



# Incorporating ecological process and environmental change into spiny lobster population models using a spatially-explicit, individual-based approach

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## Abstract

Marine fisheries and the ecosystems that sustain them are increasingly beset by environmental deterioration, yet traditional fishery models used for stock prediction typically handle these dynamics poorly if at all. To do so requires the integration of spatio-temporal change in environmental quality and its subsequent effects on habitat suitability and life history dynamics. Spatially-explicit, individual-based simulation models are particularly well suited to this task and, although they are seeing increased use in fisheries ecology and management, this approach has seen limited application in crustacean fisheries. In 1993, we began development of a spatially-explicit individual-based model (IBM) describing the recruitment of Caribbean spiny lobster (*Panulirus argus*) in the Florida Keys, Florida (USA) to investigate the impact of regional changes in environmental quality, habitat structure and postlarval supply on lobster recruitment. The shallow coastal waters of the Florida Keys ecosystem have experienced an unprecedented series of environmental perturbations over the past decade. Seagrass die-offs, cyanobacteria blooms, sponge die-offs and dramatic changes in salinity have occurred and these potentially impact the recruitment of spiny lobsters in the region via both direct and indirect means. Here I provide an overview of the unique approach that we have used to examine these dynamics, an approach that links environmental events that occur on large scales (e.g. changes in habitat structure and salinity) with their population-level consequences for lobsters via impacts that operate on the individual-level. Although not applicable in all situations, spatially-explicit IBMs should see wider use in crustacean fishery applications because of both the ecological insight they yield and their ability to integrate data across hierarchical scales of organization.

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## 1. Introduction

Many models traditionally used for fishery stock assessment rely on statistical relationships that typically do not incorporate spatial heterogeneity or changing environmental features that are so often characteristic of marine environments. Yet, the inclusion of spatial complexity and the incorporation of changing envi-

ronmental conditions are often desirable features of applied models that are likely to improve their realism and usefulness (Van Winkle et al., 1993a,b; Dunning et al., 1995; LePage and Cury, 1997; Jaworska et al., 1997; Breitbart et al., 1999; Rose, 2000; and others). Spatial models combine population dynamics with a landscape depicting the spatial distribution of salient environmental features that may vary among habitat “cells” (see Steyaert et al., 1997). The spatial resolution of these models is virtually limitless and spatial structure can be represented in many forms

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and at many scales. Each habitat cell might describe dynamics that occur on a scale of tens of centimetres or thousands of kilometres, depending on which is most appropriate to capture the key geographic features or dynamics of the system. The most detailed are “spatially-explicit” models (or “spatially-realistic” models sensu Hanski, 1996), in which unique habitat patches are distributed in agreement with real patch networks.

Many marine models describing recruitment processes incorporate some degree of spatial structure (e.g. Possingham and Roughgarden, 1990; Walters et al., 1992; Lipcius et al., 1997). Those that are truly spatially-explicit and concerned with mobile species of fishery importance are pelagic models that describe larval-oceanographic dynamics, and therefore their spatial structure is defined primarily by velocity fields, temperature, salinity and prey density (Botsford et al., 1994; Hinckley et al., 1996; Herman et al., 2001). Certainly, the dynamics affecting larval supply are often the key to establishing patterns of adult abundance, but not always. There are numerous examples, many from crustaceans, where post-settlement processes modify the settler–stock relationship through demographic bottlenecks often dependent on the interaction between habitat structure and settlement density (Steger, 1987; Wahle and Steneck, 1991; Butler and Herrnkind, 1992, 1997; and others).

Spatial models can be married to population dynamics in several ways. Population-based spatial models are those in which the dynamics of a species are modelled using population parameters that are defined separately for each spatial cell (Hassell et al., 1991; Palmer, 1992). Stage-based models permit separate formulations of important life history processes that often exist among the age or size classes of an organism (see Caswell, 2000) and, therefore, add a greater degree of complexity and realism to the model structure. Within a defined life stage, however, the ecological processes that are modelled again reflect the response of an “average” individual. In contrast, individual-based models (IBM) follow the status of each individual in the population, whose survival, growth and reproduction (i.e. fitness) is affected by individual characteristics, local conditions in the habitat cell and stochastic processes (DeAngelis and Gross, 1992; Van Winkle et al., 1993a,b; Uchmanski and Grimm, 1996). An intermediate approach is

to link IBM dynamics with simpler stage-based or population-based dynamics for those portions of the life history that are poorly described or are not the focus of the study. One might do this, for example, to close the life cycle of the species that is modelled (Rose et al., 1996). Only a few individual-based, spatially-explicit models exist for marine species (e.g. Hinckley et al., 1996; Herman et al., 2001).

Our investigations of the ecology of the Caribbean spiny lobster (*Panulirus argus*) in the Florida Keys have greatly benefited from our use of a spatially-explicit IBM, first developed in 1993. As far as we know, ours is the first non-pelagic crustacean population model that sets individual-based dynamics within a large-scale, spatially-explicit geographic context. Not only has this model served as a formal framework within which our empirical studies are cast and with which hypothetical ecological processes can be investigated, it has also permitted us to investigate the practical implications of changing environmental conditions on the recruitment of spiny lobster in south Florida; hence the potential impact on the fishery for this species.

Spiny lobsters are big business in south Florida. As the target of large commercial and recreational fisheries, the Caribbean spiny lobster is of major economic importance not only in Florida but also throughout the Caribbean (see reviews in Phillips and Kittaka, 2000). Since 1986, the commercial lobster fishery in Florida has consistently ranked as the first or second most valuable fishery in the state (Harper, 1995). However, the true economic value of *P. argus* in Florida is difficult to pinpoint because the value of the recreational sport diving fishery (estimated at 29% of the commercial landings; Bertlesen and Hunt, 1991) and the associated tourist business it supports is unknown, though undoubtedly substantial.

Thus far, we have used reformulations of the same spatially-explicit, IBM to investigate a variety of fishery related issues, including: (1) the potential effect of a massive loss of nursery habitat structure due to a sponge die-off on lobster recruitment (Butler, 1994; unpublished data), (2) the consequences of temporal and spatial variation in postlarval supply on recruitment (Butler et al., 2001), (3) the effect of nursery habitat structure and geographic specificity on recruitment (Butler et al., 2001) and (4) the direct and indirect consequences of altered salinity on recruitment

(Butler, unpublished data). We also have used a version of this same model to investigate the population-level consequences and potential selective benefits of different behaviours affecting social aggregation (Dolan and Butler, unpublished data). This paper provides an overview of the model's structure, describes how it was modified to address disparate questions pertinent to fishery management issues and summarises the respective predictions and implications of each model formulation.

