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RECRUITMENT IN DEGRADED MARINE HABITATS: A SPATIALLY EXPLICIT, INDIVIDUAL-BASED MODEL FOR SPINY LOBSTER

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Abstract. Coastal habitats that serve as nursery grounds for numerous marine species are badly degraded, yet the traditional means of modeling populations of exploited marine species handle spatiotemporal changes in habitat characteristics and life history dynamics poorly, if at all. To explore how nursery habitat degradation impacts recruitment of a mobile, benthic species, we developed a spatially explicit, individual-based model that describes the recruitment of Caribbean spiny lobster (*Panulirus argus*) in the Florida Keys, where a cascade of environmental disturbances has reconfigured nursery habitat structure. In recent years, the region has experienced a series of linked perturbations, among them, seagrass die-offs, cyanobacteria blooms, and the mass mortality of sponges. Sponges are important shelters for juvenile spiny lobster, an abundant benthic predator that also sustains Florida's most valuable fishery.

In the model, we simulated monthly settlement of individual lobster postlarvae and the daily growth, mortality, shelter selection, and movement of individual juvenile lobsters on a spatially explicit grid of habitat cells configured to represent the Florida Keys coastal nursery. Based on field habitat surveys, cells were designated as either seagrass or hard-bottom, and hard-bottom cells were further characterized in terms of their shelter- and size-specific lobster carrying capacities. The effect of algal blooms on sponge mortality, hence lobster habitat structure, was modeled based on the duration of exposure of each habitat cell to the blooms. Ten-year simulations of lobster recruitment with and without algal blooms suggest that the lobster population should be surprisingly resilient to massive disturbances of this type. Data not used in model development showed that predictions of large changes in lobster shelter utilization, yet small effects on recruitment in response to blooms, were realistic. The potentially severe impacts of habitat loss on recruitment were averted by compensatory changes in habitat utilization and mobility by larger individuals, coupled with periods of fortuitously high larval settlement. Our model provides an underutilized approach for assessing habitat effects on open populations with complex life histories, and our results illustrate the potential pitfalls of relying on intuition to infer the effects of habitat perturbations on upper trophic levels.

Key words: algal blooms; Carribean spiny lobster; Florida Keys, USA; habitat degradation; individual-based modeling; lobster; Panulirus argus; *recruitment; spatial modeling; sponge die-off.*

INTRODUCTION

Global climate change, physical destruction of habitat, water pollution, invasions by nonindigenous species, and overexpoitation of fishery resources summarize the anthropogenic activities that threaten the ecological integrity of coastal marine communities (National Research Council 1995). Yet, integrating the collective dynamics of diverse environmental perturbations to predict their impact on marine populations or communities is perhaps the biggest challenge for coastal resource management. Concern for the sustainablity of marine fisheries is particularly widespread, and has moved beyond simple considerations of the direct impacts of fishing in recognizing the additional peril posed by the loss of ''essential nursery habitat'' (National Research Council 1999). Although larval supply is undoubtedly the key to predicting the population dynamics of many marine fish and invertebrates, postsettlement survival is equally important to others and often intimately tied to coastal habitat features (see Morgan 2001, and Underwood and Keough 2001, for reviews).

The inclusion of spatial complexity, changing environmental conditions, and individual organism response (e.g., dispersal, growth, reproductive success)

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to changes in habitat quality is necessary to improve the realism and usefulness of ecological models, especially those used for conservation and management (Van Winkle et al. 1993, Tischendorf 1997, Rose 2000). Yet, few model depictions of marine populations incorporate the kinds of spatially explicit benthic dynamics that govern postsettlement processes, and fewer still incorporate the effects of environmental degradation (but see Jaworska et al. 1997, LePage and Cury 1997, Breitburg et al. 1999), which is now a common characteristic of so many marine environments.

The Florida Keys (Florida, USA), like many coastal areas, has experienced a suite of environmental disturbances in recent decades. Some of these perturbations appear to be linked and thus have been described as a ''cascade of disturbances'' (Butler et al. 1995). Water quality is rapidly declining and thousands of hectares of seagrass have disappeared in episodic die-offs (Roblee et al. 1991, Fourqurean and Roblee 1999, Zieman et al. 1999, Fourqurean et al. 2003). Extensive and repeated algal blooms have swept over the shallow coastal seas of the Florida Keys, covering hundreds of kilometers of seagrass and tropical hard-bottom habitat. Some of those blooms, particularly those dominated by cyanobacteria, have sparked massive die-offs of the sponge assemblage found in the region. Large sponges, many ~1 m in diameter, are a conspicuous feature of hard-bottom habitat in south Florida, and they provide shelter for numerous species of fish and invertebrates, some of which are obligate inhabitants of sponges (Pearse 1950, Erdman and Blake 1987, Duffy et al. 2000).

Large sponges are the single most important shelter for juvenile Caribbean spiny lobster (*Panulirus argus*), a species of ecological and economic importance in the region because it is an abundant, large, benthic predator and the target of the most valuable fishery in Florida and the Caribbean (see reviews in Phillips and Kittaka 2001). Thus, the rapid and long-lasting loss of the community of large, slow-growing sponges over large areas of the Florida Keys is indeed loss of essential fish habitat. Butler et al. (1995) observed declines in juvenile lobster abundance and shifts in their use of shelter in the Florida Keys following algal blooms and the subsequent sponge die-offs that ensued in the early 1990s. Although lobster densities in the area directly affected by the sponge die-off (~20% of the total nursery) declined by >50%, on a regional scale, Florida's spiny lobster population actually increased during this period. Possible reasons that have been proposed for the resistence of the spiny lobster population to these seemingly huge losses of nursery habitat are the availability of alternative shelters in impacted areas, a healthy nursery elsewhere in the region into which juvenile lobsters migrated, and unusually high larval supply during this period (Butler et al. 1995, Herrnkind et al. 1997*b*).

To evaluate these hypotheses, we constructed a spatially explicit, individual-based model that recreates the cascade of disturbances in the nearshore nursery of the Florida Keys from algal blooms, to the destruction of sponges, to the impact on juvenile spiny lobster population dynamics.

In this paper, we describe the model, show how we corroborated it with independent data, present predictions of the effects of algal blooms and sponge die-off on spiny lobster recruitment, and evaluate potential explanations for the resiliency of the lobster population to such large perturbations. In addition to providing a better understanding of the recruitment process in spiny lobster, our results demonstrate a general approach for assessing habitat effects on open populations with complex life histories, and illustrate the potential pitfalls of relying on intuition to infer the effects of habitat perturbations on upper trophic levels.

Spiny Lobster Life History

The Caribbean spiny lobster (*Panulirus argus*) is an abundant, widespread, and heavily fished species of lobster that dwells in shallow coastal regions from Bermuda to Brazil. Both the offshore distribution of larvae (Yeung and McGowan 1991) and genetic evidence indicate that Florida lobsters are part of a pan-Caribbean population (Silberman et al. 1994, Silberman and Walsh 1994). Late-stage larvae (called postlarvae) arrive in the coastal area year-round during new moon flood tides (Little 1977, Acosta et al. 1997). Upon arrival, postlarval lobsters seek structurally complex vegetation, particularly red macroalgae within hard-bottom habitat, in which they settle and metamorphose into the first benthic juvenile stage (Marx and Herrnkind 1985, Herrnkind and Butler 1986, 1994, Butler and Herrnkind 1991, Field and Butler 1994). The early benthic stage juveniles remain in vegetation for several months, where they are sheltered from predators (Herrnkind and Butler 1986, Butler et al. 1997) and have abundant food (Marx and Herrnkind 1985, Herrnkind et al. 1988). Upon reaching ~15 mm carapace length (CL), the ''postalgal-stage'' juveniles emerge from vegetation and take up daytime refuge in crevices provided mainly by sponges (~70% of shelters) and other kinds of crevice-bearing structures (Forcucci et al. 1994, Butler et al. 1995, Herrnkind et al. 1997*a*, *b*). Postalgal-stage juveniles initially venture only a few meters from their shelter each night. When they reach a size of ~50 mm CL (about one-year postsettlement), they become more nomadic and begin associating with adult lobsters in large natural shelters. Spiny lobsters become increasingly social and aggregate more often in communal shelters as they grow larger. Juveniles leave the nursery area and move offshore to join the adults after about one to two years. Natural mortality during the larval and postlarval stages is thought to be high but has not been directly estimated (Acosta and Butler 1997). Mark–recapture studies indicate that only 2–4% of the settled postlarvae survive their first few months on the bottom (Butler et al. 1997), but natural mortality rapidly declines once lobsters exceed 50 mm CL (Eggleston et al. 1990, Smith and Herrnkind 1992). In contrast, injuries and mortality due to fishing increase as lobsters near the legal size (76 mm CL) established for the large commercial and recreational fisheries in Florida and the Caribbean (see reviews in Phillips and Kittaka 2001). It is estimated that >90% of the legal-sized lobsters are harvested each year in Florida (Hunt 2001). Despite heavy fishing pressure over the last two decades, adult population abundance in Florida has not declined (Hunt 2001) and is undoubtedly sustained by the supply of postlarvae from outside the system. However, the widespread degradation of nursery habitat for lobsters (i.e., the destruction of the sponge community) in the Florida Keys raises questions about the continued sustainability of the adult population.

