaries were derived using species-specific dispersal dynamics (Figure 1) that were based on the mechanistic description of species movement among available habitats rather than *a posteriori* flux rates observed at boundaries. This simplistic model allowed for predictions of the potential population size of a mobile species given its recruitment rate, movement behavior, and the spatial characteristics of the refuge.

Populations of spiny lobsters and queen conch in the harvest refuge of the Glover's Reef Marine Reserve were predicted to reach equilibrium levels within three to four years. With effective enforcement since 1998, the populations rapidly increased, leveling off near the equilibrium population sizes predicted by the model. The population of spiny lobsters increased greater than three-fold in the refuge, whereas the queen conch population increased five-fold. MacDiarmid and Breen (1992) also showed a logistic-type trajectory in a protected New Zealand rock lobster population that increased five-fold within five years. Further research indicated that these patterns were linked to depth and reef habitat distribution (Kelly *et al.*, 2000). In a large reserve (456 km²) in the Bahamas, Stoner and Ray (1996) found queen conch densities that were 15–31 times greater than in the fished areas. At Glover's Reef, the higher rates of diffusion by spiny lobsters may have resulted in a smaller equilibrium population size compared to queen conch. This suggests that dispersal might play a key role impacting densities of these species in space-limited harvest refuges.

The magnitude of recruitment did not impact the population trajectories of spiny lobsters or queen conch populations. Sensitivity analysis indicated that the equilibrium population sizes fluctuated in step with increases or decreases in the number of recruits (Figure 6). However at low recruitment levels, the curve fit becomes less precise for both lobsters ($R^2=0.62$) and conch ($R^2=0.73$). The rate of loss at moderate to high recruitment appeared to have had the greatest effect on the refuge population sizes.

The combined effects of a compact refuge shape, reduced absorbing boundary, and increased refuge area had variable impacts on the population sizes of spiny lobsters and queen conch. Simplifying the shape of the refuge and decreasing the absorbing boundary by 50% may result in a further 30% increase in the equilibrium density of spiny lobsters, whereas the population of the

less-mobile queen conch was not expected to increase in this refuge. In contrast, an additional 50% increase in the size of the refuge was expected to result in a further 110% increase in the lobster population and a 50% increase in the queen conch population. Refuge size had a dominant effect on the less mobile species, whereas both refuge size and boundary conditions impacted the more mobile species.

Assumptions of the model

Several simplifying assumptions were made in the model for its applicability in rapid assessment of refuge efficacy in the absence of long-term population data. First, the input of new individuals via larval recruitment was assumed to be relatively constant at the temporal scale of years, and larval supply was assumed to be even over available nursery habitats such as seagrass and other vegetation. However, environmental and stochastic factors may cause high inter-annual variability in larval supply and pre- and post-settlement mortality (Connell, 1985; Roughgarden *et al.*, 1985). A more conservative estimate of recruitment is the density of juveniles colonizing adult habitat (Connell, 1985; Keough and Downes, 1982). In this context, the densities of juvenile spiny lobsters and queen conch leaving nurseries for adult habitat were relatively constant over five years in both the refuge and the fished zone at the Glover's Reef atoll.

Because natural mortality often declines with increasing individual size (Paine, 1976), loss of mobile adults was attributed solely to emigration from the refuge to fishing grounds where fishing mortality may be several orders of magnitude greater than natural mortality (Beverton and Holt, 1957). For example, natural mortality of adult lobsters in coral reef habitat declines rapidly (to <0.10) from that experienced by smaller juveniles (Smith and Herrnkind, 1992), whereas fishing mortality of adult lobsters at Glover's Reef may exceed 60% annually (Acosta, 2000). The primary consideration in the model was thus given to the spatial factors that influence the emigration of mobile adults leading to high mortality outside the refuge.