## 2. A general description of the model

### 2.1. Spatial structure

The model's general structure is described in detail in earlier reports and papers (Butler, 1994; Butler et al., 2001), so it is described only briefly here. The spatial framework of our model simulates the Florida Keys region stretching from Key Largo to Key West, including most of the bayside spiny lobster nursery habitat and a narrow 1–2 km oceanside strip of bottom

that is suitable for lobster recruitment (Fig. 1). There are 245 habitat cells in the model each representing approximately 12 km<sup>2</sup> of actual seafloor and positioned in a 7 × 35 grid; seven cells north–south and 35 cells stretching east to west. Each cell's habitat designation corresponds with the actual spatial distribution of seagrass and hard-bottom habitat in the region, as determined from diver-based field surveys at nearly 200 sites (Herrnkind et al., 1997). Macroalgae-covered hard-bottom habitat is the preferred settlement and nursery habitat of juvenile *P. argus*, whereas seagrass is used to a lesser extent (Marx and Herrnkind, 1985; Herrnkind and Butler, 1986; Butler 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.

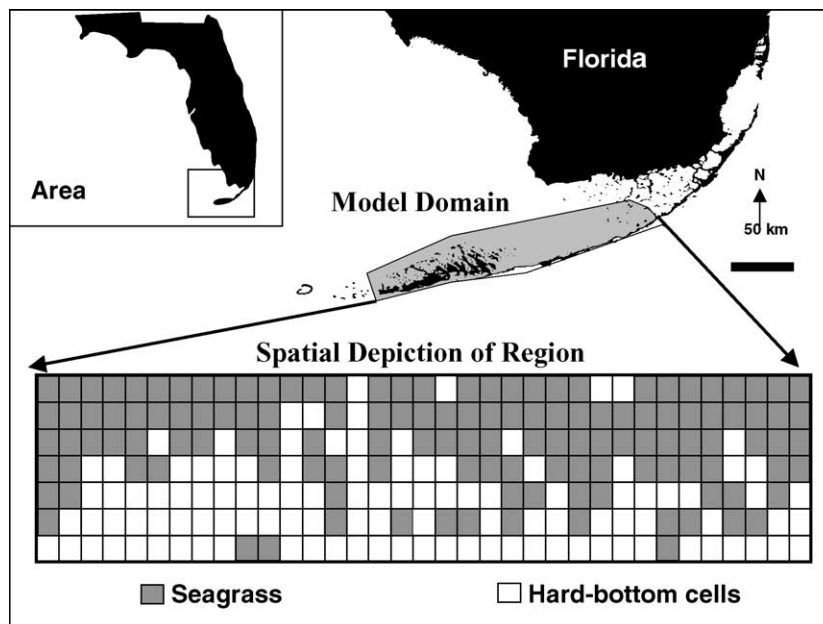


Fig. 1. Diagram depicting the model's geographic domain and spatial structure. The model's spatial domain represents the waters surrounding the Florida Keys and is divided into 256 square cells representing seagrass or hard-bottom habitat; the habitat locations mirror the dominant habitats in the actual region. Within each hard-bottom cell, the shelter availability for lobsters is also independently defined.

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/shelter type that we observed in our surveys. Temperature varies daily in the model using a sin function with a summer high of 30 °C to a winter low of 18 °C; it does not vary among habitat cells. Two other spatially-explicit environmental conditions (i.e. sponge-killing plankton blooms and variations in salinity) can be inputted to the model and these can vary daily among individual cells.

## 2.2. Modelling the recruitment process

The ecological aspects of *P. argus* recruitment included in our model start with the arrival of postlarvae in the nearshore nursery and terminate when larger juveniles begin to enter fishermen's traps and are thus first impacted by the fishery (Hunt and Lyons, 1986). A complete description of spiny lobster recruitment, and the recruitment of *P. argus* in particular, is given elsewhere (Butler and Herrnkind, 2000). The recruitment process is explicitly incorporated 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. 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, which we are now incorporating. Lobsters begin to enter traps at about 50 mm CL and individuals of this size can be legally deployed live in traps by fishermen as social attractants for legal-sized lobsters. Therefore, we remove individuals from the model and record them as "pre-recruits" to the fishery once they attain 50 mm CL. On average, it takes a lobster that is 50 mm CL about 1.5 years to attain the legal fishable size of 76 mm CL (Forcucci et al., 1994).

Each of the lobster biology subroutines (e.g. settlement, growth, shelter selection, mortality and among-cell movement) is described in detail elsewhere (Butler, 1994, unpublished data; Butler et al., 2001), so I only summarise them here. Each of the processes (e.g. mortality, movement, etc.) 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 curvilinear functions to empirical data (Tablecurve, Ver. 1.12 software, Jandel Scientific).

Every new moon, the program generates a cohort of new postlarvae whose abundance fluctuates each month in accord with historical data on postlarval supply (see Acosta et al., 1997). New settlers are randomly assigned a size between 5.0 and 7.0 mm CL. For most of our simulations, new postlarvae were distributed randomly among spatial cells with approximately 80% settling within macroalgae in hard-bottom cells and 20% settling in seagrass beds; this ratio is based on laboratory settlement choice studies (Herrnkind and Butler, 1986). However, in one set of simulations (see section on impacts of variable postlarval supply) we specifically investigated whether the pattern of postlarval supply significantly altered predictions of recruitment (Butler et al., 2001). To initially populate the model, we run simulations for 2 years (26 lunar months) prior to the time period of interest and use the long-term mean postlarval supply for each month as input during this spin-up period. Preliminary runs of the model using monthly-averaged postlarvae supply demonstrated that the abundance of large juveniles >50 mm CL stabilised after 18 months; hence, our choice of a 2-year initialisation 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 actual 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.

