

## Modelling the effect of spatial variation in postlarval supply and habitat structure on recruitment of Caribbean spiny lobster

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**Abstract.** Many field studies have shown that recruitment of the Caribbean spiny lobster, *Panulirus argus*, is sensitive to variation in both postlarval supply and local nursery-habitat structure. We used a spatially explicit individual-based model, to investigate the effects of (i) spatio-temporal variation in postlarval supply and (ii) changes in the spatial structure of the nursery habitat on lobster recruitment to the Florida Keys, Florida (USA). By simulating eight different regional scenarios describing postlarval supply, we investigated whether differences in the spatio-temporal delivery of postlarvae to the Florida Keys alters recruitment of subadult lobsters. Our results indicate that random geographical variation in postlarval supply yields the highest predicted recruitment, whereas persistently patchy settlement yields the lowest. Field observations of postlarval supply suggest that the random model is the most realistic. In separate simulations, we determined the sensitivity of the model to changes in the geographic arrangement of nursery habitat and the spatial resolution of habitat structure. The most spatially explicit depictions of habitat structure yielded small, but marginally significant differences in lobster recruitment as compared with more generalized spatial scenarios. These differences may well be magnified when more detailed depictions of postlarval settlement are implemented in the model.

*Extra keywords:* *Panulirus argus*, puerulus, Florida Keys

### Introduction

The association between larval supply, habitat structure, and subsequent adult population size remains a central focus of lobster research world-wide because of the intriguing ecological complexities of this relationship and its practical promise for fishery management. A consensus is growing that meso- to large-scale oceanographic phenomena that affect cross-shelf transport strongly affect the supply of lobster postlarvae to specific nursery regions (Phillips *et al.* 1991; Polovina and Mitchum 1992; Caputi and Brown 1993; Caputi *et al.* 1996; Katz *et al.* 1994; Acosta *et al.* 1997; Incze *et al.* 1997; Lipcius *et al.* 1997; Yoshimura *et al.* 1999; and others). Depending on the structure of the local habitat within the nursery, the subsequent settlement of postlarvae and postsettlement survival of juveniles can be limited in a density-dependent manner by shelter-imposed thresholds (Eggleston *et al.* 1990, 1998; Wahle and Steneck 1991; Butler and Herrnkind 1992, 1997; Eggleston and Lipcius 1992; Mintz *et al.* 1994; Parrish and Polovina 1994; Polovina *et al.* 1995; Arce *et al.* 1997). Therefore, integrating spatial and temporal heterogeneity in habitat

structure with spatio-temporal patterns in larval supply is important if we are to scale up descriptions of local dynamics to predict population-level consequences.

For nearly two decades, we have studied the recruitment and early life history of the Caribbean spiny lobster (*Panulirus argus*) in the Florida Keys (see Butler and Herrnkind 2000). Results from field studies indicate that postsettlement mortality poses a demographic bottleneck for juveniles of this species at locations where shelters for large juveniles are limiting (Eggleston *et al.* 1990, 1998; Butler and Herrnkind 1992, 1997; Eggleston and Lipcius 1992; Mintz *et al.* 1994). Of course, postlarval supply ultimately determines the potential magnitude of recruitment region-wide, and locally its effects are most pronounced where shelter is plentiful (Forcucci *et al.* 1994; Butler and Herrnkind 1997). Knowledge of these processes is particularly important for the Caribbean spiny lobster, which is the target of intensive commercial trap and recreational sport-diving fisheries that together constitute one of the most valuable fisheries in Florida and the Caribbean (Harper 1995; Hunt 2000).

Obtaining accurate measures of postlarval supply to different regions of the nursery is a critical element for predicting recruitment of spiny lobsters. The supply of postlarval lobsters to coastal nurseries is monitored by means of artificial collectors that mimic the structure of settlement habitat, and large monitoring programs are in place in Australia, New Zealand, and Cuba among other countries (see Phillips and Booth 1994 for review). In Western Australia, for example, fishery researchers have used collectors to estimate postlarval supply and have successfully predicted the stock size of *P. cygnus* several years later (Morgan *et al.* 1982; Phillips 1986; Caputi and Brown 1993; Caputi *et al.* 1995). This situation is especially desirable because these predictions, based on postlarval supply, provide sufficient lead time for fishers and managers to adjust to potentially large changes in the fishery. The design of monitoring programs like the one in Western Australia evolved over many years during which numerous locations were sampled and those data analysed to produce the most efficient and reliable programs possible.

We too have monitored postlarval supply in the Florida Keys for the past 15 years, but until recently our monitoring was limited to a single site; a second long-term site was added 5 years ago. Despite its limitations, this monitoring program provides the only long-term data available in Florida. Temporal patterns of postlarval supply and their possible coupling with meteorological events have been examined with those data (Acosta *et al.* 1997). Those data are also used as a primary input variable in a model used by managers to predict stock size (Muller *et al.* 1997), as well as in the recruitment model that we have developed (Butler 1994, unpublished data; Dolan and Butler unpublished data) and discuss further here. Yet, we do not know whether data obtained from five collectors at a single site represent a reliable or accurate depiction of the true supply of postlarval lobsters to the Florida Keys.

Therefore, two years ago we expanded our postlarval monitoring to eight sites distributed along the length of the ~200-km chain of islands comprising the Florida Keys. It takes years to obtain sufficient empirical data to describe the spatio-temporal pattern of postlarval delivery to a system, but modelling allows us to simulate the most likely scenarios describing postlarval supply, whereupon we can examine their respective effects on predictions of recruitment.

