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Spatially-Explicit Agent-Based Modeling of Ecosystem Change and Epizootiological Impacts on Caribbean Spiny Lobster, *Panulirus argus*

Thomas William Dolan III
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SPATIALLY-EXPLICIT AGENT-BASED MODELING OF
ECOSYSTEM CHANGE AND EPIZOOTIOLOGICAL IMPACTS
ON CARIBBEAN SPINY LOBSTER, PANULIRUS ARGUS

by

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B.S. May 1990, College of William & Mary
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A Dissertation Submitted to the Faculty of
Old Dominion University in Partial Fulfillment of the
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Agent-based models explicitly incorporate interactions and variation at the individual level, just as in the real world. As a result, agent-based models are realistic, intuitive, and generally less complex mathematically than their analytical counterparts. Their primary disadvantage is the large amount of detailed data required to construct and parameterize them. Although the use of agent-based simulation is increasing in ecology, they are highly specific, so are rarely used for development of theory. To demonstrate the flexibility and utility of this approach I developed a multi-species, agent-based, spatially-explicit model of the spiny lobster nursery of southern Florida that incorporates changing salinities, temperatures, and harmful algal blooms, and used it to evaluate the likely consequences of changes in hydrology due to the Comprehensive Everglades Restoration Program on the spiny lobster and associated hard-bottom communities. I found that water quality changes associated with the restoration effort will likely reduce lobster recruitment in Florida Bay 6–24% and will likely prevent the restoration of loggerhead sponges and vase sponges on which the lobster depends for shelter in Florida Bay. Then, I extended the model, incorporating disease dynamics appropriate to Panulirus argus Virus 1, including disease states, contact transmission, and two density-independent transmission mechanisms, to explore
the effects of changes in host sociality on disease dynamics. I showed that when susceptible hosts avoid diseased conspecifics in a manner consistent with that demonstrated by *P. argus* in a system dominated by contact transmission, persistence of the disease requires an exogenous source. I also examined the effects of increased host aggregation on disease transmission. I found that in the absence of disease avoidance, outbreaks occurred rapidly, and by the end of the 10 year simulation, PaV1 was maintained continuously at unrealistically high levels. However, the disease avoidance behavior reduced simulated outbreak intensities and durations, and in the absence of other sources of PaV1, resulted in extinction of the disease within five years. Both the density independent infection of EBJs and the simulated arrival of infected cohorts of postlarvae maintained the disease in the larger population as a consequence of the long period between exposure and death.
This thesis is dedicated to the two most important women in my life: my mother, Dona Brizzi, who made it possible for me to begin this work, and my wife, Linda Spalding, who gave me endless support along the way and made it possible for me to finish it. I may stand on the shoulders of giants, but I did not get there alone.
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CHAPTER I

INTRODUCTION

In modeling ecological processes and systems, a fundamental decision must be made regarding the appropriate level of detail for the phenomena of interest. Model complexity ranges from compartmental differential equations that assume homogeneous mixing of individuals under uniform conditions to spatially-explicit, agent-based models that explicitly represent each individual and their spatial relationships across landscapes with varying ecological conditions. The former emphasize mean effects, whereas the latter place more emphasis on variance. In the field of epidemiology, for example, compartmental models have been used effectively to predict epidemics and recommend effective management strategies (see reviews by Barlow 1995, Heesterbeek and Roberts 1995). These models have the advantages of being mathematically tractable, requiring relatively little data, and, in some cases, have been extended to allow for spatial heterogeneity and stage-structured populations (see reviews in Grenfell and Dobson 1995). However, there is no representation of individuals in even the most complex of these models, which are mathematically dense, and their interpretation non-intuitive.

On the other hand, in agent-based models (also referred to as "individual-based"), interactions and mechanisms are applied at the individual level, just as they

The journal model for this dissertation is Ecology.
operate in the real world, and they explicitly incorporate variation at the individual level. As a result, agent-based models are realistic, intuitive, and generally less complex mathematically. Their primary disadvantage is the amount of detailed data required to properly construct and parameterize them. Agent-based models are also computationally intensive, but the rapid development of high-speed computer processors has nearly rendered this a non-issue. There is a perception, however, that agent-based models tend to be developed *ad hoc* and are not broadly applicable, which is a misperception. As a case in point, I present two very different applications of a spatially-explicit, agent-based model of the population dynamics of juvenile Caribbean spiny lobster (*Panulirus argus*) in the Florida Keys, Florida (USA). The first (Chapter II) is an ecosystem-based application with the applied goal of predicting how proposed changes in freshwater management within the Everglades, that in turn influence salinity and the potential for harmful algal blooms in the adjacent marine ecosystem, are likely to impact sponges, octocorals, and juvenile lobsters. In Chapter III, I extend the model to include a recently discovered disease and use it to explore a more theoretical topic, specifically, the impact of host behavior and habitat structure on the spread of disease in social organisms.