MODEL DESCRIPTION

Overview

The model simulated the arrival of individual postlarval lobster and their subsequent daily settlement, growth, shelter selection, mortality, and movement until they reached 50 mm CL on a spatial grid of 245 habitat cells that corresponded to the nursery habitat in the Florida Keys. Ten-year model simulations were performed using monthly postlarval supply observed for 1987 to 1997. Each individually modeled lobster was tracked for ~18 months to allow for all lobsters to either die or reach 50 mm CL. We used 50 mm CL as the final size for recruitment to adulthood because the dynamics of lobsters longer than 50 mm CL are complicated by the activities of the fisheries. Juveniles between 50 mm and 70 mm (full adults) are captured by fishermen and used as ''live decoys'' in traps (Lyons and Kennedy 1981, Forcucci et al. 1994). The initial focus of this model is on recruitment dynamics, not fisheries, although our prediction of survivors to 50 mm CL should yield reasonable predictions of new recruits to the fishable adult population.

Spatial structure of the model

We simulated the Florida Keys region stretching from Key Largo to Key West, including most of the bay-side spiny lobster nursery habitat and a narrow 1–2 km ocean-side strip of bottom that is suitable for lobster recruitment (Fig. 1). The region was represented with 245 square habitat cells in a 7 × 35 cell grid (Fig. 1A): 7 cells north to south (columns) and 35 cells east to west (rows). The habitat designation for each cell, either seagrass or hard-bottom, corresponded to the actual spatial distribution of these habitats in the region as observed in field surveys made at 239 sites throughout the region (Herrnkind et al. 1997*b*) and later from GIS benthic habitat data.

Although differences in habitat structure among the model's spatial cells were indicative of those in the Florida Keys region when divided into 12-km^2 areas, the actual numerical representations of lobster dynamics and shelter abundance in each habitat cell were on a scale approximating a 1000-m^2 area, which matched the scale at which our empirical data were based. In essence, we modeled lobster dynamics and habitat structure in each cell at an ecologically realistic scale (1000 m^2) considered to be representative of the larger region (12 km^2) it was meant to depict. This approach is similar to that used in forest succession models that simulate every tree in a specified size plot within a region of forest, rather than the entire forest (Shugart and West 1977). Had we simulated the true number of lobsters in habitat cells in a 12-km^2 area, we would have needed to model billions of individuals, which was beyond our computing capability. Even so, the number of individual lobsters that we tracked in the model during a single 10-year simulation exceeded 1 million.

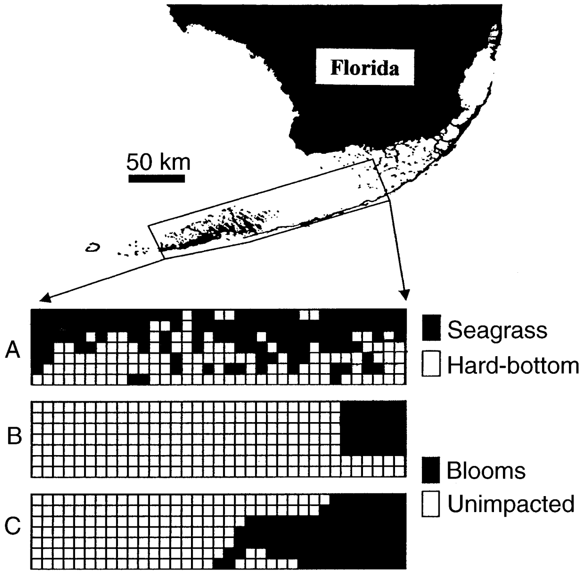

FIG. 1. (Map) The geographic domain of the model within the Florida Keys region, (A) the distribution of habitat types (seagrass and hard-bottom) among cells, and (B and C) the distribution of the two successive algal blooms. The general distribution of seagrass and hard-bottom habitat in the model (panel A) is based on data from habitat surveys conducted at over 200 sites thoughout the Florida Keys. Additional spatial substructure specified within each hard-bottom cell includes the abundance of different shelters (e.g., loggerhead sponges, other sponges, solution holes, other shelters) used by juvenile lobsters. Locations of the 1991 (panel B) and 1992 (panel C) algal blooms were based on monthly aerial overflight observations.

Whereas seagrass cells were considered as a single habitat type for all lobsters, the habitat in hard-bottom cells consisted of macroalgae for algal-stage lobsters and five types of shelter habitat for postalgal-stage lobsters. We used field data and diver observations of shelter utilization by lobsters (Butler and Herrnkind 1997, Herrnkind et al. 1997*b*) to divide hard-bottom shelter habitat into loggerhead sponges, other sponges, solution holes, octocoral-sponge complexes, and other shel-

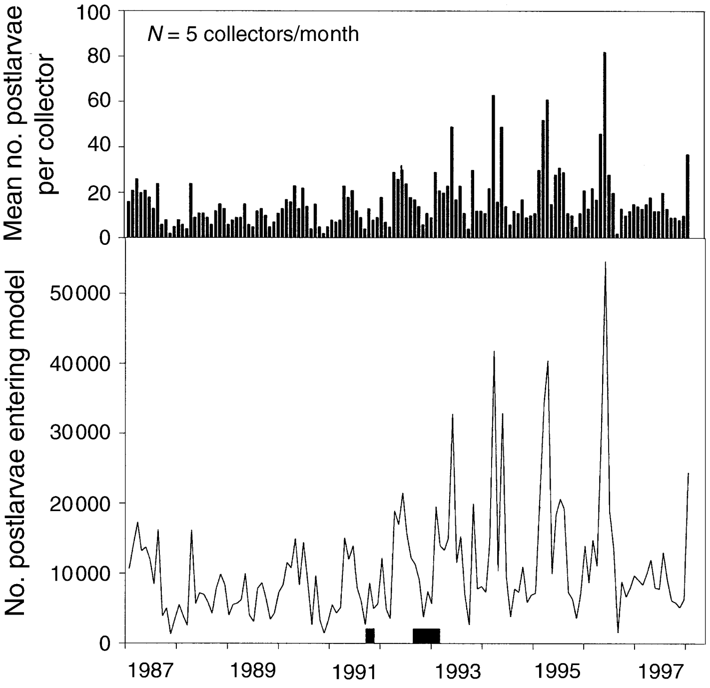

FIG. 2. Monthly time series of postlarval spiny lobster supply to a site near Big Munson Key, Florida, USA, from March 1987 to December 1997 (top panel) and, based on these data, the standardized monthly postlarval supply used in model simulations (bottom panel). The two black bars along the *x*-axis represent the periods when the algal blooms occurred. Note the high late-winter and early-spring peaks in postlarval supply during 1992–1996.

ters (mainly scleractinean corals). We specified a lobster carrying capacity (maximum number of lobsters in the 1000 m^2) for each of the five shelter types in each of the hard-bottom cells based on diver surveys of shelter densities, and maximum numbers of lobsters per shelter, measured at 128 field sites throughout the Florida Keys (Herrnkind et al. 1997*b*). Thus, hard-bottom cells had unlimited macroalgal shelter for algal-stage lobsters, and potentially limiting shelter for post-algal-stage lobsters, depending on the degree of crowding. For postalgal-stage lobsters, the size and availability of open shelters among the five types affected their mortality rate.

Arrival and settlement

Superimposed on this spatial landscape is an individual-based lobster model depicting the settlement, growth, shelter selection, mortality, and emigration of spiny lobsters. Every 28 days in the 10-year simulation, new lobsters entered the model, mimicing the natural, pulsed, lunar arrival of postlarvae to the coastal environment (Fig. 2). Postlarvae arrive inshore within a few days of the new moon each month (Acosta et al. 1977). Monthly variation in postlarvae arrivals was based on a 10-year time-series measured at collectors deployed near Big Munsen Key, in the Florida Keys (Acosta et al. 1997). Measurements of postlarvae at this location have been shown to reflect the magnitude and temporal pattern of settlement in the general region (Herrnkind and Butler 1994). Typical postlarval densities at settlement were 0.041 settlers/m^2 (Marx and Herrnkind 1985, Herrnkind and Butler 1994, Butler et al. 1997), which converted to an initial value of 10 000 model individuals (0.041 settlers/m^2 × 245 cells × 1000 m^2/cell). The number entering the model each month was obtained by multiplying the monthly deviation from the long-term average by 10 000 individuals.