The dynamics of lobster recruitment in the Florida Keys are also influenced by spatial heterogeneity and temporal changes in nursery habitat structure. Macroalgal settlement habitat and crevice shelters for juvenile lobsters vary substantially both among regions and among locales within a region (Herrnkind *et al.* 1997). In addition, these important features of the nursery habitat are not static. The availability of macroalgae for postlarval settlers can fluctuate dramatically within and among sites over a period of months

(Butler *et al.* 1997). The abundance of crevice shelters can change abruptly as well. In 1991–92, a massive die-off of large sponges (the most important crevice shelter for juvenile lobsters in Florida), caused by cyanobacterial blooms, virtually destroyed the sponge community over ~20% of the Florida Keys nursery (Butler *et al.* 1995). The impact of the sponge die-off on juvenile lobster abundance varied geographically, depending on the severity of the sponge loss, the availability of alternative shelters, and the initial abundance of lobsters, but in many localities it was severe (Herrnkind *et al.* 1997). Therefore, knowledge of spatial and temporal heterogeneity in habitat structure is important if we are to use site-specific dynamics to predict population-level consequences in this changeable system.

In 1992, we developed a spatially explicit individual-based model describing the recruitment of Caribbean spiny lobster (*Panulirus argus*) in the Florida Keys that has since provided a useful framework for our continued investigations. Here, we describe how we modified this model (1) to examine the effects of spatio-temporal variability in postlarval supply on predictions of lobster recruitment and (2) to determine whether changes in the spatial resolution and structure of the habitat in the model alter model predictions of lobster recruitment.

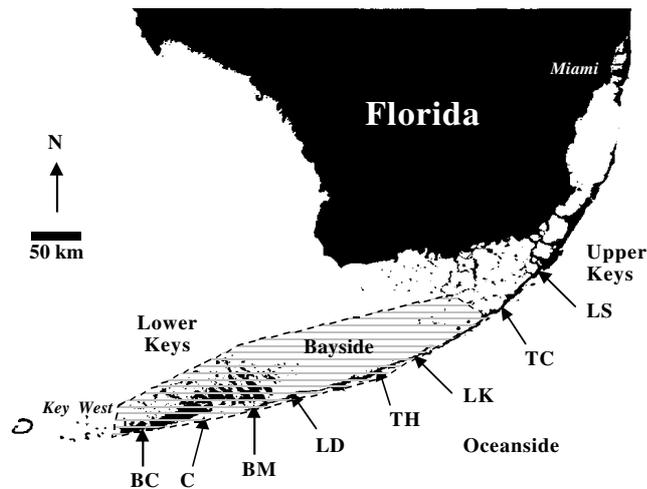
## Methods

### *Spatial Structure of Model*

The model's general structure is similar to that described in detail in other reports and papers (Butler 1994; Butler *et al.* unpublished data; Dolan and Butler unpublished data), so it is described only briefly here. The model is currently written in Fortran 90 (Microsoft Fortran Powerstation 4.0) and runs on a PC. The spatial framework of our model simulates 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- to 2-km ocean-side strip of bottom that is suitable for lobster recruitment (Fig. 1). The model includes 245 habitat cells, each approximately 12 km<sup>2</sup>, positioned in a 7 × 35 grid; 7 cells north to south (=1 column) and 35 cells stretching east to west (=1 row). Each cell's habitat designation corresponds with the actual spatial distribution of sea-grass and hard-bottom habitat in the region, as determined from diver-based field surveys at nearly 200 sites (Herrnkind *et al.* 1997).

Each hard-bottom habitat cell includes specific information that reflects the abundance of various hard-bottom structural features that serve as shelter for postlarval-stage lobsters (e.g. number of sponges, octocorals, stony corals, solution holes). The 'lobster carrying capacity' for each habitat cell is a function of the abundance of the shelter type and the number of lobsters that typically shelter under them. This information was obtained from the field surveys (Herrnkind *et al.* 1997) and is also spatially explicit. That is, model simulations for realistic habitat simulations use cell-specific lobster carrying capacities that match in geographic position the shelter abundance we observed in the field as well as the mean number of lobsters per shelter type that we observed in our surveys.

Two other spatially explicit environmental conditions (i.e. sponge-killing plankton blooms and variations in salinity) can be added to the model and have been used in other simulations (Butler 1994; Butler *et al.* unpublished data), but these were set at default states for the simulations described here. That is, no plankton blooms occurred in



**Fig. 1.** Map of the Florida Keys (USA) study area. The shaded region depicts the approximate geographic coverage of our model. Waters to the south of the main chain of islands that form the Florida Keys are referred to as 'oceanside', whereas those to the north are called 'bayside'. Locations referred to in the text are also shown in this figure, as are the locations of our postlarval sampling, sites labelled: BC = Boca Chica, C = Cudjoe, BM = Big Munson, LD = Little Duck, TH = Tom's Harbor, LK = Long Key, TC = Tavernier Creek, LS = Largo Sound.

these simulations, and salinity was uniform across the model domain and constant at 35.0 (Practical Salinity Scale 1978). Temperature varies daily in the model from a summer high of  $\sim 30^{\circ}\text{C}$  to a winter low of  $\sim 18^{\circ}\text{C}$ ; it does not vary among habitat cells.