The Caribbean spiny lobster, *Panulirus argus*, and its population dynamics are the central focus of both modeling exercises. It is a species of great economic interest in the Caribbean, because it supports the most valuable fishery in the region (Ehrhardt et al. 2010), but it also serves as a good ecological model for other abundant coastal species with similar life cycles that are also subject to fishing. *Panulirus argus* has a complex life cycle with several life stages requiring different habitats, and individuals
undergo ontogenetic shifts in gregariousness, habitat preference, and shelter preference that lead to a spatially and socially structured population. Shallow hard-bottom communities within the area serve as the primary nursery habitat for *P. argus*, which later populate the nearby barrier reef as adults. Postlarvae settle in nearshore habitats dominated by macroalgae (Marx and Herrnkind 1985), and after metamorphosing to the early benthic juvenile stage, seek food and solitary refuge in algal clumps for three to five months postsettlement (Herrnkind and Butler 1986, Herrnkind et al. 1988, Childress and Herrnkind 1996). Upon reaching approximately 15 mm carapace length (CL), individuals leave the macroalgae to reside in crevice shelters provided by corals, cavities in the limestone bedrock, and large sponges whose abundance is an important factor regulating lobster recruitment in the Florida Keys (Berrill 1975, Forcucci et al. 1994, Childress and Herrnkind 1996, Herrnkind et al. 1997b). Above 45 mm CL, juveniles become increasingly nomadic within the nursery habitat, and eventually migrate to offshore reefs, where they live as adults (Forcucci et al. 1994, Acosta 1999). Juvenile lobsters and the sponge shelters on which they depend are both sensitive to changes in salinity and to sponge-killing harmful algal blooms that can occur in this shallow water nursery.

Florida Bay and the shallow (< 3 m deep) waters surrounding the Florida Keys provide the ecological stage upon which both models described here operate. Historically, Florida Bay received large inflows of oligotrophic fresh water from the Everglades. More recently, development and the need for flood control led to channelization and diversion of that flow, greatly diminishing the storage capacity of the wetlands. Together with in-filling of many of the channels between islands during
the early 20th Century for the building of the Overseas Railroad, these changes have stifled water flow and lead to extreme fluctuations in salinity in the northeastern portion of the bay, and generally higher salinities and eutrophication throughout. The goal of the Comprehensive Everglades Restoration Plan (CERP) (www.evergladesplan.org) is to restore more natural water flow through the Everglades and is expected to impact salinity in Florida Bay, which may have consequences for the marine communities there and those in the adjacent Florida Keys marine ecosystem. Several alternative water management plans in CERP are under consideration but the degree and spatial extent of their consequences on the marine ecosystem are unknown. Spiny lobsters are among several species of special concern to CERP, because of the high commercial value of the lobster fishery (the second most valuable in Florida) and the ecological importance of lobsters both as predator and prey. The highly specific, applied nature of this project and the spatial heterogeneity of the environmental landscape demanded a spatially-explicit approach that closely mimicked the real system. In addition, the complexity of the social structure of the lobster population compounded with changes in lobster behavior and ecology associated with environmental change was most conveniently and accurately modeled on a probabilistic individual basis. Thus, this was the goal and rationale of my first model application described in Chapter II.

In Chapter III, I extended the previous model to include the effects of a pathogenic virus that infects Caribbean spiny lobsters, and then used model simulations to explore the effects of disease-induced behavioral changes, different transmission mechanisms, and changes in habitat structure on the epizootiology of the disease. In 1999, the first known viral pathogen of lobsters, designated PaV1 (Panulirus argus
Virus 1), was discovered in Caribbean spiny lobster dwelling in Florida Keys, Florida, USA (Shields and Behringer 2004). In late stages of infection, lobsters become lethargic, cease grooming and molting, and their hemolymph (i.e., blood), normally clear or amber, becomes chalky white. Shields and Behringer (2004) found that 38% of lobsters died within 80 days of inoculation with the disease. Surveys of >100 sites throughout the Florida Keys in 2002 revealed the virus to be widespread among crevice-dwelling juveniles with a mean prevalence between 6–8% (Shields and Behringer 2004, Behringer et al. 2006), and annual surveys of a subset of those sites since then indicate that prevalence is stable (5–10%), although local prevalence can be as high as 70% on a site (Behringer et al. 2010). There is also evidence that lobster size plays a role in susceptibility, with algal-dwelling juveniles being the most susceptible and having the highest prevalences of PaV1 (15–25%), whereas adults have the lowest prevalence (~10%). The disease can be transmitted to *P. argus* juveniles by injection, ingestion of infected tissue, and by contact, and among the smallest juveniles it can spread via waterborne transmission over short distances (Butler et al. 2008). Recent evidence also suggests that the virus is carried by postlarvae, and presumably also by the larvae, which spend 6–8 months in the plankton of the open sea (Goldstein et al. 2008) and disperse from their spawning sites hundreds if not thousands of kilometers (Butler et al. in press).