The postlarvae entering the model domain each month were allocated among the 245 spatial cells based on habitat type. Individuals were assumed to have just molted from the postlarval stage to the first benthic juvenile stage (i.e., arrivals were new algal-stage juveniles). Newly arrived individuals were distributed uniformly among cells of similar habitat without regard to the geographic location and proximity of these cells to other cells. We did so because settlement studies conducted in the Florida Bay nursery (Field and Butler 1994, Herrnkind and Butler 1994) have revealed no repeatable decline in settlement magnitude with distance into the nursery (i.e., no settlement shadow). Based on experiments involving habitat preferences at settlement (Herrnkind and Butler 1986), we distributed (''settled'') 17% of the new individuals each month in seagrass cells and 83% of the new individuals in the macroalgae shelter type in hard-bottom cells.

All newly entering algal-stage individuals were assigned a cell number, a shelter type (seagrass for seagrass cells and macroalgae for hard-bottom cells), and an initial length. Initial lengths were randomly assigned to individuals from a truncated normal distribution with a mean of 6.3 mm CL and ±1 SD of 0.3 (Lellis and Russell 1990, Butler and Herrnkind 1991, Field and Butler 1994). Because individuals were assumed to have just molted from postlarvae to algal-stage juveniles, the number of days since their last molt (which

TABLE 1. Size-specific juvenile spiny lobster shelter preference rankings (1, most preferred; 5, least preferred) used to simulate shelter selection in the model.

Lobster size class (mm CL)	Rank order of preference for each shelter type				
	Loggerhead sponge	All other sponges	Solution hole	Octocoral–sponge complex	Other shelters
<20.0	2	1	NA	3	4
20.1–25.0	2	1	NA	4	3
25.1–30.0	1	2	4	5	3
30.1–35.0	1	2	3	5	4
35.1–40.0	1	4	2	NA	3
40.1–45.0	2	4	1	NA	3
45.1–50.0	2	NA	1	NA	3
>50.0	2	NA	1	NA	3

Note: Some sizes of lobster are rarely, if ever, found associated with certain shelter types, so those shelter types are not included in the rank preferences for that lobster size class (CL = carapace length).

affects growth rate) was assigned an initial value of zero.

Growth

Growth of individual lobsters was simulated in discrete steps, reflecting the molting process of arthropods. Individuals were evaluated daily to determine whether they molted, and if molting occured, then growth in length was determined. The probability of molting (P_m) was determined for each individual based on its size (S; mm CL) and the number of days since its last molt (x):

$$P_m = \begin{cases} 1.01/\{1 + e^{[-0.31\times(x-22.8)]}\} - 0.02 \\ \quad \text{if } S < 25 \text{ mm CL}, \quad \text{and} \\ 1.02/\{1 + e^{[-0.18\times(x-34)]}\} - 0.02 \\ \quad \text{if } S \geq 25 \text{ mm CL}. \end{cases} \qquad (1)$$

These equations were based on laboratory growth experiments (Lellis and Russell 1990). The probability that a juvenile lobster will molt within 10 days of its last molt is zero. However, the probability rises quickly to 1.0 after 34 days post-molt for small individuals (<25 mm CL), and rises somewhat less steeply to 1.0 after 55 days for larger juveniles (>25 mm CL). If a generated uniform random number was $<P_m$, then the individual molted and its counter for ‘‘days since last molt’’ was reset to zero.

If an individual is designated to molt, the incremental increase in length (G; mm CL) was then determined from the individual’s current length (S) as $G = 0.463 + 0.111 \times S$. This relationship was again based on laboratory and field determinations of molt increments (Lellis and Russell 1990, Forcucci et al. 1994).

Shelter selection

Shelter selection depended on lobster body size, lobster density, and the habitat cell type (i.e., seagrass or hard-bottom cell). The type of shelter selected affected lobster mortality and the movement of lobsters among cells, which was represented in other subroutines. Shelter selection rules were represented separately for algal-stage juveniles (<12 mm CL) and postalgal-stage juveniles (25–50 mm CL). Transitional juveniles (13–25 mm CL) shelter both in the macroalgae, as algal-stage juveniles do, and in crevice shelters, as do postalgal juveniles. As they grow larger, they are less often found in macroalgae (Childress and Herrnkind 1996); therefore, we modeled the daily probability that a lobster in this size range would choose a crevice shelter (P_T) as an increasing function of its size (S, mm CL):

$$P_T = 0.0045e^{(0.216\times S)}. \qquad (2)$$

If a generated uniform random number was $<P_T$, then the individual was treated as a postalgal-stage juvenile; otherwise, the individual was treated as an algal-stage juvenile.

Shelter selection rules were formulated for algal-stage and for postalgal-stage juveniles based on field data and laboratory investigations of habitat choice (Childress and Herrnkind 1994, 1996, Forcucci et al. 1994, Butler and Herrnkind 1997). All lobsters were assumed to be quiescent in shelter during the day and assumed to forage most of the night. Algal-stage juveniles remain in seagrass or macroalgae while foraging, and thus we assumed they spent both day and night in their seagrass habitat if in seagrass cells or in their macroalgae habitat in hard-bottom cells. Postalgal-stage juveniles leave their daytime shelters to forage in surrounding areas each night. Postalgal stage juveniles in seagrass cells, regardless of size, were therefore assigned to seagrass shelter. Shelter selection of postalgal juveniles in hard-bottom cells, where five different shelter types were represented, was a more complex process.

Postalgal-stage individuals in a hard-bottom cell were assigned one of the five shelter types based on size-dependent shelter preferences and shelter availability. We first used lobster size to determine the shel-

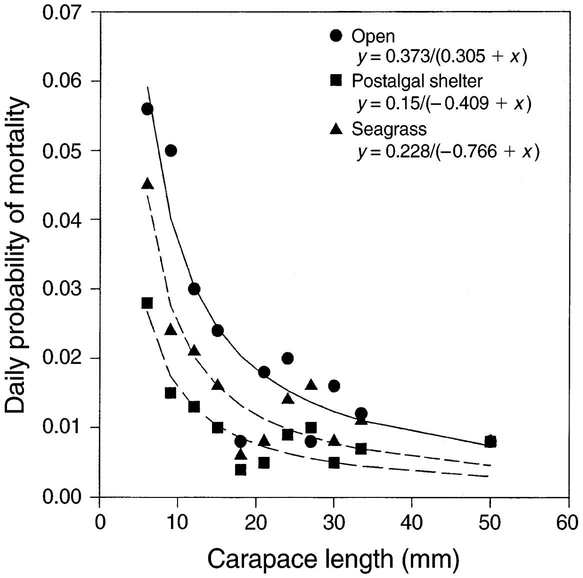

FIG. 3. Functions describing the size-specific and shelter-specific daily probability of mortality for juvenile spiny lobsters used in model simulations. The shapes of the functions were determined by least-squares fit to field data describing the survival of juvenile lobsters tethered in the open (λ), in seagrass (σ), or in shelter (e.g., sponges, solution holes, etc.; ν).

ter preference of an individual for each of the five shelter types (Table 1). These preferences were determined using Manly's alpha (Chesson 1978), an electivity index, calculated separately for eight size classes of lobsters (15–50 mm CL in 5-mm size increments). The electivity index was determined from field observations of shelter use by >10 000 juvenile lobsters at 27 field sites (0.2–0.7 ha in area), wherein shelter abundance had been determined (Herrnkind et al. 1997*b*; M. J. Butler, W. F. Herrnkind, and J. H. Hunt, *unpublished data*). For each individual lobster, the most preferred shelter type that was below its carrying capacity was selected. If all of the shelter types were filled to capacity, then the individual was assigned the open (no shelter) category.

Mortality

The daily probability of mortality (P_D) was computed as a weighted sum of day, night, and twilight mortality probabilities, with each dependent on lobster size and shelter type. Daytime was considered to be 12 hours, twilight was 2 hours, and nighttime was 10 hours. We determined the probability of mortality for each of the daytime, twilight, and nighttime periods based on the shelter inhabited by the lobster for each of the periods, and then computed a total daily probability by weighting the three probabilities by the hours of each period. Daily probabilities of mortality for juvenile lobsters of a given size (S; Fig. 3) were as follows:

$$P_o = 0.373/[24 \times (0.305 + S)] \qquad (3)$$

for lobsters in the open;

$$P_s = 0.15/[24 \times (-0.409 + S)] \qquad (4)$$

for lobsters in macroalgae or postalgal shelters; and

$$P_g = 0.228/[24 \times (-0.766 + S)] \qquad (5)$$

for lobsters in seagrass.