#### The Recruitment of Caribbean Spiny Lobster in Florida

The ecological aspects of *P. argus* recruitment that are included in our model are summarized here, starting with the arrival of postlarvae in the nearshore nursery and terminating when juveniles begin to enter traps and are thus affected by the fishery (Hunt and Lyons 1986). A more complete description of spiny-lobster recruitment, and the recruitment of *P. argus* in particular, is given elsewhere (Butler and Herrnkind 2000). Postlarval *P. argus* move onshore year-round at night in monthly pulses during new-moon flood tides; pulses are higher in late winter-spring (Little 1977; Little and Milano 1980; Heatwole *et al.* 1992; Acosta *et al.* 1997). Those that come into contact with structurally complex vegetation, particularly macroalgae within hard-bottom habitat, settle and metamorphose into the first benthic juvenile stage (Marx and Herrnkind 1985; Herrnkind and Butler 1986, 1994; Butler and Herrnkind 1991). The early benthic juveniles remain hidden in vegetation for several months, but at approximately 15 mm carapace length (CL) they begin to emerge and take up daytime refuge in crevices provided mainly by sponges (approximately 50% of shelters), although many types of shelter are occupied (Childress and Herrnkind 1994, 1996; Butler *et al.* 1995; Herrnkind *et al.* 1997). These 'postalgal-stage' juveniles are exposed to an array of piscine and invertebrate predators capable of inflicting very high mortality, so their use of shelter is critical to survival (Eggleston *et al.* 1990; Smith and Herrnkind 1992; Mintz *et al.* 1994). We estimate that mortality ranges from 96 to 99% during the first benthic year (Butler *et al.* 1997; Sharp *et al.* 2000). Initially, the postalgal juveniles occupy a relatively small home range, but at 45–50 mm CL ( $\sim 1$  year after settlement) they become nomadic and constitute a portion of the trap-caught lobsters (Lyons *et al.* 1981).

#### Modelling the Recruitment Process

We explicitly incorporate the various aspects of the recruitment process just described into our model by superimposing on the model's spatial landscape the daily ecological processes faced by juvenile spiny lobsters: settlement, growth, shelter selection, mortality, and movement. Thus, the model literally tracks each hypothetical lobster from settlement until its recruitment to 50 mm carapace length (CL). Ours is an ecological model of recruitment and so does not yet include adult dynamics or fishery effects. Lobsters begin to enter traps at about 50 mm CL, and individuals of this size can be legally deployed in traps by fishermen as attractants for legal-sized lobsters. We therefore remove individuals from the model and record them as 'prerecruits' to the fishery once they attain 50 mm CL. On average, it takes a 50-mm CL lobster about 1.5 years to attain the legal fishable size of 76 mm CL (Forcucci *et al.* 1994).

Each of the lobster-biology subroutines (settlement, growth, shelter selection, mortality, and among-cell movement) is described in detail elsewhere (Butler 1994; Butler *et al.* unpublished data), so we only summarize them here. The settlement algorithm is particularly pertinent to this study so it is described in somewhat more detail. Each of the processes is modelled on a daily time step for each individual in the population, except for settlement, which occurs once every lunar cycle (i.e. every 28 days). Nearly all processes are probabilistic, and whenever possible, the functions describing the probability of a particular event were obtained by fitting of curvilinear functions to empirical data (Tablecurve Ver. 1.12 software, Jandel Scientific Co.).

For all simulations, postlarval supply varied among lunar months (i.e. temporally) in the same way, based on a 10-year record of postlarval supply at one site (Big Munson Key) in the Florida Keys. These data have been described in detail elsewhere (Acosta *et al.* 1997; Muller *et al.* 1997). Although the supply of postlarvae in the model fluctuates realistically from month to month, we scaled the total number of individual postlarvae entering the model to fit the model's spatial domain. To do so, we set the mean monthly supply of postlarvae in the model at 10,000 individuals, using the product of the mean density of settlers estimated from field studies (approximately  $0.041$  settlers/ $\text{m}^2$ ; Marx and Herrnkind 1985; Herrnkind and Butler 1994; Butler *et al.* 1997) and the habitat area encompassed by the model. Monthly deviations in postlarval supply to the model depend on the observed variation from the long-term mean number of postlarvae caught per collector (10.5 postlarvae/collector). Therefore, if the actual postlarval supply in a particular month is 30% greater than the long-term mean (e.g. from 10.5 to 13.7 postlarvae/collector), then that change is mirrored in the model and results in 13,000 new recruits to the model that month. The way in which these settlers are distributed to specific habitat cells varied from simulation to simulation and was the focus of the first set of simulations described in the next section ('Postlarval Supply Simulations').

To populate the model initially, we ran the model for 2 years (26 lunar months) prior to the time period of interest and used the long-term mean postlarval supply for each month as input during this spin-up period. Thus, during the population phase of the model the supply of postlarvae during consecutive months differed, but the annual patterns were the same. Preliminary runs of the model using monthly averaged postlarvae supply demonstrated that the abundance of large juveniles  $>50$  mm CL stabilized after 18 months, hence our conservative choice of a 2-year initialization period. To complete a model run, we ran the model 2 years beyond the end date of interest in the same way, so we could observe the fate of the last cohort of postlarvae. Using real postlarval-supply data and populating and depopulating the model in this manner, we typically modelled over 1 million individual lobsters in a single 10-year simulation.

New settlers are randomly assigned a size between 5.0 and 7.0 mm CL. Individual lobster growth is then modelled as a discontinuous

process using empirically determined probability distributions to specify moult increments and intermoult intervals, which vary as a function of current size, time since last moult, and temperature. There is no evidence that growth of *P. argus* in nature is density dependent (see Butler and Herrnkind 2000), so we model it as a density-independent process with no food resource limitation.