Individual lobster growth is modelled as a discontinuous process using empirically determined probability distributions to specify moult increments and intermoult intervals, which vary as a function of an individual's current size, the days elapsed since that individual's last moulting event and the current water 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, etc.) 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 determined by summing the independent probabilities of mortality determined for the daytime, night-time and crepuscular periods of a day. The time each individual spends in a shelter versus the open during these periods, along with its size, figures prominently in the calculation of these respective mortality probabilities. We explore the potential effects of shelter density, group defence and the guidepost effect (Childress and Herrnkind, 1994, 1996) on individual mortality and its effect on recruitment in another paper (Dolan and Butler, unpublished data).

Movement of lobsters among habitat cells is random in direction and its probability depends upon 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 because in reality differences in habitat, salinity and depth limit lobster movement in those directions. Movement across the east and west boundaries is "wrapped", so that lobsters exiting the eastern edge of the model then enter at the corresponding cell on the western edge. This approximates natural immigration and emigration of lobsters east and west of the modelled region.

Each set of the model runs usually requires 1–3 h of run time, depending on the number of years simulated, number of replicate simulations and the processor speed and RAM of the computer on which it is run. The model was originally written in Fortran 77, but it has been rewritten in C++. Verification of model results has been accomplished in two ways. We first verified the output of isolated routines (e.g., growth, shelter selection, etc.) using the appropriate independent empirical data sets, and then compared the results of an actual model simulation of the effects of habitat disturbance on lobsters with the results of a large-scale field survey of lobster recruitment (see Section 3.1). Later simulations (see the sections describing simulations 2 and 3) were not validated and were thus run as "what-if" scenarios, because

the necessary empirical data for the validation of large-scale results were unavailable.

### 3. Model applications: variation on a theme

#### 3.1. *The effect of habitat disturbance on lobster recruitment*

The Florida Keys marine ecosystem has experienced a cascade of environmental disturbances over the last decade. Water quality has declined and thousands of hectares of seagrass have disappeared in episodic die-offs, first documented in 1987 (Robblee et al., 1991; Zieman et al., 1994). Perhaps linked to the release of nutrients from seagrass die-off, extensive and repeated blooms of cyanobacteria swept over much of Florida Bay near the Middle Keys since at least 1999. In turn, those blooms sparked a massive die-off of the sponge community in ~20% of the available lobster nursery in south Florida. Coincident with the sponge die-off were shifts in the abundance and shelter use of juvenile spiny lobsters (Butler et al., 1995), which use several species of sponge as a primary shelter. Thus, our first use of the model (Butler, 1994, unpublished data) 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.

##### 3.1.1. *Simulations*

We ran two simulations: a "control" simulation was run without cyanobacteria blooms, followed by a "bloom" simulation that recreated the timing and spatial distribution of the actual 1991 and 1992 bloom events. In the bloom simulation, the 1991 bloom began in November, lasted 49 days and covered ~10% of the model's spatial domain, mostly in the northeast portion of the modelled region. The 1992 bloom began in October and proceeded in two phases: the first bloom covered the same area as the 1991 bloom and lasted 47 days, then it swept over an even larger area (~35% of the model region) extending to the south and west of the first bloom and it persisted for 119 days. For this set of simulations, the presence of a bloom in a habitat cell resulted in the incremental die-off of sponges in the effected cell, with loggerhead sponges dying at a slower rate than other sponge



species. Thus, the shelter capacity that supports lobsters in each cell is dynamic and changes in a unique way depending on the initial shelter structure in a cell, the duration of bloom exposure for each cell and the subsequent shelter requirements of lobsters in each cell, which itself is size-dependent.

### 3.1.2. Results

The results of those simulations suggested that the lobster population should be surprisingly resilient to the sponge die-off (Fig. 2A). Although nearly the entire sponge community was decimated over ~20% of the nursery, this loss of habitat was predicted to result in only a 16% decline in lobster recruitment in the perturbed region and a 2% decline over the entire Florida Keys region. Why should this be so? An important feature of IBMs is the level of “process detail” that one can obtain and output from any subroutine, which permits ready evaluation of various hypotheses to explain the result.

For example, it just so happened that coincident with the timing of the sponge die-off, actual postlarval supply nearly tripled. Florida’s lobster populations are undoubtedly sustained by postlarvae arriving from elsewhere in the Caribbean (Lyons, 1980; Silberman et al., 1994), so his serendipitous increase in larval supply may have boosted recruitment in undisturbed or marginally disturbed areas and helped mask the effect of the sponge die-off. Fortunately, the mechanistic structure of the model permits us to examine explanations such as this. We replaced the actual postlarval supply with the long-term mean monthly postlarval supply to examine the effects of the sponge die-off without the confounding effect of changing postlarval supply. The results of this second set of simulations were remarkably similar to the first; only a 1% loss in recruitment region-wide and a 13% loss in the perturbed region (Fig. 2A). Thus, the sponge die-off, regardless of postlarval supply scenario, had remarkably little effect on lobster recruitment. What other processes could compensate for the expected effect of habitat loss on lobster recruitment? Our modelling results suggested that more severe impacts on recruitment were averted for two reasons.

First, the model predicted that juvenile lobsters residing in areas affected by the sponge die-off would switch their habitation to previously underutilised, al-

ternative shelters (e.g. solution holes, coral heads, etc.; Fig. 2B). Although lobsters of different sizes select certain types of shelters over others, their preference is reasonably plastic and we know of no measurable impact on their survival when alternative shelters are used (Childress and Herrnkind, 1994). Second, the model predicted the movement of significant numbers of large juvenile lobsters out of the perturbed region into nearby unaffected areas (Fig. 2C). These model generated “explanations” for the asymmetrical response of lobsters to habitat loss were supported by field evidence. The abundance of recent settlers and more mobile lobster size classes increased on non-impacted sites and lobsters displayed dramatic shifts in shelter use on sites impacted by the sponge die-off (Butler et al., 1995; Herrnkind et al., 1997).