Emigration of mobile animals is inversely related to patch area (e.g., Karieva, 1985; Turchin, 1986), but patch shape and boundary permeability may significantly impact rates of loss (Schonewald-Cox and Bayless, 1986; Stamps *et al.*, 1987). Species-specific dispersal behavior ultimately determines population spread, and thus, the probability of encountering permeable boundaries. The correlated random walk approach used here was appropriate for nomadic movement in which refuge size and the length of absorbing boundary were the primary influences on the instantaneous rate of loss (Okubo, 1980; Turchin, 1998). However, habitat patchiness may impact the spatial dynamics of dispersal and density distribution (Turchin,

1986; With *et al.*, 1999). For example, movement of reef fishes may often be associated with habitat distribution rather than defined "home ranges" (Appeldoorn *et al.*, 1997; Attwood and Bennett, 1994; Holland *et al.*, 1996). The efficacy of a reserve for species without behavioral home ranges may depend on habitat distribution, as well as refuge size, boundary conditions, and dispersal range. If the distribution of critical habitat is even between refuge and fished areas, then dispersal of a mobile species (defined as D in the model) is sufficient to quantify loss across a given refuge boundary.

Seasonal or ontogenetic movement may also have important consequences for loss from a refuge. In the Cape Rodney Marine Reserve in New Zealand, the abundance of rock lobsters *Jasus edwardsii* has increased substantially over time even though large adults, particularly males, may undertake seasonal migrations that may take some lobsters outside the reserve boundaries (Kelly *et al.*, 2000; MacDiarmid and Breen, 1992). However, no increase has been observed in the abundance of the congeneric *J. verreauxi* population that may undertake more extensive migrations as adults. Similarly, most adult *P. argus* leave the protected area in Florida Bay, Everglades National Park (USA), due to the lack of suitable adult shelter in this area (Davis and Dodrill, 1980). At the Glover's Reef Marine Reserve, lobsters and conch undertake ontogenetic movement from juvenile nurseries to abundant adult habitat nearby, but there was no evidence of seasonal migrations of adults associated with depth or other physical factors (Acosta, 1999, this study). The distribution of adults was instead primarily associated with their increased mobility allowing for exploitation of resources farther away from juvenile nurseries. Large adult lobsters up to 180 mm CL sheltered with small juveniles in coral patches <1 m deep but exclusively occupied deep forereef habitat. Similarly, adult queen conch ranged farthest away from seagrass nursery habitats. The efficacy of a marine reserve would be extremely limited if the reserve contained only adult or juvenile habitat.

Conclusions

Marine reserves hold great potential for the conservation of overexploited species, but a number of important issues remain unresolved. Paddock and Estes (2000) summarized the large amount of observational literature citing increased abundance of exploited species in reserves in the absence of time series or experimental data. They noted the difficulties in attributing causal relationships between reserves and abundance/biomass increases, particularly when reserves are small. Most marine reserves will practically be space-limited, and spatial factors including habitat quality will have primary impacts on populations of mobile species

(Crowder *et al.*, 2000). The spatial and temporal scale of dispersal then becomes a primary factor that impacts the loss of exploited species from a harvest refuge. Therefore, the assertion that small reserves contribute significantly to the buildup and persistence of exploited populations (e.g., Roberts and Hawkins, 1997; Roberts *et al.*, 2001) remains highly dubious.

The replenishment of harvested populations and the subsequent increase in reproductive output are the primary benefits of marine reserves (Carr and Reed, 1993), and therefore, assessment of within-refuge dynamics is important for determining whether these goals will be attained in a particular refuge. In addition to increasing the population size in a harvest refuge, the restocking of adjacent fishing grounds with dispersing adults is also necessary to offset the economic loss due to closure to local fishing (Attwood and Bennett, 1994; Russ and Alcalá, 1996). A suitable tradeoff between increases in population size and transfer of a proportion of adults to adjacent fisheries can only be reached if refuges are large enough to intercept a large number of larval recruits and if boundaries effectively control the rate of loss of adults.

Mathematical models are powerful tools to elucidate refuge function, but parameterizing these models with mechanistically derived spatially explicit estimates is difficult. The results of this study indicated that simple rate models may be useful for rapid assessment of the efficacy of a proposed marine harvest refuge for a target species. The observed population trajectories for spiny lobster and queen conch appeared to support the model predictions that were derived from data on recruitment rates and movement dynamics. A more comprehensive assessment of marine refuge dynamics requires consideration of data-intensive models with parameters that are difficult to define and complex results that may be difficult to interpret (Hastings and Botsford, 1999). More testing and validation of spatially explicit population models of harvest refuges are currently needed.

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