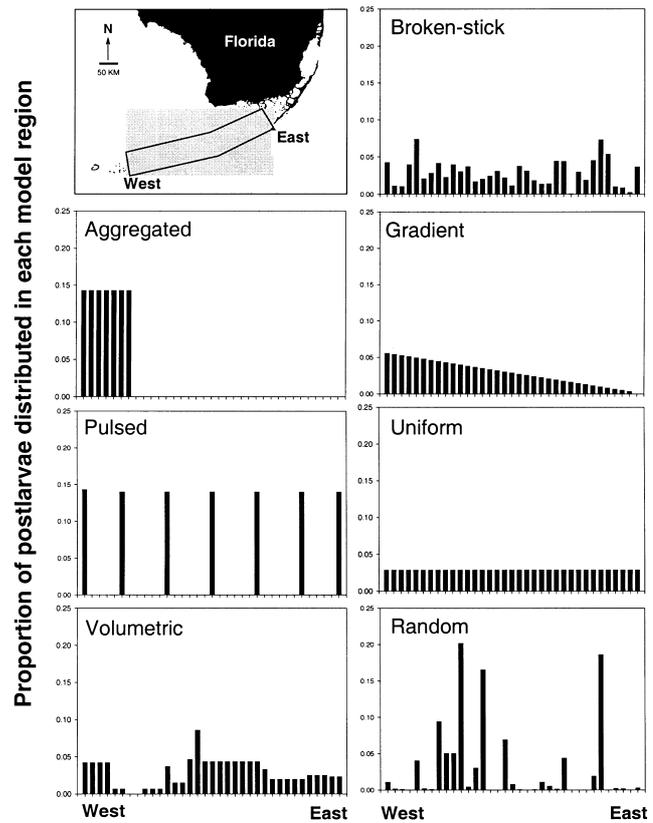
Within a habitat cell, selection of specific types of shelters (e.g. loggerhead sponge, other sponges, solution holes) by lobsters is modelled as a complex, probabilistic process. That process includes ontogenetic (size-specific) changes in shelter preference, the cell-specific availability of different types of shelter, the respective lobster sheltering capacity of each shelter type, and the current residency in each shelter by other lobsters. An individual's daily probability of mortality is the sum of the independent probabilities of mortality determined for the daytime, nighttime, and crepuscular periods of a day. The times each individual spends in a shelter and in the open during these periods, along with its size, figure prominently in its daily probability of mortality. We explore the potential effects of group defense and the guide effect (Childress and Herrnkind 1994, 1996) on reducing individual mortality in another paper (Dolan and Butler unpublished data).

Movement of lobsters among habitat cells is random in direction, and this probability depends on individual size and shelter availability in the current cell (e.g. individuals who cannot locate suitable shelter and are left in the open vacate the current cell with higher frequency). No movement is permitted across the northern or southern edges of the model domain, a condition that mimics the real system, where habitat, salinity, and depth limit movement in those directions. Movement across the east and west boundaries is wrapped, so lobsters exiting the eastern edge of the model enter at the corresponding cell on the western edge. This pattern approximates natural immigration and emigration of lobsters east and west of the modelled region.

*Postlarval Supply Simulations*

Our first modelling objective was to determine whether altering the spatial delivery of postlarvae to regions of the model affects projected recruitment. To answer this question, we first simulated six different scenarios describing the most plausible schemes for the spatio-temporal delivery of postlarvae to different regions of the model. These simulations included (1) Uniform (2) Volumetric (3) Gradient (4) Static broken-stick (5) Variable broken-stick, and (6) Random deliveries of postlarvae. In addition to these six scenarios, we conducted two less realistic simulations (Pulsed, Aggregated) to examine model predictions under extreme conditions. Fig. 2 provides a graphical depiction of the patterns of postlarval supply resulting from these simulations.

For all simulations, cells of similar habitat (i.e. sea-grass or hard bottom) within each column received the same proportion of new postlarvae each month. On the basis of settlement data from a laboratory study (Herrnkind and Butler 1986), 17% of the postlarvae within a column of cells are allocated to sea-grass cells and 83% to hard-bottom cells. For example, in a column consisting of three hard-bottom and four sea-grass cells, the hard-bottom cells would each receive one-third of the 83% of the postlarvae assigned to hard-bottom cells in that column. The four sea-grass cells would each receive one-fourth of the 17% of the postlarvae assigned to sea-grass in that column. Thus, each column in the habitat grid was treated as a unit that received a percentage of the total postlarval influx each month. Each habitat cell within a column (region) received a percentage of the postlarvae assigned to the region (column) based on its designated habitat (i.e. more postlarvae settle in hard-bottom cells than in sea-grass cells). Each column of cells in the model is thus roughly equivalent to regions in Florida Bay into which rush tidally driven water and postlarvae from the interisland channels between the Keys. We believe this to be a reasonable first approximation for two reasons.



**Fig. 2.** An illustration of the model's spatial domain (upper left panel) and the various patterns of postlarval supply examined in model simulations. In each panel, each histogram represents the proportion of the total supply of postlarvae that enter each of 35 subregions of the model domain each month. Eight different simulations were run; only seven are shown here because the 'broken-stick' scenario was run with either a static distribution (shown here) or a similar distribution constructed from independent randomizations each month of the 10-year simulation run. Likewise, the 'Random' scenario (bottom right panel) is an example of one randomization outcome, but for this simulation new random distributions were determined each month.

First, the currents through the interisland channels are tidally driven and strongly influence water flow in the shallow (<3 m), bay-side waters surrounding the Florida Keys (Wang *et al.* 1994; Smith 1994). Second, an earlier study (Herrnkind and Butler 1994) demonstrated that postlarval settlement within a region of the nursery downstream of an interisland channel adequately reflects the abundance of postlarvae passing through the channel.

The Uniform postlarval supply scenario is the one used in the original model and so serves as a benchmark for comparison with our earlier results. In this scenario, each region (i.e. column of cells) received the same proportion of the postlarval supply (i.e. 1/35) in any given month.