### 3.2. Ecosystem restoration: the impact of altered salinity on lobster recruitments

Many of the environmental problems facing the south Florida marine ecosystem have been traced back to the management of freshwater flow from the Everglades south into Florida Bay. The Everglades is an enormous freshwater marsh stretching from Lake Okechobee in central Florida south to Florida Bay. Its natural hydrography has been drastically altered by the construction of canals and levees for flood control and the reclamation of land for urban development and agriculture. Natural variation in rainfall along with these alterations to the Everglades natural hydrography result in dramatic annual and sub-annual differences in salinity and water temperature in Florida Bay (Brewster-Wingard and Ishman, 1999). Portions of Florida Bay that were historically estuarine are now marine, and other areas vacillate dramatically in salinity by as much as 50 ppt or more a year. The US government has begun a multi-billion dollar effort to restore natural water flow to the Everglades, which is expected to significantly alter the amount and character of the water entering Florida Bay. The potential impact of changing salinities on the marine communities in south Florida, and spiny lobsters in particular, is largely unknown. Thus, another use of our model was to explore the potential impact of changing salinity on hard-bottom habitat, with special emphasis on spiny lobster (Butler et al., unpublished data).

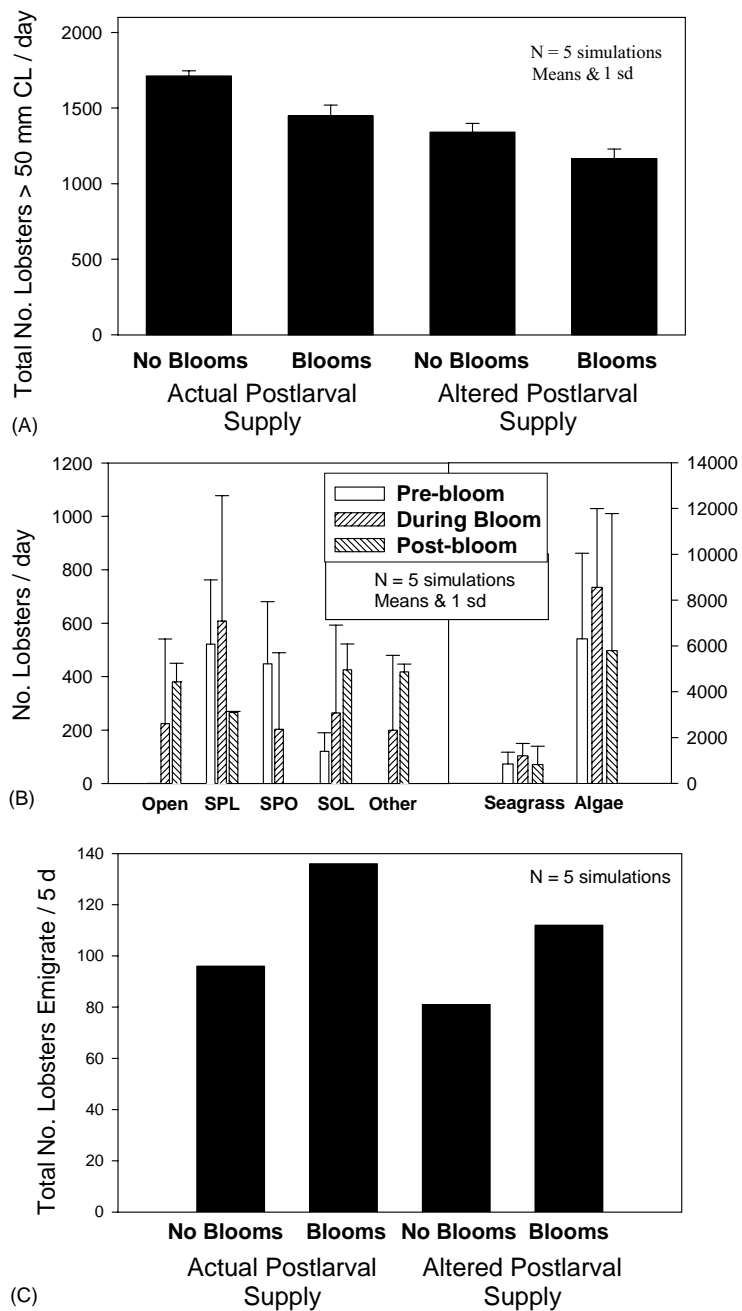


Fig. 2. Summary of results of model simulations of juvenile lobster recruitment, shelter change and emigration under four simulation scenarios: (1) with or without cyanobacteria blooms and (2) actual postlarval supply or an altered supply of postlarvae that varies among months but not years. (A) Predicted recruitment of juvenile lobsters under the four model simulations; (B) the changing number of juvenile lobsters occupying seven different shelter types prior to the cyanobacteria blooms, during the blooms and after the blooms. Habitat codes used in this panel are—open: no shelter; SPL: loggerhead sponge; SPO: other sponges; SOL: solution hole; other: other large shelters. (C) The mean number of juvenile lobsters that emigrated from the region impacted by the blooms under the four model simulation scenarios.

### 3.2.1. Simulations

The extreme salinities and temperatures that occur in portions Florida Bay are lethal to lobster postlarvae (Field and Butler, 1994), and recently completed laboratory experiments reveal that early benthic stage juveniles are equally susceptible (Butler, unpublished data). Surprisingly, the survival and growth of larger juveniles (20–60 mm CL) are unaffected by these extreme salinities and temperatures after up to 6 weeks of exposure. However, the movement of large juvenile lobsters (>35 mm CL) significantly increases when they are exposed to abnormally high or low salinities (Butler, unpublished data). Thus, to investigate the potential effects of changing salinity on lobster recruitment throughout the Florida Keys region, we incorporated these kinds of size-dependent responses to different salinity–temperature regimes into the model's survival and movement subroutines.

Ideally, we would have liked to have run simulations exploring the impact of various proposed hydrological restoration efforts in the Everglades on salinity in Florida Bay, and hence on lobster recruitment. However, water circulation, transport and evaporative pathways are insufficiently known in this region to permit realistic estimates of likely salinities resulting from potential water management practices. We therefore resorted to modelling salinity effects on lobster recruitment by comparing results for salinity regimes based on empirical data available during the wettest (1995) and driest (1993) years during the last decade. Under this simulation scenario the spatio-temporal patterns in salinity represent upper and lower bounds, as should the resultant effects on lobster recruitment. As in other simulations, lobster populations were permitted to build over two simulation years, at which time the populations had attained a dynamic equilibrium. During this initialisation period, salinity fields within the model cells remained stable at 35 ppt. After initialisation, salinities in the model cells varied independently among cells and on a weekly time step in accordance with empirically measured changes for the wet or dry year. We therefore modelled salinity changes in much the same way as we did the occurrence of cyanobacteria blooms in our initial modelling efforts, and like those earlier simulations, the direct effects of salinity were limited to ~20% of the lobster nursery where salinity varies naturally. Water temperature was modelled as before;

that is, water temperature changed incrementally each day in the model reaching a maximum of 30 °C in the summer and a minimum of 18 °C in the winter.