All lobsters in seagrass habitat cells remained in seagrass all of the time, so we used Eq. 5 for the day, twilight, and night periods ($P_D = P_g$). Algal-stage lobsters in hard-bottom cells remained in macroalgae all of the time, so we used Eq. 4 for all three time periods ($P_D = P_S$).

The calculation was more complicated for postalgal-stage lobsters, and for transitional lobsters acting like postalgal-stage lobsters, in hard-bottom cells. Transitional and postalgal-stage juveniles were in shelters (if available) or were in the open during the day (either Eq. 3 or Eq. 4), spent variable amount of twilight time in the open searching for shelter (Eq. 3), and were in the open at night (Eq. 3). Thus, their daily probability of mortality was

$$P_D = \{P_s \text{ or } P_o\}[12 + (10 - 10T_f) + (2 - 2T_P)] + P_o(10 + 10T_f + 2T_P) \qquad (6)$$

where Tp is the fraction of twilight spent searching for shelter and therefore in the open, and T_f is proportion of nighttime spent foraging for food. The fraction of twilight hours spent searching was assumed to be inversely proportional to the total availability of all shelters in that cell:

$$Tp = 1/(K_T - N_t) \qquad (7)$$

where K_T is the total lobster carrying capacity of the cell (summed over shelter types) and N_t is the current number of lobsters in the cell and already in shelters. For each lobster, if a generated random deviate was $<P_D$, the lobster was assumed to have died and was removed from the simulation.

Eqs. 3–5 were determined through least-squares fitting of equations to size-specific and shelter-specific mortality data derived from tethering studies (Smith and Herrnkind 1992). However, tethering data only yielded relative estimates of mortality among sizes and shelters; thus, the appropriate intercepts for these functions were unknown. We estimated the intercept terms in the equations using model simulations. Mark–recapture studies of microwire-tagged, first benthic stage juveniles outplanted in macroalgae indicate that only 1–4% survive to 35 mm CL (Butler et al. 1997, Sharp et al. 2000). Therefore, we iteratively altered the intercept in Eq. 4 and ran a single cohort of juveniles through the growth, shelter selection, and mortality routines with the constraint being that lobsters only accessed hard-bottom habitat where they could move between macroalgae and hard-bottom structures of unlimited lobster carrying capacities. From these simulations, we chose a mortality function for lobsters dwelling in hard-bottom cells that resulted in 1–4% of the model individuals surviving to 35 mm CL. Based on tethering results, we then assumed that survival of lobsters in open water was one-half that of those in hard-bottom cells with unlimited shelter, and so selected an intercept for Eq. 3 that resulted in 0.5–2% survival to 35 mm CL. Tethering studies also suggest that survival of juveniles in seagrass falls midway between that measured in the open and in hard-bottom structures or macroalgae (Herrnkind and Butler 1986). We therefore chose an intercept for Eq. 5 (lobsters in seagrass) that resulted in survival intermediate to the survival in the open and in hard-bottom cells.

Movement among habitat cells

Movement of lobsters among habitat cells depended upon lobster size and the availability of shelter in their current cell. The functions below (Eq. 8) that describe the size-specific probability of movement for lobsters in different types of shelter was based on mark–recapture records for over 500 individual lobsters in 24 2500-m^2 (50 × 50 m) field sites within hard-bottom habitat (Schratwieser 1999; M. J. Butler, *unpublished data*). Each site was divided into four 25 × 25 m survey areas, and survey methods adapted to the Jackson/Jolly-Seber mark–recapture method (Jackson 1939, Manly 1985) were used to separate estimation of emigration and mortality. Movement of lobsters in the open was based on our intuitive expectation that the likelihood of cell departure of large juvenile lobsters (e.g., 50 mm CL) with no shelter would be 10 times that of similar-sized individuals with access to shelter. Movement from seagrass was derived by assigning probabilites of moving that were intermediate between those with shelter and those without. Small juvenile lobsters that have found shelter rarely move to other shelters, and typically forage at night within a meter or two of their daytime shelter (Andree 1981, Schratwieser 1999). Thus, in the model, individuals <30 mm CL that occupyied a shelter were assumed to remain in their cell. For all other individuals, we determined the probability of leaving their current cell (P_M) based on their current shelter type (seagrass, open, macroalgae, or one of the five hard-bottom shelter types) and size:

$$P_\text{M} = \begin{cases} 0 \quad \text{if } S < 30 \text{ and the lobster is in shelter} \\ -0.00005 + (0.0025 \times S) \\ \quad \text{if } S \geq 30 \text{ and the lobster is in shelter} \\ -0.000275 + (0.01375 \times S) \\ \quad \text{if the lobster is in seagrass} \\ -0.0005 + (0.0250 \times S) \\ \quad \text{if the lobster is in the open.} \end{cases} \tag{8}$$

If a uniform random number was $<P_\text{M}$, then the individual moved to a randomly selected cell from among the four neighboring cells. Nondirectional movement appears to be the norm for postalgal stage juvenile lobsters (M. J. Butler, *unpublished data*), although large juveniles and adults often participate in nightly and seasonal migrations requiring directional movement (Herrnkind 1969, Cox et al. 1997, Boles and Lohman 2003). No movement was permitted across the northern or southern edges of the model cell grid, which mimics the real system where habitat, salinity, and depth prohibit movement in those directions. Movement across the east and west boundaries was wrapped, so that lobsters exiting the eastern edge of the cell grid then entered at the corresponding cell on the western edge. This approximates natural immigration and emigration of lobsters from areas east and west of the modeled region.

Individuals designated to move from a cell were only permitted to move into an adjacent habitat cell, thus one cell per day. As discussed in the section *Spatial structure of the model* above, the habitat structure (i.e., type and proportion of each shelter available) of each cell was constructed to be *indicative* of a ∼12-km^2 area in the Florida Keys and in a position in the array of habitat cells that corresponded with its real position in nature. However, the actual number of shelters, number of lobster, and dynamics of lobsters (e.g., rates of movement) were scaled to match those typical in a 1000-m^2 area (the scale at which we have good empirical data). Therefore, the movement probabilities that we used should not be viewed as the probability of movement of an individual from the center of one 12-km^2 area to the next (a distance of ∼3.5 km in one night). Instead, the distance the juvenile lobster traverse in one night if they change cells in the model is roughly equivalent to 30–50 m. Conceptually, this is no different than lobsters moving from a 1000-m^2 area at the edge of one large 12-km^2 habitat cell into the adjacent 1000-m^2 area in the next 12-km^2 habitat cell. Portraying movement among habitats (i.e., emigration/immigration) in this way was a necessary consequence of an individual-based formulation, and the way in which the spatial structure of the model was conceptualized to avoid having to model billions of individuals at a time. It is an abstraction of reality, but we believe it to be a realistic and reasonable one.

Before arriving at this depiction of movement, we conducted sensitivity analyses by decreasing the above empirically based movement probabilities by 10%, 50%, and finally by two orders of magnitude. The most extreme scenario represented rates of movement expected between 1000-m^2 areas situated in the center of 12-km^2 habitat cells. This extreme scenario resulted in virtually no exchange of lobsters among habitat cells, which is clearly unrealistic. Most individuals died or grew out of the model before ever emigrating to a new habitat cell. Deceasing movement by 10% and 50% resulted in reductions in recruitment under no algal bloom or sponge die-off conditions of 0% and 8%, respectively.

Details of simulations

Each day we randomly chose the order in which habitat cells, and individuals within habitat cells, were evaluated. Settlement was determined at the beginning of each day. For each individual, the biological processes were evaluated in the order of shelter selection, mortality, growth, and movement. The only exception was new postlarval arrivals to a habitat cell, which occurred only after the current residents were finished choosing shelters. Random ordering of cells and individuals minimized any artifical results that can arise from a fixed-order evaluation of cells or lobsters.

Each 10-year simulation was begun two years before the period of interest (e.g., 1989–1997) and continued for two years past this period. The initial two years used the long-term mean postlarval supply for each month as input, and was designed to minimize effects of initial conditions. Running the model for two years after the period of interest ended was done to follow the fate of all lobsters in the model who entered during the last year of interest in the simulation (i.e., 1997). We performed replicate simulations of each condition (see below), and in each we used different random number sequences that affect the stochastic aspects of settlement, growth, shelter selection, mortality, and movement. All mean values reported for the simulations were computed as the average of the specified response variable for the replicate simulations. The program is written in FORTRAN 90, using Microsoft FORTRAN Powerstation 4, and simulations were run on a Pentium III platform.