The Volumetric delivery simulation reflects differences in tidal flow through channels between the Keys. For example, the model area simulating the region adjacent to the largest channel with the greatest tidal volume in the Florida Keys (i.e. 7-mile bridge near our Little Duck postlarval sampling site) received more settling postlarvae (8% of the total postlarval supply) than portions of the model that depict zones in the Upper Keys where channels are few and small. Because tidal-flow values are not available for all of the channels between the

Keys, we estimated their relative flow (hence their capacity to deliver postlarvae into the bay) by taking the product of the mean width and depth of each channel.

Coastal oceanography (Lee *et al.* 1992, 1994), offshore concentrations of *P. argus* larvae and postlarvae in the plankton off the Florida Keys (Yeung and McGowan 1991), and juvenile lobster densities (Herrnkind *et al.* 1997) suggest the existence of an east–west gradient in postlarval supply and therefore that fewer postlarvae are available for recruitment to the upper Keys. Our Gradient simulation therefore mimicked a situation in which postlarval supply diminishes smoothly from west to east in increments of 5%, so fewer postlarvae were available for recruitment to the upper Keys than to the lower Keys.

The Static broken-stick and Variable broken-stick simulations both relied on a ‘broken-stick’ model to allocate postlarvae to regions, but they differed in the way that postlarvae were allocated to cells each month. A broken-stick allocation procedure is analogous to considering the total postlarval supply equal to a line segment 1.0 unit long. Then, 34 random numbers between 0 and 1.0 were selected without replacement, each representing a break point along the line segment. The length of each of the resulting 35 line segments thus represents the proportion of the total postlarval supply apportioned to each of the 35 columns in the model spatial domain. Because of the large number of ‘breaks’ required in our broken-stick randomization procedure, it generally resulted in fewer extreme values than a completely random algorithm. For the Static broken-stick scenario, we used the first randomization iteration to determine how postlarvae would be allocated among regions each month during the 10-year model run. That is, once the proportional allocation of postlarvae among model regions was determined, it remained the same and did not change from month to month. We reran the randomization procedure each month for the Variable broken-stick simulations. The Variable broken-stick procedure usually resulted in a relatively uniform distribution of postlarvae, similar to that for the Static broken-stick simulation, but because the randomization procedure was repeated each lunar cycle under the Variable broken-stick scenario, a model region occasionally received a large proportion of the total postlarval supply (i.e. 10–20%).

For the Random simulation, we chose 35 random numbers between 0 and 0.3 with the restriction that they sum to 1.0. In this way, no model region could receive more than 30% of the total postlarvae arriving in a lunar period. We repeated this randomization procedure for each lunar month (i.e. when each cohort of postlarvae are distributed in the model), thus producing a different pattern of postlarval allocation each lunar period. During any particular lunar month, this procedure produced the most variable postlarval supply among those simulations that we considered the most plausible explanations for actual postlarval supply.

The Pulsed and Aggregated simulations were run as ‘out-groups’ to examine the model’s sensitivity to extreme scenarios of postlarval supply. The Pulsed scenario delivered 14.3% (i.e. 1/7) of the postlarvae each month into each of seven uniformly spaced small regions of the model (spatial columns) representing 14% of the total model area.

Therefore, 86% of the model area received no postlarval settlement, although juvenile lobsters could later emigrate into those areas. In the Aggregated scenario, all postlarvae settled into a single, contiguous area representing a portion of the lower Florida Keys, and again only 14% of the total model area received settlers.

#### Habitat-Structure Simulations

Our second series of simulations was designed to test the importance of spatial continuity and habitat structure to our model results. We ran six separate sets of simulations, altering (1) the geographic position of sea-grass and hard-bottom nursery habitat cells in the model space (real, random) and (2) the spatial-scale over which shelter-structure density varied (cell-specific, regional, homogeneous), yielding a  $2 \times 3$  completely crossed design (Table 1). The pattern of postlarval supply in these simulations was the same for all treatments and was identical to that in the Uniform scenario described above.

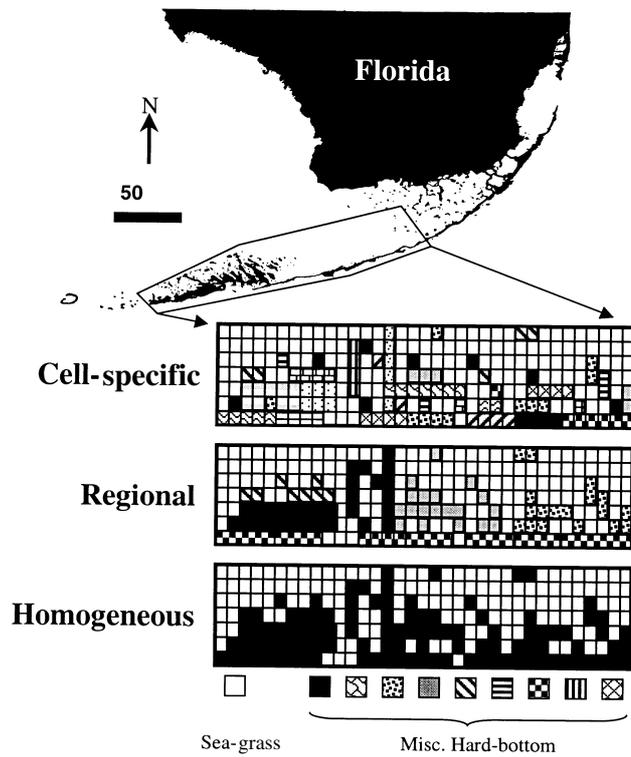
The geographic arrangement of habitats among model cells was either (i) a ‘Real’ positioning of habitat types based on field data or (ii) a ‘Random’ positioning of habitats. The Real positioning of habitats is the distribution that we have used in all of our other model runs. The geographic specificity with which shelter density was allocated within model habitat cells took one of three forms (Fig. 3). The first was a ‘Cell-specific’ simulation using the realistic distribution of shelter types and densities obtained from field data, so every model cell was unique in its shelter structure (i.e. type of shelters and density). The second was a ‘Regional’ simulation in which within-cell shelter structure was homogeneous within five large nursery regions but differed from region to region. The last was a ‘Homogeneous’ simulation, in which shelter structure was the same across all model cells (i.e. the mean based on data from all the cells in the Cell-specific scenario).