### 3.2.2. Results

The results of our simulations on the effects of salinity change on lobsters in Florida Bay suggested that lobster recruitment during a very wet or dry year would be similar. In both cases, recruitment declined by ~25% in the area directly affected by salinity change which resulted in ~5% decline in recruitment over the entire Florida Keys region, as compared to control simulations where salinity was stable at 35 ppt (Fig. 3). Although large juveniles are capable of emigrating from areas experiencing inappropriately high or low salinity and did so in the model, the effects of this movement on recruitment were inconsistent and of little overall impact. This occurred because the smallest size classes that are most effected by altered salinities cannot emigrate great distances. However, these simulations lacked some potentially important dynamics for which we have no data. For example, we did not assign any differential “costs” to large juveniles that stay in their home cell versus those that emigrate in response to changing salinity. Also, these simulations did not include the potential indirect effects that altered salinity is likely to have on lobster recruitment via changes in the habitat, prey or predator structure of hard-bottom communities. Still, these results offered managers useful predictions of the minimum impacts that might be expected when the Everglades restoration effort is fully implemented.

### 3.3. Does geographic specificity in postlarval supply or habitat structure affect recruitment?

In addition to the more practical application of the lobster recruitment model presented thus far, we have also used this same model, with minor modifications, to investigate the extent to which the spatio-temporal representation of postlarval supply and habitat structure influence model predictions of recruitment (Butler et al., 2001). This could be viewed as a purely theoretical investigation of the appropriateness of the model's spatial structure and depiction of postlarval supply. However, these simulations yielded results of practical importance as well.



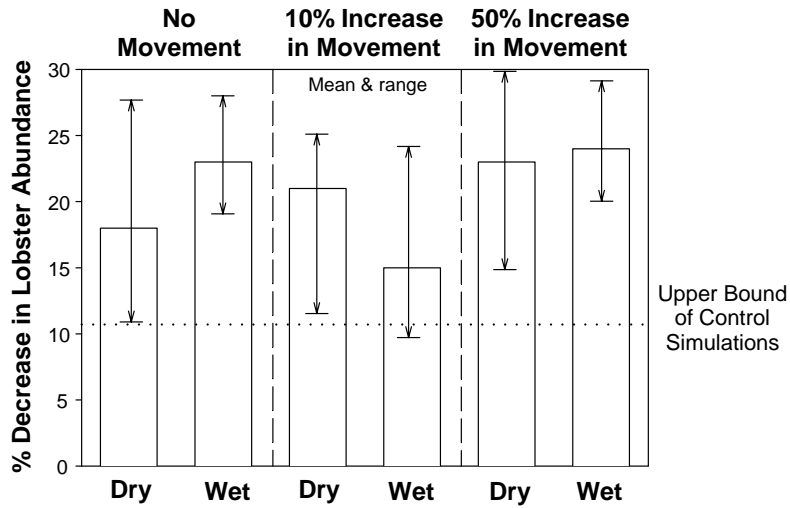


Fig. 3. Summary of six model simulations investigating the potential impact of extreme salinity and lobster emigration on the recruitment of juvenile lobsters. Results are expressed as the percent decrease in recruitment (i.e. higher values indicate a greater negative impact on recruitment). The dotted line depicts the upper bound attained for the control simulations. Results are shown for simulations of the wettest and driest years (i.e. most extreme salinity) in the past decade.

#### 3.4. Recruitment and the configuration of habitat structure

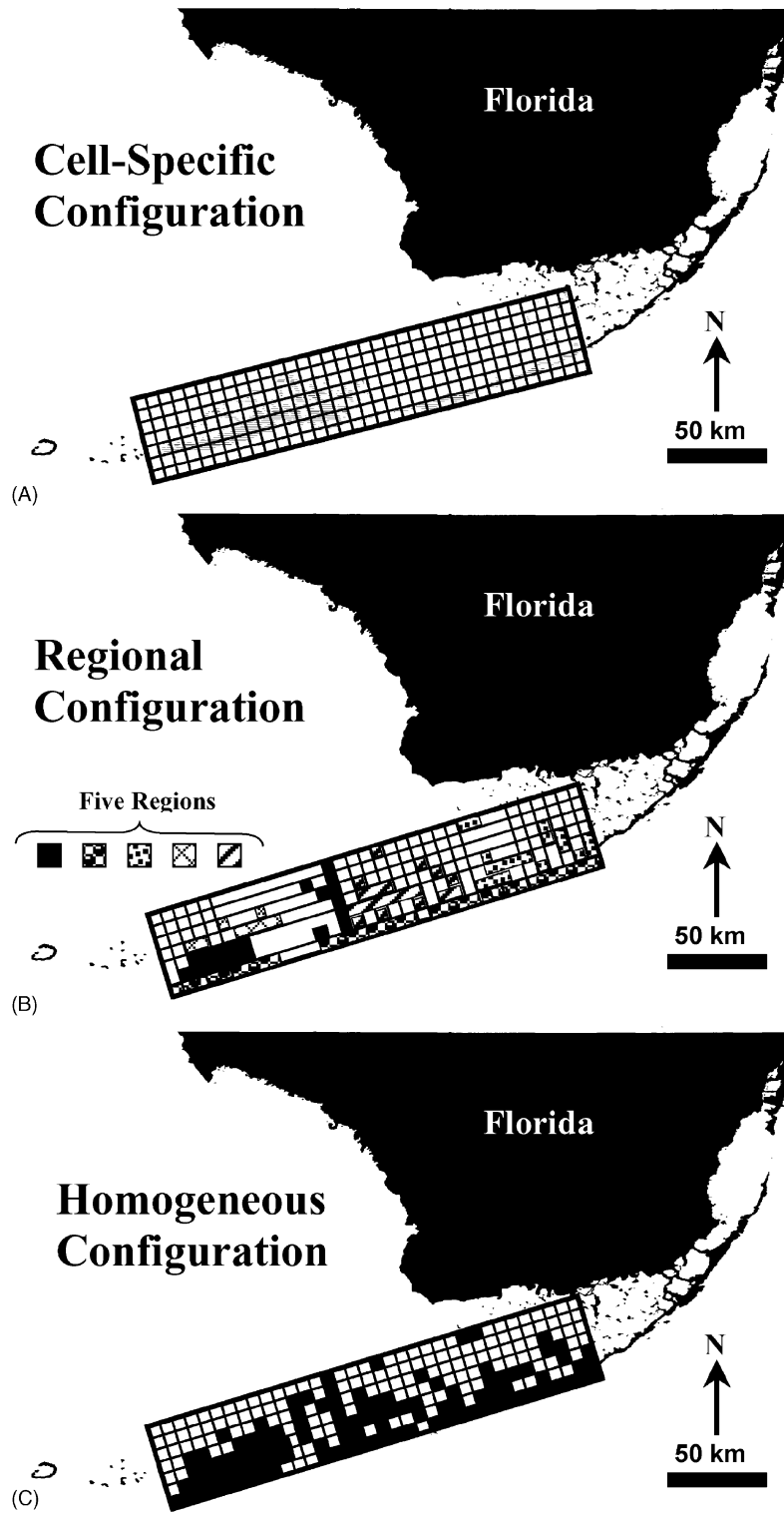
The effect of habitat spatial configuration on recruitment processes is directly relevant to the protection of essential nursery habitat and the essential features of those habitats that effect their function (e.g. size, location, structural complexity, etc.). Most models for species that are fished implicitly assume that small-scale variation in habitat–recruitment relationships “average out” over the large spatial scales over which fisheries typically operate. But is this really so? Both theoretical and empirical examples, mostly from terrestrial systems, suggest that habitat patchiness and connectivity have great consequences for population dynamics and sustainability (Huffaker, 1958; Hanski, 1996; Bascompte and Sole, 1996; Rohani et al., 1996; Pascual and Levin, 1999; and others).