DESIGN OF MODEL SIMULATIONS

Model corroboration

We corroborated the growth and shelter selection processes by comparison of model predictions of lobster sizes and shelter utilization to independent field data. We compared the predicted growth (mm CL) of a single cohort of model lobsters for one year post-settlement to growth estimated from microwire-tagged lobsters released into the wild in the Florida Keys (Sharp et al. 2000) and in Cuban waters (Phillips et al. 1992).

To corroborate the shelter selection process, we compared predicted shelter utilization with observed shelter utilization for a field study conducted in early November 1991, prior to the 1991 algal bloom. The field study involved measuring the shelter use and sizes of lobsters in each of four hard-bottom shelter types (octocoral-sponge complexes were not quantified) at six hard-bottom sites (160–740 m^2 in area) in Florida Bay (Herrnkind et al. 1997*b*). The cell grid used in the model simulation was designed to mimic the field conditions and contained all hard-bottom cells, with field data used to set the types and numbers of four shelter types and the initial numbers and lengths of lobsters in each cell. We simulated lobsters selecting shelters with no growth, mortality, or movement for 10 days. We compared predictions on day 10 from the model with observed field values for the mean ± SD of the percentage of lobsters, and the mean ± SD of the lengths of lobsters, in each of the four shelter types. Means and standard deviations were computed from 10 replicate model simulations.

Algal bloom effects on lobster recruitment

Our objective in these simulations was to predict the potential impact of the massive 1991 and 1992 cyanobacteria blooms and the associated sponge die-offs on spiny lobster recruitment in the Florida Keys. We performed 10-year simulations without (baseline) and with the 1991–1992 algal blooms and associated sponge die-offs. The 1991 bloom was from 15 November through 2 January (49 days) and occurred in 30 model cells (Fig. 1B). The 1992 bloom was simulated in the same 30 cells as the 1991 bloom for 1 October through 16 November (47 days), and additionally in 85 cells for 1 October though 27 January (119 days; Fig. 1C). Thus, the 1991 bloom covered ~10% of the model cell grid, and in 1992 the bloom affected ~10% of the grid in the first event and ~35% in the second event.

The effects of the blooms on lobster habitat were simulated by decrementing by 0.0225% each day the loggerhead sponge carrying capacity and by decrementing by 0.125% each day the carrying capacity of the other sponge shelter type during the bloom periods. Field data indicates that the algal blooms killed loggerhead sponge (*Spheciospongia vesparia*) at the lowest rate, whereas the vase sponge (*Ircinia campana*), several species of commercial sponges (*Hippospongia* and *Spongia*), and other similar-sized sponges (*Ircinia* sp.) all died quickly (Butler et al. 1995, Herrnkind et al. 1997*b*). The combination of bloom durations and daily percentages of reductions in carrying capacity resulted in a loss of sponges in the simulation that approximated the loss of sponges that were observed in the field. In both simulated blooms, ~60% of the loggerhead sponges and all of the other sponge shelter type were lost by the end of each bloom. Observed losses were ~45% for loggerhead sponges and 100% for other sponges after three months of exposure (Butler et al. 1995, Herrnkind et al. 1997*b*). No sponge regrowth was simulated because the regrowth of sponges typically used as shelter by lobster was minimal in the region during the 10-year simulated period (Stevely and Sweat 1999).

To determine the robustness of model predictions to postlarval supply, we repeated the baseline and algal bloom simulations using the long-term average postlarval supply for the entire simulation, rather than the actual values observed for the period (which were high-

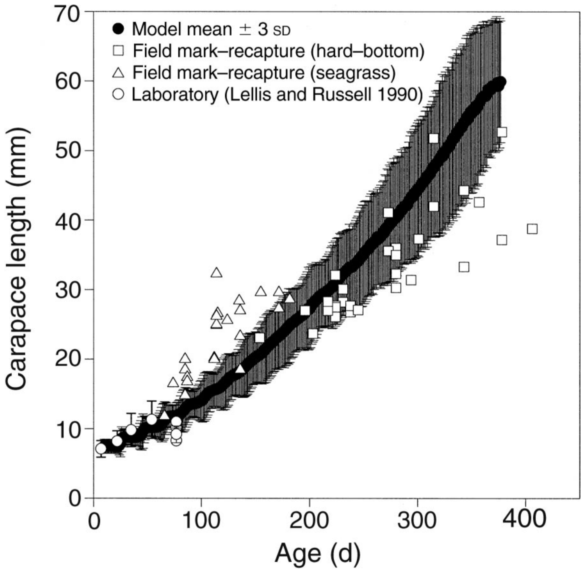

FIG. 4. Growth subroutine validation: predicted and observed growth (in carapace length) of juvenile spiny lobsters over a one-year period. Predicted growth was from a single cohort of 100 lobsters from settlement to one year, using the probability of molting algorithm and the length-increment equation. Observed growth was obtained from laboratory and field studies.

er than average; see Fig. 2). We report the daily average numbers of lobsters reaching 50 mm CL for the cells impacted by the bloom (''perturbed region'') and for the entire model cell grid (''entire domain'') for the bloom simulation and the baseline simulation. We summarized the difference between the bloom and baseline simulations by computing the average difference between the number of lobster reaching 50 mm for each day, and then computed the average of these difference over days for all days after the onset of the first bloom. We used predicted shelter use and predicted movement out of the impacted cells to help understand the differences in predicted recruitment between bloom and baseline simulations. Shelter use was summarized by the predicted mean numbers of lobsters per shelter for each day, and then averaged by shelter type for the pre-, during, and post-bloom periods. Movement was reported as the numbers of lobsters moving out of bloom-impacted cells under baseline and bloom simulations. Based on the model formulation of lobster movement, any changes in movement were due to the behavior of individuals >30 mm CL because smaller individuals were not permitted to move among cells. Five replicate simulations were performed for the baseline and bloom simulations; all mean values are averages over the five replicate simulations. For several comparisons, we applied a one-factor model I ANOVA to the model predictions to determine the statistical significance of predicted changes between between baseline and bloom simulations.

SIMULATION RESULTS

Model corroboration

Predicted lobster growth and shelter selection were similar to observed values. Predicted growth of lobsters over the year was similar to observed growth for lobsters <30 mm CL, but the simulation slightly overestimated the growth of lobsters >30 mm CL (Fig. 4). The overestimation of growth for larger juvenile lobsters was likely due to our temperature-independent representation of growth, and our use of laboratory information on growth at warm, summer temperatures. Predicted shelter selection was also similar to observed values (Fig. 5). Both simulated- and observed-shelter selection showed most lobsters in loggerhead sponges, intermediate numbers of lobsters in solution holes, and relatively few lobsters in other sponges and other shelters (Fig. 5A). Predicted and observed lengths of lobsters in shelter types were also similar, except for predicted mean lengths being shorter than observed in the ''other shelters'' category (Fig. 5B). The generally

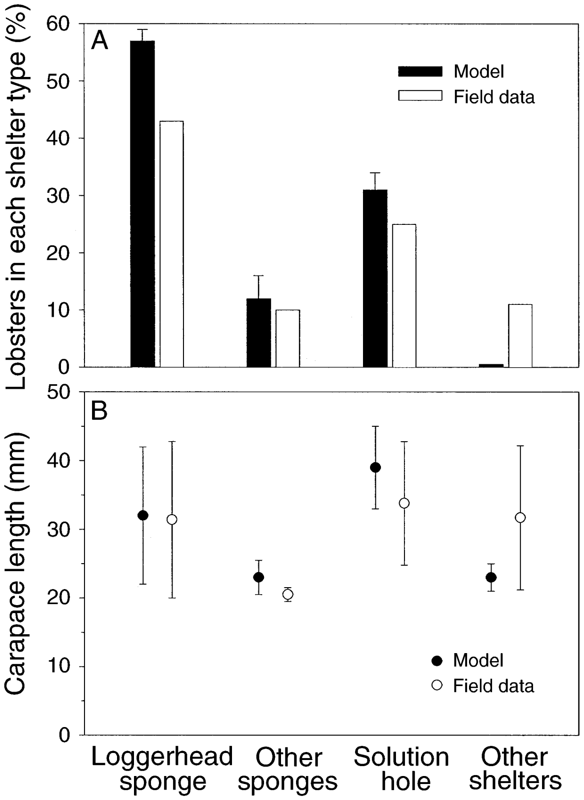

FIG. 5. Shelter use subroutine validation: (A) predicted and observed shelter usage and (B) lengths of lobsters in each of four types of shelter. Observed values were from a field study of six hard-bottom sites in Florida Bay in November 1991. Predicted values were from 10 replicate simulations on a cell grid designed to closely mimic the field conditions; only the shelter-selection algorithm was used in these validation simulations. Shelter usage is defined as the percentage of lobsters found in each shelter type.