#### Results

For each postlarval-supply and habitat-structure scenario, we ran five simulations. Previous modelling exercises indicate that five replicate runs are sufficient to capture most of the variance in the simulations (Butler 1994; Butler *et al.* unpublished data). Numerous kinds of output are possible from the model (size structure of lobsters, size-specific shelter use, locations of individuals, etc.), but we chose to compare among simulations the number of lobsters recruiting to 50 mm CL over the 10-year model period. We used a one-factor model I ANOVA to test for differences in recruitment among the postlarval supply simulations and a  $2 \times 3$  model I ANOVA to test for differences in recruitment among the habitat structure simulations. A Tukey HSD test was used to test for differences among individual simulation results. Both of the data sets tested in these analyses were normally distributed (all *P*-values >0.37; Shapiro-Wilk test).

**Table 1. Table showing the  $2 \times 3$  crossed design of the habitat-structure simulations**  
For each combination of habitat arrangements (real, random) and habitat-structure specificity (cell-specific, regional, homogeneous) we ran five simulations

Geographic specificity of habitat structure	Geographic arrangement of habitat areas	
	Real	Random
Cell-specific	5 simulations	5 simulations
Regional	5 simulations	5 simulations
Homogeneous	5 simulations	5 simulations



**Fig. 3.** The portion of the Florida Keys region encompassed by the model’s spatial domain is shown by the shaded area on the map at the top of the figure. The three grids at the bottom of the figure represent graphical examples of how the geographic specificity of habitat structure was depicted in three types of habitat simulations. In each grid, sea-grass habitat is shown as an open cell, whereas hard-bottom habitats with different habitat structures are shown with various fill patterns. In the ‘Cell-specific’ model simulations, each hard-bottom cell in the spatial domain received a unique habitat structure, so each cell was in fact unique with respect to the presence and abundance of four types of crevice shelters. In the ‘Regional’ model, hard-bottom cells within a region were identical in structure (as indicated by the same fill pattern) but differed among regions. All hard-bottom cells in the ‘Homogeneous’ model were identical in habitat structure.

The postlarval-supply data had homogeneous among-group variances ( $P = 0.15$ ; Levene’s test); variances among the habitat-structure simulations were somewhat heterogeneous ( $P = 0.02$ ; Levene’s test) but could not be improved by transformation. Therefore, in both cases the ANOVAs were performed on the raw simulation data.

*Postlarval-Supply Simulations*

Varying the spatio-temporal supply of postlarvae to our model resulted in significant ( $F = 108.56$ ; d.f. = 7, 30;  $P < 0.0001$ ) differences in recruitment among the eight simulation scenarios (Fig. 4). The Random supply of postlarvae yielded the highest predicted recruitment of any modelled scenario; the mean recruitment from that simulation was ~15% higher than those of the other five

realistic models. With the exception of the Random simulation, differences in recruitment among the remaining five most plausible simulations were small (<4%), although some of these differences were statistically significant. The recruitment predicted from the Uniform and Variable broken-stick models, for example, was significantly greater than that from the Volumetric scenario. The two most extreme scenarios, the Pulsed and Aggregated simulations, yielded significantly lower recruitment than the other simulations and also differed significantly from each other.

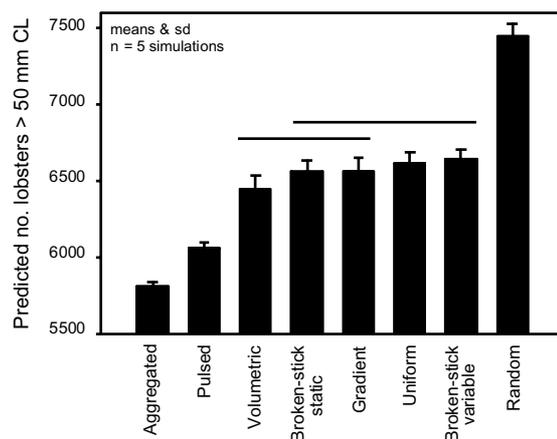
*Habitat-Structure Simulations*

None of the changes in the spatial configuration of shelter structure that we simulated in our model resulted in dramatic changes in the predicted recruitment of lobsters (Fig. 5), but a small (~2%) difference among the simulations comparing the geographic resolution with which shelter structure within hard-bottom habitat areas was modelled (i.e. cell-specific, regional, homogeneous scenarios) was of borderline significance ( $F = 3.154$ ; d.f. = 2, 24;  $P = 0.061$ ) despite the low power of the test ( $1 - \beta = 0.55$ ). The geographic positioning of sea-grass and hard-bottom habitat cells in model space (i.e. real or random position) did not significantly alter predictions of lobster recruitment ( $F = 0.25$ ; d.f. = 1, 24;  $P = 0.876$ ), nor did the interaction between them ( $F = 0.248$ ; d.f. = 2, 24;  $P = 0.783$ ).