Furthermore, a detailed spatial depiction of habitat structure seemed particularly appropriate for our model of *P. argus* in south Florida where the primary settlement habitat is heterogeneous and dynamic. Unlike other species that settle into rock crevices, the distribution of which is relatively stable (Wahle and Steneck, 1991; Parrish and Polovina, 1994; see review in Butler and Herrnkind, 2000), *P. argus* settles pref-

erentially into hard-bottom habitat covered by clumps of the red macroalgae, *Laurencia* sp. (Marx and Herrnkind, 1985; Herrnkind and Butler, 1986). In south Florida, hard-bottom habitat is widely dispersed and patchy, and the abundance of red macroalgae on sites is ephemeral and uncorrelated with postlarval supply (Butler et al., 1997). If the distribution or structure of nursery habitat affects habitat choice by settlers or their post-settlement survival, then we cannot easily infer the recruitment of juveniles from postlarval supply.

##### 3.4.1. Simulations

These simulations were designed to test the importance of spatial continuity in habitat structure on model predictions of lobster recruitment. We ran six independent simulations ( $2 \times 3$  completely-crossed design) where we altered the position of habitat cells and the spatial uniformity of habitat structure within cells in different combinations. The geographic position of seagrass and hard-bottom nursery habitat cells within the model domain was run as either a real or random geopositioning of habitat cells. The spatial scale over which shelter structure density varied took one of the three forms: cell-specific, regional or homogeneous. In the “cell-specific” simulations, the habitat structure



within each habitat cell was unique (Fig. 4A). The second scenario was a “regional” simulation where the abundance and types of shelters within each habitat cell was homogeneous within a specified region but differed among the five regions we created in the model (Fig. 4B). These five regions roughly corresponded with actual biogeographic regions identified in the Florida Keys based on the structure of sessile benthic communities (Herrnkind et al., 1997). The last scenario was a “homogeneous” simulation where shelter structure was identical in all model cells (Fig. 4C).

#### 3.4.2. Results

Marginally significant differences (1-factor model I ANOVA;  $F = 3.154$ ; d.f. = 2, 24;  $P = 0.061$ ; Butler et al., 2001) in recruitment occurred when we varied the geographic resolution with which hard-bottom shelter structure was modelled (i.e. cell-specific, regional, homogeneous scenarios). The lowest recruitment consistently occurred when we simulated habitat structure in the most realistic, cell-specific format. However, those effects were relatively small (~5% difference in predicted recruitment) and from a practical standpoint had relatively little impact on predictions of lobster recruitment.

One might conclude from these results that the addition of georeferenced spatial depictions of habitat structure to our model is an unnecessary complexity. Perhaps, but we have already demonstrated that having such complexity has permitted us to examine the impact of habitat change on lobster recruitment. Moreover, those earlier simulations incorporating habitat details allowed us to determine that shifts in shelter use probably contributed to the remarkable resilience to disturbance exhibited by the spiny lobster population in Florida. These kinds of results also prompted an introspective look at potentially important dynamics absent from the model.

In this case, we suspect that the position and structure of habitat would be more consequential if our

model better captured more of the dynamics relevant to the settlement process. In particular, our model now over-simplifies the way in which postlarvae are distributed to specific habitats, and omits the effects of local hydrodynamics or local habitat structure on settlement patterns. In the model’s current configuration, habitat structure only impacts upon lobsters through its effects on shelter use by larger juveniles, not settlement patterns. In our defence, the simplistic rules governing settlement in the model were not an oversight, but a deliberate attempt to minimise the impact of dynamics about which we knew little. In retrospect, the minor impact of habitat reconfiguration on our simulation results is somewhat of a vindication of this approach, but it is an unsatisfying result just the same.

Although settlement magnitude differs between habitat cells designated as seagrass versus hard-bottom, we do not alter cell-specific settlement rates in the model based on the abundance of macroalgae or the density of seagrass in the cell. In reality, the distribution and abundance of red macroalgae into which most lobsters settle is dynamic (Butler et al., 1997) and seagrasses are subject to massive die-offs (Robblee et al., 1991; Zieman et al., 1994). 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, but we are now conducting experiments to determine this.