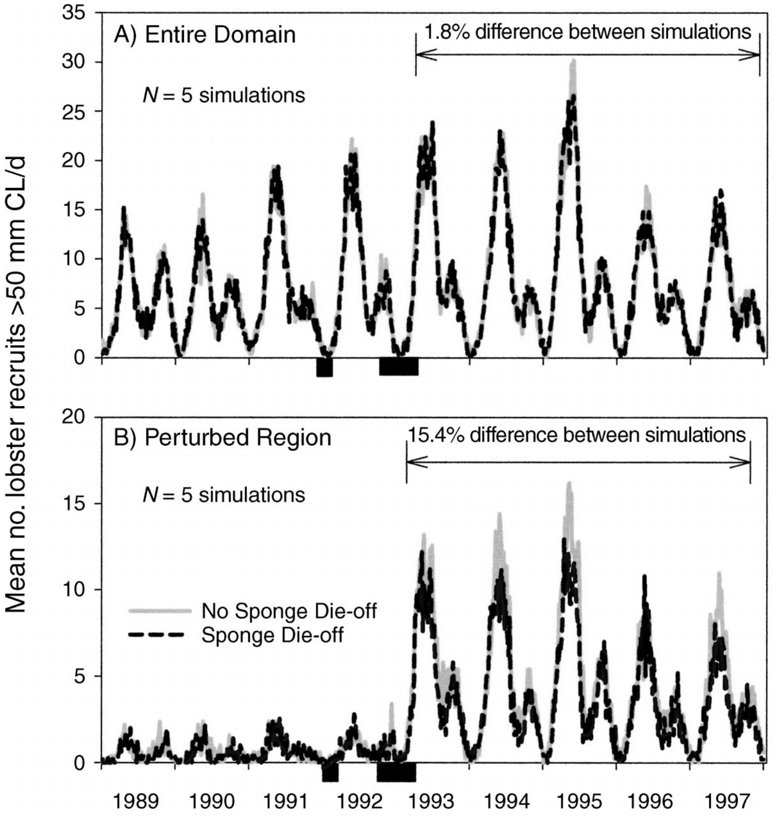

FIG. 6. Model predictions of the daily mean number of lobster recruits (individuals larger than 50 mm CL) for the 10-year simulations without (baseline) and with the algal blooms for the (A) entire system and (B) local region impacted by the blooms. The percentage of difference in post-bloom lobster recruitment between baseline and bloom simulations is shown. The two black bars along the *x*-axes represent the periods when the algal blooms occurred.

good agreement between predicted and observed growth and shelter selection suggested that the representation of these two important processes in the model was reasonable.

Algal bloom effects on lobster recruitment

The algal blooms and associated sponge loss had significant localized effects on lobster recruitment, but surprisingly small effects when the entire Florida Keys was considered (Fig. 6). After 15 November 1991 (the onset of the first bloom), the percentage of difference between the cumulative number of lobsters recruiting to 50 mm CL under baseline and algal bloom simulations averaged 15.4% in the cells affected by both blooms (Fig. 6B), but only 1.8% for the entire grid (Fig. 6A). The reduction of 15.4% was statistically significant ($F_{1,9} = 77.38$, $P < 0.001$), whereas the 1.8% reduction was not. Thus, despite the loss of the prime lobster shelter over 35% of the nursery area, the predicted recruitment of lobster was reduced by only 15.4% in the impacted area and by only 1.8% over the entire Florida Keys. Indeed, in terms of actual numbers of recruits, total recruitment was 58% higher for the two years after the blooms than for the two years prior to the onset of the first bloom. The increase in actual numbers just after the blooms was due to higher than average postlarval supply during the preceeding years, which more than offset the loss of lobster due to the blooms and associated sponge die-off.

The smaller than expected reductions in local and system-wide recruitment was also due to increased movement of lobsters out of the impacted cells, and greater use of normally underutilized shelter types under periods of high postlarval settlement. The number of lobsters moving from the bloom-impacted cells to adjacent unimpacted cells increased by 42% under bloom conditions as compared to baseline conditions ($F_{1,9} = 5.169$, $P = 0.011$). Prior to the first algal bloom, lobster densities were predicted to be highest in loggerhead sponge shelters and second highest in other sponge shelters (Fig. 7A, B). During the algal blooms, use of loggerhead sponges by lobster was predicted to increase slightly, their use of other sponges was predicted to decline, and their use of solution hole and other shelters predicted to increase. After the blooms, model simulations predicted lower use of loggerhead sponges, continued lower use of other sponges, and continued increased use of solution holes and other

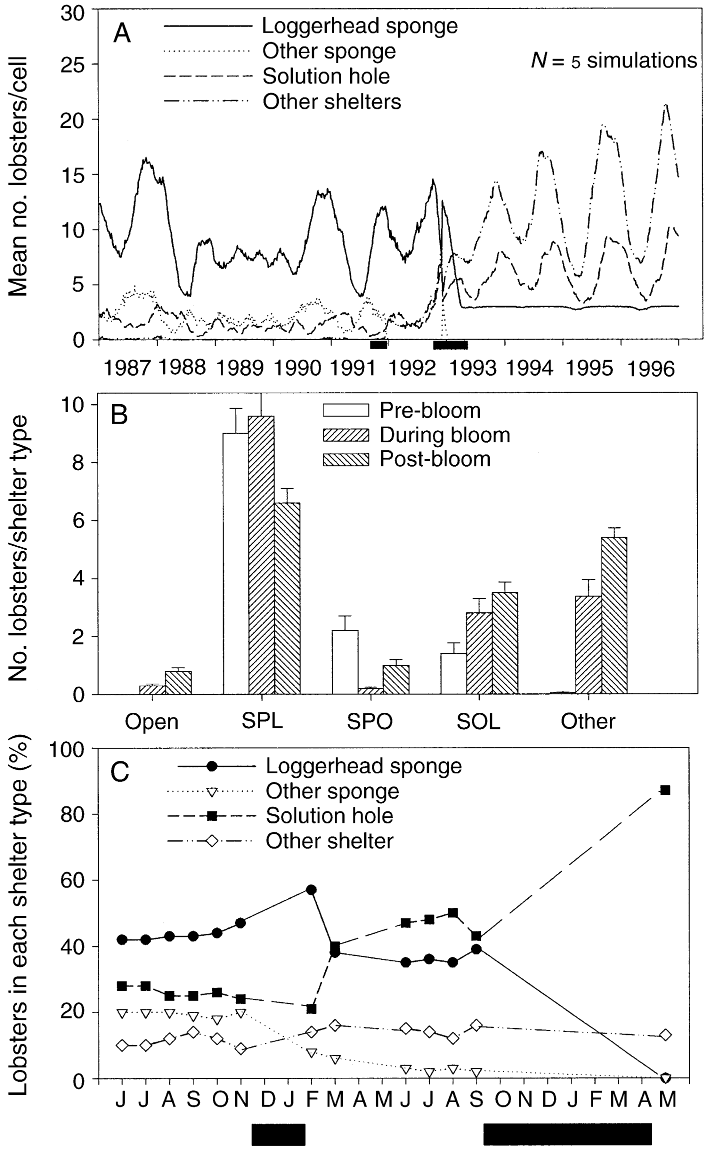

FIG. 7. Model predictions and field observations of changes in shelter use by lobsters in response to the plankton blooms and sponge die-offs. (A) Predicted mean daily number of lobsters in each of four shelter types in the local region impacted by the blooms for the 10-year simulations. (B) Predicted mean (±1 SD) number of lobsters per shelter type per day for the five shelter types for three time periods: prior to the first bloom, during the two blooms, and after the second bloom. These results are a summary of the daily predictions shown in panel (A). The shelter-type designations in panel (B) are: Open, not in shelter; SPL, loggerhead sponge; SPO, other sponges; SOL, solution hole; and Other, other shelters such as corals and octocorals. The two black bars along the *x*-axis represent the periods when the cyanobacteria blooms occurred. (C) Field observations during June 1991–May 1993 of juvenile lobster shelter usage at 27 hard-bottom sites within south-central Florida Bay that were exposed to the blooms. These data were not used in model formulation. The two black bars along the *x*-axis represent the periods when the blooms occurred.

shelters. These predicted changes in shelter use are virtually identical to changes that we observed in the field, which we detail in the *Discussion*.