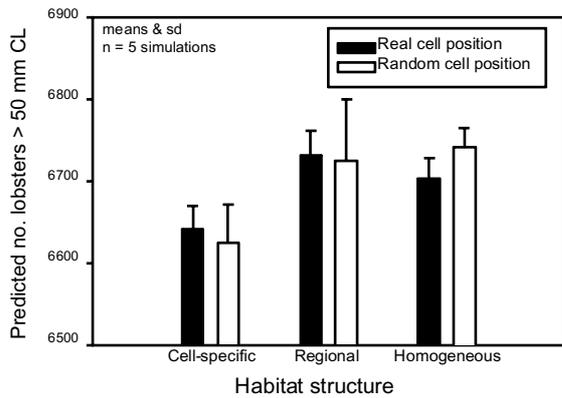
**Discussion**

*Postlarval Supply: Modelling versus Reality*

An implicit assumption of most fishery models is that the effects of small-scale spatio-temporal variation in postlarval



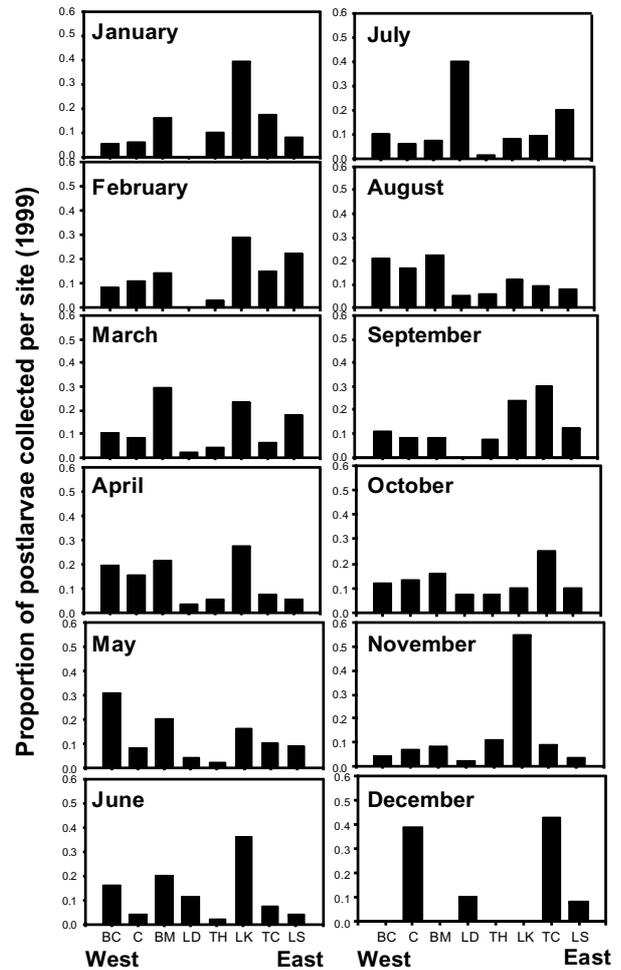
**Fig. 4.** The mean recruitment of lobsters (>50 mm CL) predicted from simulations depicting eight different patterns of postlarval supply. Shown are means and one standard deviation determined from five replicate simulations per postlarval supply scenario. Histograms that share a horizontal line indicate simulations that did not differ significantly ( $P > 0.05$ ) from one another as determined by a Tukey HSD test.



**Fig. 5.** The mean recruitment of lobsters (>50 mm CL) predicted from simulations depicting six different patterns of habitat structure. Shown are means and one standard deviation determined from five replicate simulations per habitat-structure scenario.

supply or habitat structure on recruitment ‘average out’ at the large scales over which fishery stock predictions are made. This may be true for some systems with predictable patterns of postlarval supply or where the distribution of nursery habitats remains unchanged (e.g. cobbles or holes in rock), but the nursery habitat in Florida is spatially and temporally dynamic, as is the supply of postlarvae. Our modelling results suggest that differences in the regional pattern of postlarval supply affect recruitment. Random patterns and those that are consistently patchy result in markedly different predictions of recruitment.

This result begs the question of which postlarval-supply scenario we modelled best describes the real pattern observed in nature. At the beginning of this project we had no idea what the spatio-temporal pattern of postlarval supply might be along the Florida Keys archipelago, which in part was the rationale for our modelling. The entire four-year data set, for which we plan an exhaustive analysis, is not yet available, but we now have some field data with which to compare field and modelling results. Field data from 1999 for our eight sampling sites spanning the length of the Florida Keys (Fig. 6) suggest that postlarval abundance indeed varies randomly among sites and months (i.e. significant interaction in two-factor ANOVA testing site  $\times$  month;  $F = 4.573$ ; d.f. = 71, 269;  $P < 0.0001$ ). Again, a more complete analysis of the multiyear data will be forthcoming and will permit us to determine whether this conclusion from 1999 holds true for other years. If so, then the modelling and field results imply that future monitoring of postlarval supply must continue to include multiple locations for accurate estimation of monthly or regional patterns of postlarval supply. This is not to say that the long-term data from one site are useless. In fact, because estimates of fishery recruitment are based on annual summaries of postlarval supply, a single or perhaps few sites



**Fig. 6.** Field observations of the proportion of postlarvae obtained from Witham-type collectors ( $n = 5$ /site) at each of eight sites for each month in 1999. The sites are arranged from east to west, and the site designations (BC = Boca Chica, C = Cudjoe, BM = Big Munson, LD = Little Duck, TH = Tom’s Harbor, LK = Long Key, TC = Tavernie Creek, LS = Largo Sound) are listed along the x-axis. The geographic locations of these sites are shown in Fig. 1.

may be sufficient to capture most of the annual variation among sites.