We also do not include the effects of local hydrodynamics on postlarval settlement, although we have modelled and investigated regional variation in postlarval supply that are most likely tied to meso-scale oceanographic events (see next section). At the present time, 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 (Smith, 1994; Wang et al., 1994), but the complex bathymetry of the region, as well as the timing of

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Fig. 4. Graphical representation of the three spatial scales over which juvenile lobster crevice shelter types and abundances varied in simulations examining the effect of habitat spatial structure on lobster recruitment. In the cell-specific (A) simulations, shelter type and abundance differed among each of the habitat cells. Shelter structure within each habitat cell in the regional (B) simulations varied among the five regions, but was the same within a region. Shelter structure was the same in every cell in the homogeneous (C) simulations. For each of the three spatial scale configurations shown, we also ran simulations where the position of each hard-bottom cell was realistic (as shown) or randomly assigned.

wind events, has so far prevented the development of accurate physical descriptions of local current fields suitable for our model. There is some progress being made on this front, so we intend to add a more realistic means of delivering postlarvae to specific habitat cells in our model. Based on these empirical advances, future model improvements in the way we settle postlarvae with respect to habitat structure are likely to significantly improve the realism, accuracy and usefulness of this model, as well as its sensitivity to habitat configuration.

### 3.5. The consequences of spatial variation in postlarval supply on recruitment

For palinurid lobsters, the focus of studies on postlarval supply has generally been on temporal patterns and the environmental features that influence them, rather than the determination of spatial variation in the supply of postlarvae to a region (see Butler and Herrnkind, 2000 for review). Yet, the distribution of meroplanktonic larvae can be remarkably variable along a coast. If we only monitor spiny lobster postlarval supply at just a few sites, are we missing settlement dynamics that are important to predictions of recruitment? The answer depends largely on the natural pattern of postlarval supply and whether different patterns result in appreciably different recruitment outcomes. In Florida, for example, the supply of *P. argus* postlarvae has been monitored for over a decade at only a single site; a second site was established ~5 years ago. Despite its limitations, this monitoring program provides the only long-term data set available to managers in Florida for use in generating predictions of recruitment to the fishery (Muller et al., 1997), and we use it as a primary input variable in our model. Do these data, obtained from a single site, yield reliable estimates of the supply of postlarval lobsters to the entire Florida Keys? Until we complete the analysis of our data from a 4-year multi-site postlarval monitoring study, we will not know the true pattern of postlarval supply. But we have used our model to investigate the possible effect of various patterns of supply on recruitment.

To determine whether altering the spatial delivery of postlarvae to regions of the model affects projected recruitment, we simulated eight different scenarios for the spatio-temporal delivery of postlarvae within the model domain: (1) uniform, (2) volumetric, (3) gradi-

ent, (4) static broken-stick, (5) variable broken-stick, (6) a random, (7) pulsed and (8) aggregated delivery of postlarvae (Fig. 4). We considered the first six model scenarios as the most plausible; the last two scenarios were run to examine model predictions under extreme, and probably unrealistic, conditions.

#### 3.5.1. Simulations

For all simulations, each column in the model's habitat grid was treated as a unit that received a certain percentage of the total postlarval influx each month, depending on the simulation scenario. Thus, each column of cells in the model was considered to be roughly equivalent to regions in Florida Bay into which rush tidally-driven water and postlarvae from the inter-island channels between the Keys. As in previous simulations, all cells of similar habitat (i.e. seagrass or hard-bottom) within each column received the same proportion of new postlarvae each month, and hard-bottom cells received more settlers (83%) than did seagrass (17%).

The details of each model scenario are presented elsewhere (Butler et al., 2001), so I only summarise the general mechanics of each here (Fig. 4). In the *uniform* supply scenario, each column of cells received the same proportion of the postlarval supply (i.e. 1/35) in any given month. The *volumetric* delivery scenario simulated what would occur if postlarval supply depended on differences in tidal flow among the channels between the islands of the Florida Keys, through which postlarvae pass on their way to the nursery. The *gradient* simulation mimicked a situation where postlarval supply diminishes smoothly from west to east in increments of 5%. The *static* broken-stick and *variable* broken-stick simulations both relied on a "broken-stick" type randomisation scenario (sensu MacArthur, 1957) to randomly allocate postlarvae to cell columns. They differed in that the first random allocation of postlarvae was used repeatedly throughout the *static* broken-stick simulations, whereas a new random allocation was calculated each lunar period in the *variable* broken-stick simulations. These two broken-stick formulations resulted in fairly uniform distributions because of the large number of "breaks" in the distribution of postlarvae, so we also constructed a completely random simulation. For the *random* simulation a different pattern of postlarval allocation was determined each lunar period with the restriction

that no column could receive more than 30% of the total postlarval supply in a lunar period. During any particular lunar month, this procedure produced the most variable postlarval supply among the first six simulations. Finally, we ran a *pulsed* simulation and an *aggregated* simulation to examine the model’s sensitivity to extreme scenarios of postlarval supply. The *pulsed* scenario delivered 1/7 of the postlarvae each month into each of the seven uniformly spaced columns in the model. The *aggregated* scenario was created by again delivering 1/7 of the postlarvae each month into each of the seven columns, but this time into seven adjacent columns (Fig. 5).

3.5.2. Results

Varying the spatio-temporal supply of postlarvae to our model resulted in significant differences in recruitment among the eight simulation scenarios (Table 1). Recruitment in the random supply simulation was ~15% higher than those of the other five “realistic” models (i.e., uniform, volumetric, gradient, static broken-stick, variable broken-stick); differences in recruitment among those five simulations were small (<4%). The two most extreme scenarios, the pulsed and aggregated simulations, yielded significantly lower recruitment than the other simulations, with the aggregated scenario yielding the lowest recruitment.