Model robustness

The robustness simulations showed that model predictions of bloom effects on lobster recruitment were sensitive to changes in the magnitude of postlarval supply. Reducing postlarval supply to the long-term average beginning with the onset of the first bloom resulted in only a slightly larger reduction in recruitment in the local area (20% vs. 15.4% decline in number of recruits to 50 mm CL), but much larger reductions in system-wide recruitmemt (14% vs. 1.8% decline in recruits). Subsequent simulations in which the spatial pattern of postlarval supply to the nursery was altered in various ways (e.g., uniform, east–west gradient, aggregated, various randomized permutations, flow-dependent supply, etc.) also showed that model predictions were sensitive to changes in the spatial delivery of postlarvae (Butler et al. 1997). Recruitment varied by nearly 25% among the different spatial delivery scenarios we tested, with the random postlarval supply model yielding the highest levels of recruitment. The recruitment of lobster under a uniform postlarval delivery scenario, which we used in the original model formulation described here, was ~12% lower than that predicted by the random delivery model, but indistinguishable from most of the other spatial simulations of postlarval supply. Which of these spatial depictions of postlarval supply is the most realistic is not known, although preliminary empirical evidence suggests that the random model may be best (Butler et al. 1997).

Subsequent model simulations also showed that predicted recruitment was insensitive to the spatial location of hard bottom cells and to spatial heterogeinty of shelters assigned to model cells. Results reported in this paper used a habitat grid with the locations of hard bottom cells and the assignment of shelter types and densities to cells based on empirical data for the Florida Keys. In subsequent analyses (Butler et al. 1997, Butler 2003), we examined the sensitivity of predicted recruitment to the locations of hard bottom cells and to the types and densities of shelters assigned to cells. Six combinations were simulated that used empirically based or random assignment of hard bottom cells combined with empirically based assignment of shelters to cells, regional homogeneity in shelters, and complete (grid-wide) homogeneity in shelters. Regional homogeneity in shelters consisted of setting the types and densities of shelters in cells to the averaged values from the empirically based grid for each of five regions, with all cells within a region being assigned the same values. Predicted recruitment under average postlarval supply varied by $<5\%$ among the six combinations of hard bottom cell locations and spatial homogeneity in shelter types and densities.

Discussion

Model predictions and field observations

Our model results suggest that the recruitment of spiny lobster to the subadult stage in the Florida Keys was remarkably resistent to the massive and episodic destruction of structural complexity in a large portion of their nursery habitat. The magnitude of those effects depended on postlarval supply. Sponges are the primary shelter for juvenile lobsters. Yet, the nearly complete loss of the dominant sponge community in ~20% of the lobster nursery area resulted in a predicted reduction of only 15% in lobster recruitment in the affected area and a 2% reduction for the entire Florida Keys region. These results are surprising given the observed degree of habitat damage, although they are consistent with the results of field surveys of lobster population change made subsequent to our modeling and thus not used in the model's formuation. Field estimates put juvenile lobster loss at ~30% on sites directly impacted by the sponge die-off (Herrnkind et al. 1997*b*). However, this figure varies widely among sites, depending largely on the structural complexity remaining on a site after the die-off (Herrnkind et al. 1997*b*). Local lobster populations in some areas impacted by the sponge die-off were seemingly unaffected, whereas their abundance on other sites declined by 50%. Those same field surveys suggested that over the entire Florida Keys, the sponge die-off would result in ~4% fewer juvenile lobsters, which is similar to the model prediction of a 2% decline.

Model predictions of the effects of the sponge die-off on shelter use by lobster were also similar to those that we independently observed in field surveys. The model predicted a shift in shelter use in the bloom area from loggerhead sponges and ''other sponges'' to solution holes and ''other shelters'' (Fig. 7A, B). Field observations made after the blooms showed a similar shift in shelter usage by lobsters. At the time of the algal blooms, we had been following juvenile lobster shelter use at 27 hard-bottom sites within south central Florida Bay, an area affected by the blooms (see Butler et al. 1995, Herrnkind et al. 1997*b*). Fig. 7C summarizes the temporal change in lobster shelter use observed at those sites during the period that includes the blooms. Field observations and model predictions both indicate that the blooms initially resulted in a decline in the use of ''other sponges,'' which died first in response to the algal blooms. This, in turn, lead to a temporary shift to greater lobster occupancy of loggerhead sponges until those too died. Thereafter, lobsters sheltered increasingly within solution holes and other formerly underutilized shelters, such as small coral heads and octocorals.

When the effects of the blooms are expressed as absolute number of recruits, rather than comparisons of change between simulations with and without blooms, the model predictions and observed values were also similar. Postlarval supply to the Florida Keys was substantially higher than average during the years of the sponge die-off (Fig. 2), so model simulations actually predicted a 58% increase in the number of lobster recruits in the two years following the algal blooms as compared to the two years before. Fishery landings of lobsters in the two years after the blooms were similarly up 38% over the years preceeding the blooms. Thus, both model predictions and field observations suggest that the sponge die-off had an imperceptible impact on lobster recruitment that, for other reasons, was booming. There is no fishery-independent time-series of data available for assessing adult lobster abundance in Florida. However, fishery landings may be a good proxy for adult abundance in the Florida Keys because the fishery is severely overcapitalized, a majority of the legal-sized lobster are harvested each year, and there has been no change in the long-term mean landings despite a four-fold change in fishing effort (Hunt 2001). Regardless, fishery-dependent landings data are all that is available.

Reasons for population resistance

Empirical evidence and modeling results offer several possible explanations for the resistance of the spiny lobster population to such a dramatic loss of nursery habitat. First, coinciding with the onset of the algal blooms, higher than average concentrations of postlarvae arrived in the Florida Keys during the peak winter and spring settlement season for four consecutive years (Fig. 2). The nursery areas for lobster in the Florida Keys are a mosaic of sites that vary in habitat structure and local delivery of postlarvae (Field and Butler 1994, Herrnkind and Butler 1994). Experimental studies indicate that as a consequence, recruitment at a particular site may be limited by either larval supply or postsettlement mortality, depending on the local interplay between the availability of postlarval settlers and appropriately scaled shelter (Butler et al. 1997). Our model suggests that the additional settlers that arrived during algal bloom years may have saturated previously underpopulated nursery sites, thus boosting recruitment outside the zone impacted by the sponge die-off. Additional settlers also arrived within the impacted area, and many of those individuals sought shelter in previously under-utilized and presumably ''suboptimal'' shelters that nonetheless afforded them some refuge. The way in which the relationships between shelter availability and both lobster movement and mortality were represented in the model also contributed to the predicted resistance of the spiny lobster population.

Juvenile spiny lobsters display size-specific preference for shelter (Eggleston et al. 1990, Forcucci et al. 1994, Butler and Herrnkind 1997), but their choice is strongly influenced by the type of shelter available (Butler and Herrnkind 1997) and the presence of conspecifics in existing shelters (Eggleston and Lipcius 1992, Childress and Herrnkind 1994, 1997, Ratchford and Eggleston 1998, Butler et al. 1999). Flexible behavior along with the availability of alternative shelters at many sites resulted in a shift by lobsters to habitation of those previously underutilized shelters following the sponge die-off. This shift in shelter use is evident in both model results and field observations (Fig. 7). On average, sites within the perturbed region have a large number of potential alternative shelters (e.g., solution holes, complex octocorals) that were unaffected by the sponge die-off, or, in some cases, even increased in abundance (Herrnkind et al. 1997*b*; M. J. Butler, *unpublished data*). In the field, we noted an increase in the number of solution holes at sites where sponges died. These holes were either beneath the now-missing sponges and, therefore, overlooked in our pre-bloom surveys of shelter abundance, or they were newly excavated holes created by taxa (e.g., stone crabs; *Menippi mercenaria*) that also seek shelter in crevices and are more capable burrowers than spiny lobster. This is an extraordinary example of the type of unanticipated response of biological communities to disturbances that can destroy the validity of statistical or mathematical constructs based on unperturbed systems. Dynamics such as these are reminders of the need for flexible models based on observation and experimentation under different environmental conditions.

Other regions of the Florida Keys contain less-suitable expanses of nursery habitat, possibly with fewer underutilized shelters. If so, then lobster recruitment in those areas may be less resistant to the loss of prime habitat. An uneven distribution of alternative shelters among sites probably accounts for the asymmetrical change in population decline among perturbed and unpertubed regions predicted by the model and observed in the field (Herrnkind et al. 1997*b*). It also provides a possible explanation for why a change in the modeled postlarval supply from the actual supply to an average supply altered the predicted population loss in perturbed areas very little, but resulted in a much greater decline in recruitment over the entire region where habitat structure varies more. The key appears to be the plastic use of shelter by lobster and the overabundance of underutilized shelters in some areas, which in this instance were, fortuitously, those areas that were also impacted by the sponge die-off.