Perhaps the most heuristically interesting modelling result is that the Random simulation produced the highest recruitment, whereas the Pulsed and Aggregated simulations yielded just the opposite. These three simulations all created highly patchy distributions of postlarvae (Figs 2 and 4) yet differed significantly from one another in their resultant levels of recruitment. The explanation presumably lies in the temporally variable nature of the Random scenario. The Pulsed and Aggregated scenarios created persistently high densities of lobsters in specific regions, which probably resulted in high density-dependent postsettlement mortality in the model due to shelter limitation for juveniles. Although the Random

scenario also often created dense regional patches of postlarval settlement in a particular month, those patches varied in their magnitude and distribution with the arrival of a new cohort of postlarvae each lunar month. We therefore suspect that this scenario ensured that areas of good habitat received ample settlement over the long term but were unlikely to experience consistently the high levels of settlement that might result in higher density-dependent mortality. In short, the same general arguments used to explain the evolution of widespread planktonic dispersal make functional, if not evolutionary, sense at smaller regional scales too.

#### *Does Spatial Structure Really Matter?*

Our spatial structure simulations were designed to determine whether changes in the spatially explicit nature of this particular formulation of this particular model significantly altered model predictions. This specificity is important. We do not suggest that our results provide a general evaluation of the importance of spatial structure in ecological models. Ample evidence from prior field and modelling research indicates that spatial structure is indeed of major ecological consequence and can significantly improve our ability to simulate processes occurring in many systems (see Dunning *et al.* 1995 for review).

The most spatially explicit habitat scenarios that we modelled yielded small but consistently different results (~2% lower recruitment) than the more generalized regional and homogeneous depictions of habitat structure. Randomizing the spatial positioning of nursery-habitat cells, in contrast to their habitat structure, had no effect on predictions of recruitment, but we suspect that differences would have been amplified if our model better captured the dynamics relevant to the settlement process. Perhaps most important to this issue is our model's over-simplification of the way in which postlarvae are distributed to specific habitats regardless of local hydrodynamics or local habitat structure.

For example, once the appropriate portion of postlarvae from a lunar cohort are assigned to one of the 35 settlement regions (columns) in our model, their assignment to habitats (cells) within that region is not tied to hydrodynamics or within-cell habitat availability. That is, of the postlarvae allocated to each region, 17% will be evenly distributed among the sea-grass cells within the region and 83% will be evenly distributed among the hard-bottom cells, regardless of the number of cells of each type in the region. Because the numbers of cells designated hard-bottom or sea-grass within regions differ, this procedure does create different levels of local settlement among regions, which is a desirable feature of the model, but these differences in local settlement are not tied to any explicit feature of the habitat, which is probably unrealistic. We do not alter cell-specific settlement rates on the basis of the abundance of macroalgae

or density of sea-grass in the cell. In the Florida Keys, the abundance and size of clumps of red macroalgae are ephemeral (Butler *et al.* 1997) and sea-grasses are subject to massive die-offs (Robblee *et al.* 1991; Zieman *et al.* 1994). The local abundance of settlement habitat is therefore dynamic, and the timing of those dynamics does not necessarily coincide with annual cycles of postlarval supply (Butler *et al.* 1997). Beyond its presence or absence, we do not yet know how much these changes in the availability of settlement habitat alter the settlement or survival of postlarvae. We are now conducting experiments to find out. If the effect is large, then we intend to modify our model to reflect better this type of local selection of settlement habitat by postlarvae.

We also have not yet included the effects of local hydrodynamics on the distribution of postlarvae within the nursery, but we hope to do so in future versions of the model. Currently, the complicated local hydrodynamics of the shallow (<3 m) waters surrounding the Florida Keys where lobsters settle are poorly known and inadequately modelled. That these dynamics are primarily driven by tides and wind events is unquestionable (Wang *et al.* 1994; Smith 1994), but the complex and changeable bathymetry of the region, as well as the timing of wind events, has so far prevented the development of accurate physical descriptions of local current fields that we could use in our spatial modelling. Some progress is being made on this front, so we soon intend to add a more realistic means of delivering postlarvae to specific habitat cells in our model. This improvement, along with new algorithms describing postlarval settlement behaviour with respect to habitat structure (discussed above), will significantly improve the accuracy of this model.

#### *Rationale for Modelling Approach*

We chose a spatially explicit individual-based modelling approach for several reasons. Traditional fisheries models typically rely on statistical relationships between adult stocks and larval supply, or vice versa, and do not incorporate the spatial heterogeneity and temporal changes in habitat structure so characteristic of the modern Florida Keys. Nor do such models easily accommodate the probabilistic biological interactions that may interact with habitat structure to create possible compensation or feedback mechanisms affecting population dynamics (see reviews by DeAngelis and Gross 1992; Uchmanski and Grimm 1996). However, spatially explicit simulation modelling represents one approach that is flexible enough to accommodate environmental conditions, both natural and human-caused, vary over different spatial or temporal scales. This flexibility has permitted us to adapt our model quickly to investigate the possible impact on lobster recruitment of various environmental changes (e.g. sponge

die-off, salinity change, and the changes in postlarval supply and habitat structure described here).

Spatial models can be married to organism dynamics in several ways, but we chose an individual-based approach for philosophical and pragmatic reasons. It is at this level—the individual—that selection acts and through which lobster populations change and evolve. The properties of populations and communities emerge from the processes affecting individuals, and thus many believe that patterns at higher levels of organization can be predicted from a keen knowledge of the processes affecting individuals (see reviews by DeAngelis and Gross 1992; Uchmanski and Grimm 1996). It is also at the individual level that empirical data are collected, so there is a natural harmony between the kinds of data that we collect and the ‘currency’ or values used to parameterize models. An obvious disadvantage to individual-based models, especially spatially explicit ones, is that they are data hungry and often system specific, yet these features foster greater cooperation between fishery managers, modellers, and empiricists—not to mention greater ecological insight into the process of lobster recruitment.

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