Why should the random simulation produce the highest recruitment and the pulsed and aggregated simulations yield just the opposite when all three produce highly patchy distributions of postlarvae? The answer presumably lies in the temporally variable na-

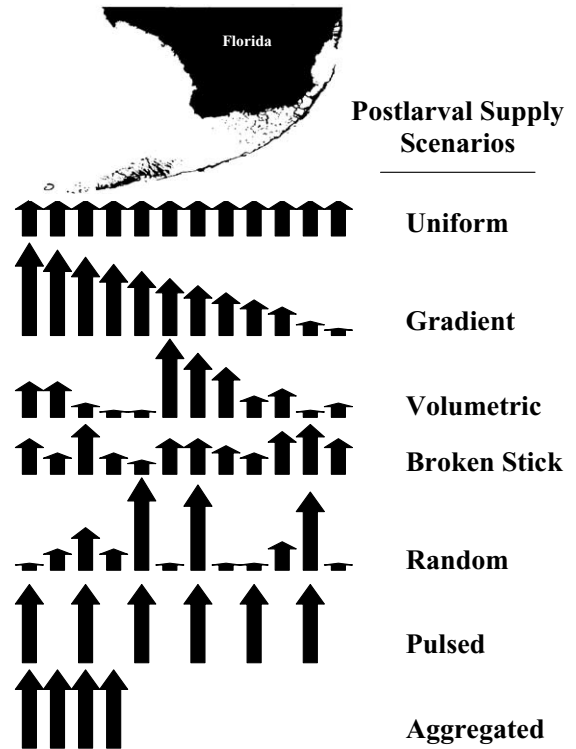


Fig. 5. Graphical representation of seven postlarval supply scenarios used in our simulations investigating the effect of spatio-temporal variability in postlarval supply on the recruitment of juvenile lobsters. Each arrow represents the supply of postlarvae into a particular region of the model (in reality, we used 35 separate inputs not the 12 shown here for simplicity). The length of each arrow corresponds to the relative magnitude of postlarval supply to that region.

Table 1

Matrix showing the percent difference in the recruitment of subadult lobsters ( $\geq 50$  mm CL) predicted in pairwise comparisons of results from each of the six model scenarios<sup>a</sup>

	Uniform delivery	Broken-stick delivery (fixed distribution)	Volumetric delivery	Broken-stick delivery (variable distribution)	East–west gradient delivery	Partially-random delivery
Uniform delivery	0	+0.2	+3.2	+4.2	+4.4	+15.9
Broken-stick delivery (fixed distribution)		0	+3	+4	+4.2	+15.7
Volumetric delivery			0	+1	+1.2	+12.4
Broken-stick delivery (variable distribution)				0	+0.2	+11.3
East–west gradient delivery					0	+11.1
Partially-random delivery						0

<sup>a</sup> Differences of 1% or less are within error limits. Simulations differed only in the spatio-temporal pattern of postlarval supply; total postlarval supply was unchanged among the simulations.

ture of the random supply scenario. The pulsed and aggregated scenarios created persistently high densities of lobsters in specific regions, resulting in shelter limitation and higher density-dependent post-settlement mortality for juveniles. Although the random scenario also often created dense regional patches of postlarval settlement in a particular month, those pulses of postlarvae varied in their magnitude and distribution with the arrival of a new cohort of postlarvae each lunar month. Thus, the random arrival of postlarvae ensured that areas of good habitat received ample settlement over the long-term, but were unlikely to experience consistently high levels of settlement that might result in higher density-dependent mortality. These patterns of abundance established at settlement are likely to be reflected in the abundance of juvenile lobsters because of limited post-settlement dispersal by juveniles. Lobsters move very little until they are ~50 mm CL and then only begin limited nomadic movements (Butler and Herrnkind, 2000).

Which scenario describing postlarval supply best reflects reality? Although our analysis of 48 months of field collections of postlarvae at eight sites along the Florida Keys archipelago is not yet complete, these data suggest that postlarval abundance indeed varies randomly among sites and months; just as in the random supply simulation. If our final analyses of the field data confirm this, then a practical outcome of these simulations will be a recommendation to include multiple locations in future monitoring, rather than the present long-term sampling of one or two sites.

#### 4. Conclusions

Our choice of a spatially-explicit individual-based approach for our computer simulation needs is based on both philosophical and pragmatic reasons. An individual-based approach emphasises the importance of differences among individuals in life history traits, physiology, and behaviour. It also highlights the significance of interactions between individuals and their local environment in shaping population processes. The idea that initial conditions matter and that small effects, like those initiated by unique individuals, are often amplified via positive feedback into large consequences (sometimes referred to as the “butterfly effect” in the terminology of chaos theory) is a

hallmark of the individual-based approach. However, this concept has often been overlooked in favour of methods that model “average” individuals.

IBMs typically require detailed autecological data for their formulation and some may view this as a detriment to their widespread deployment and an impediment to the search for more general rules governing population processes. An alternative view is that this is a positive aspect of the IBM approach, because it fosters a more active interplay between modelling and empirical research. Empirical data are collected from individuals not populations, so there is a natural harmony between the kinds of data typically collected and the values used to parameterise IBMs. Other important practical aspects of the IBM approach are its flexible structure and the diversity of output that these models generate. The mechanistic form of the computer code is easily altered to incorporate new dynamics, routines or output. However, the output from such models can be daunting and care must be taken in selecting appropriate forms, since it potentially could include counters for nearly any event that transpires at any time step in the model.

No model is perfect, and therefore most remain in a state of constant refurbishment. This may be especially true for IBMs, given the degree of detail possible in such models and the nagging allure that a more complex model may be “better” and perhaps capable of yielding more accurate predictions. Whether true or not, an IBM approach is nonetheless capable of linking the results of numerous, often disparate empirical studies into a formal, quantitative framework and thus offers this opportunity should one decide to pursue it. Our modelling studies are a prime example of this.

Although we believe that a spatially-explicit IBM approach offers great promise for resource management, it is not appropriate in all situations and should compliment, not supplant, existing modelling tools. Many existing models are very effective and efficient tools for fishery management purposes. Yet, a statistical approach to stock prediction reveals little about the underlying ecological processes that determine recruitment and they assume a steady-state environment, or more precisely, a statistical relationship between larval supply and recruitment that is unaffected by environmental perturbations. However, 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 post-settlement population dynamics. Unfortunately, environmental degradation is often the norm rather than the exception in today's world, and few fisheries operate in a "pristine" environment. The linkage between pollution and its effects on marine habitats and fisheries is a grave concern in modern fisheries management (see Rose, 2000 and associated papers; Strickland and Grosse, 2000). IBMs, many incorporating spatial structure, are seeing increased use in assessment of the potential impact of environmental contaminants, degradation and stress on the health of fisheries. Although the origins of the IBM approach lie in terrestrial ecology, this approach has found a home in fisheries management and I suspect that we will see its expanded use in marine decapod fisheries. Where habitat structure or environmental conditions are important considerations and where good biological data for the target species is available, spatially-explicit IBM models could and should see wider use.

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