Yet, shifts in shelter use from heavily used and, perhaps, preferred structures to previously underused shelters begs the question of whether there are costs associated with the shift, and if not, why a preference among shelters should exist at all. The ecological literature is rife with examples of trade-offs made by species among shelters or habitats, driven by the evolutionary necessity of balancing the risk of mortality with maximizing growth or reproduction (e.g., Law 1979, Werner et al. 1983, Power et al. 1985, 1989, Fraser and Gilliam 1992, Reznick et al. 1996, Fraser et al. 1999). Our model assumes that there is no penalty with respect to risk of mortality for lobsters that reside in one type of shelter vs. another, so a change in shelter utilization like that resulting from the sponge die-off had no impact on survival. However, shifts in shelter use to the open (when no other shelters are available) or to a seagrass-dominated cells from hard-bottom cell do result in an increase in the risk of mortality in the model. In addition, as shelters become more scarce there is an associated increase in shelter search time, which we modeled as a simple inverse relationship with shelter abundance. Thus, fewer shelters in a habitat cell results in more time spent in the open searching for shelter, and the risk of mortality is greatest for lobster in the open.

Although the details of our model formulation of these dynamics may be debatable, there is indeed empirical evidence from tethering studies that suggests that there is no discernable difference in the mortality of juvenile lobster hiding in different natural shelters (Childress and Herrnkind 1994). We recognize, however, that tethering studies may not be sufficiently sensitive to discern small, but potentially important, differences in daily probabilities of survival. Regardless, juvenile lobsters appear to exhibit size-specific shelter preferences (see *Model description; Shelter selection* section above), which is difficult to explain unless it is an adaptive behavior. Social aggregations of lobster in dens, the potential benefit of conspecifics to group defense (Ratchford and Eggleston 1998, Butler et al. 1999), or the location of suitable shelter (i.e., ''the guidepost effect''; Childress and Herrnkind 1997) further complicate the potential rules governing shelter use and its associated risk of mortality. We are investigating the consequences of these factors in a new set of simultations.

Our representation of lobster movement was also admittedly simple and had several features that set the stage for high population resistance to habitat change. In the model, lobsters paid only a small penalty for movement when searching for shelters under crowded conditions or where shelter was limiting, and paid no penalty for movement among habitat cells. There was also no penalty for arriving in an unfamiliar cell, as long as shelters were available. We know of no data for lobsters demonstrating that new arrivals in an area are at a selective disadvantage. Given the unexpected and episodic occurrence of the algal blooms, we were not prepared to monitor changes in lobster movement in the field in response to habitat loss. So, we cannot confirm whether in reality large juvenile lobsters moved from the impacted areas to other areas. However, the average size of lobsters increased on unimpacted sites near the periphery of the area impacted by the algal blooms (Herrnkind et al. 1997*b*), which is consistent with the movement of larger, more mobile lobsters into that area. Large juvenile and adult lobsters are remarkably mobile, and their movement is known to be affected by changes in water temperature, turbulence, and day length (see Herrnkind 1980).

Model limitations and improvements

We continue to improve the model. For example, in future model formulations we plan to reduce habitat cell size by an order of magnitude to create a finer grained spatial domain consisting of >3000 cells each representing 1 km^2 of seafloor. Designation of habitat cells as seagrass or hard-bottom will also be tied to GIS overlays, and the habitat structure within each cell will be updated periodically with data from new field surveys of hard-bottom habitat. We are also now incorporating in the model natural features of the spatial environment that function as barriers to lobster movement. The islands of the Florida Keys and emergent mud banks were not included in the original spatial domain. Thus, we assumed that the absence of these geographic features and their effect on lobster movement does not significantly affect the modeling results. This assumption is probably not problematic in the largely open-water Middle Keys region of the model, but in reality the movement of lobsters is probably more constrained in the Lower Keys where islands are more numerous.

The growth function may also become a temperature dependent process in future models. Field and laboratory studies indicate that seasonal differences in water temperature in the subtropical Florida Keys can alter the rate of growth of juvenile lobsters by 20–30%, with the largest changes occurring in the intermolt interval (Lellis and Russell 1990, Forcucci et al. 1994). Improvements to movement and mortality will also require new data describing how variation in shelter availablity and predator regime influence size-specific mortality rates. Sensitivity analysis of a simple spatially explicit dispersal model suggest that errors in prediction are greatest when disperser mortality and mobility are incorrectly estimated, and less so when landscape habitat structure is misclassified (Ruckelshaus et al. 1997). Improving the rules that govern individual movement and the consequences of dispersal is of continued interest to us and is especially complicated in lobsters because of their social behavior (Childress and Herrnkind 1997, Butler et al. 1999), a characteristic that they share with many finfish that travel in schools.

Significant gaps also exist in our knowledge of the factors influencing the local settlement of postlarvae. Thus, the current model depiction of postlarval supply does not distribute settlers based on local features of the benthic environment (e.g., macroalgal abundance or structure), small-scale oceanographic phenomena in the nursery environment, or variance in the competency (i.e., probability of survival based on energetic reserves) of arriving postlarvae. Model analyses to date suggest that predicted recruitment is sensitive to the magnitude and spatial delivery of postlarvae, but insensitive to the exact spatial arrangement of habitat and shelters. We require additional empirical guidance concerning the importance of these and other processes to recruitment before their dynamics can be considered in the model.

Broader implications

Marine applications of spatially explicit, individual-based modeling generally focus on the interplay between larval dynamics and physical oceanography (Possingham and Roughgarden 1990, Botsford et al. 1994, Hinckley et al. 1996, Lipcius et al. 1997, Hermann et al. 2001, and others), thus, their spatial structure is defined by features such as velocity fields, temperature, and prey density. To our knowledge, the model presented here is the first spatially explicit, individual-based model developed to describe the benthic recruitment process of a mobile marine species. While other spatial models of *P. argus* recruitment have been developed (Stockhausen et al. 2000), ours is unique in its representation of individuals and its explicit incorporation of environmental features, some biotic, others abiotic (e.g., habitat structure, cyanobacteria blooms, salinity) that also vary in space and time, and potentially impact lobster recruitment. Since our initial modeling excercises described here, we have used variations of this model to also explore: (1) the consequences of temporal and spatial variation in postlarval supply on recruitment, (2) the effect of nursery habitat structure and geographic specificity on recruitment, (3) the direct and indirect consequences of altered salinity on recruitment, and (4) the relative merit of different hypothesized mechanisms governing social aggregation in juvenile lobsters (Butler et al. 2001, Butler 2003; M. J. Butler and T. Dolan, *unpublished data*).

Our modeling analysis has been useful for the management of spiny lobster in the Florida Keys, and we think that it also has implications for assessment of changing habitat effects on coastal-dwelling shellfish and fish. Indeed, spiny lobster share many ecological attributes (e.g., mobility, sociality, changing size-specific habitat associations, etc.) with exploited finfish, which strengthens the inferences that can be drawn from our model. If one used intuition, one would have inferred that large losses of prime habitat due to the algal bloom would have had large effects on spiny lobster recruitment. Yet, when the available empirical information was formally synthesized into a quantitative model, the resulting predictions showed small reductions in lobster recruitment. The modeling also enabled us to understand why the small effects were predicted and that the same pertubations under other conditions (e.g., average postlarval supply) could have larger effects on recruitment. These results suggest that we need the full spectrum of habitat types, even those habitat types that historically may not have been heavily utilized, when characterizing essential nursery habitat. Otherwise, our models will likely be too rigid and overestimate reductions due to losses in preferred habitats.

Computer-intensive risk assessment procedures and multivariate statistical models (Fourqurean et al. 2003) are two approaches that can be used when the underlying mechanistic processes linking population dynamics to environmental change are poorly known. Yet, a purely statistical approach to population prediction reveals little about the underlying ecological processes that determine recruitment. For example, the effects of aperiodic environmental degradation on the recruitment of marine animals cannot be predicted without knowledge of its impact on the vital ecological processes that influence larval supply, nursery habitat structure, and postsettlement population dynamics. We believe that the individual-based spatial modeling approach is ideal for dealing with changing habitat effects on aquatic biota. It enables easy representation of spatially localized perturbations and their effect on populations or communities as manifested by individual responses to environmental stressors or change that vary either with stage-determined characteristics (e.g., individual size, age, phenotype, genotype) or with individual history. With the continued human development of coastal areas, resource management will ever increasingly have to deal with how the quantity, quality, and spatial arrangement of habitat affect biota that use these coastal areas. Indeed, environmental degradation is often the norm today and few, if any, marine environments are truly ‘‘pristine.’’ The linkage between pollution and its effects on marine habitats and fisheries is a grave concern (see Rose 2000, Strickland and Grosse 2000) and individual-based models, many incorporating spatial structure, are seeing increased use in assessment of the potential impact of environmental contaminants, degradation, and stress on the health of these communities (Jaworska et al. 1997, LePage and Cury 1997, Breitburg et al. 1999).

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