The complex life history of the Caribbean spiny lobster has many of the features of marine organisms that make use of typical compartmental epizootiological models questionable, including marked ontogenetic shifts in habitat use, large-scale movement of larvae by ocean currents, and social behaviors. Cohabitation by crevice-dwelling
juvenile *P. argus* seems to be mediated by size-dependent attraction to conspecific odors (Childress 1995, Ratchford and Eggleston 1998); however, the benefits of aggregation for these small lobsters are unclear (Eggleston and Lipcius 1992, Childress 1995, Childress and Herrnkind 1997, Dolan and Butler 2006). On the other hand, a number of costs are associated with social aggregation, including increased rates of disease transmission. Because PaV1 is transmitted by proximity, the aggregative behavior of juvenile *P. argus* would seem likely to enhance the spread of the disease through the population. However, infection by PaV1 results in two behavioral changes that counter this effect. First, lobsters in the latter stages of the disease (i.e. those with visible symptoms) have markedly lower movement rates than uninfected lobster (Behringer et al. 2008). This likely reduces transmission between local populations and may reduce exposure of healthy individuals on smaller scales as the infected lobsters tend to remain in their dens rather than forage (Loehle 1995). It may also reduce transmission from the nursery habitat to the adult population on the reef. Second, healthy lobsters avoid and rarely cohabit with visibly diseased lobsters, resulting in social isolation (Behringer et al. 2006, Behringer and Butler 2010), which may act further to reduce disease transmission (Loehle 1995, Kiesecker et al. 1999). These changes in behavior may reduce the spread of the disease both within and among populations.

Given these behavioral changes, it is also possible that individual variation in the course of the disease and detectability of the infection may result in variability in the effective contact rate (contacts that result in disease transmission) among individuals. This could lead to outbreaks, similar to those seen in so-called superspreading events.
like the Severe Acute Respiratory Syndrome (SARS) global epidemic in 2003 (Shen et al. 2004). Superspreading occurs when a relatively small group of host organisms have disproportionately high degrees of connection with other hosts. Due to the presence of these highly connected hosts, the disease can persist at lower levels and with a lower epizootic threshold than predicted by compartmental models. This kind of dynamic is increasingly modeled using static networks in which individuals, represented as nodes, can have varying numbers of contacts. The \textit{P. argus-PaV1} system has an additional complication, however, in that the associations of individual lobsters are quite fluid, changing frequently within the infectious period of the disease. In addition, the behavioral responses to the disease itself alter the pattern of connections, so static networks do not accurately represent the system. A spatially-explicit agent-based approach, however, can capture these dynamics in a natural and intuitive manner.

Therefore, in Chapter III, I altered the spatially-explicit agent-based model previously developed for lobsters to include the known disease dynamics of PaV1 and its effects on lobster behavior and ecology. I then used that new model in a theoretical exploration of the effects of host behavior, mode of pathogen transmission, and habitat structure on the spread of disease in social, marine animals.
CHAPTER II

IMPACTS OF THE COMPREHENSIVE EVERGLADES RESTORATION PLAN ON LOBSTER AND HARD BOTTOM COMMUNITIES OF FLORIDA BAY: A SIMULATION STUDY

INTRODUCTION

The Everglades is a complex freshwater ecosystem that stretches from central Florida (USA) to Florida Bay at the southern terminus of the Florida Peninsula. Since the late 1800s the Everglades have been increasingly impacted by human development. In the late 1800s and early 1900s agriculture was the primary mode of economic development in Florida, and the main impediment to agricultural development in south Florida was flooding. Therefore, a series of water management projects was undertaken by the State of Florida and the Federal Government to reduce flooding, culminating in the Central and Southern Florida Project for Flood Control and Other Purposes (C&SF Project), authorized by Congress as part of the Flood Control Act of 1948 (Flood Control Act 1948). Major components of the C&SF Project included the channelization of the Kissimmee River, drainage of approximately 27% of the historic extent of the Everglades immediately south of Lake Okeechobee to form the Everglades Agricultural Area, and establishment of an ~1100 km perimeter levee, blocking sheet flow to the easternmost 16% of the Everglades so that those lands would be protected from flooding (Sheikh and Carter 2008). The C&SF Project has been successful in preventing flooding of urban and agricultural land, but a number of unintended consequences have
also occurred (reviewed by USACE and SFWMD 1999). In summary, loss of over 50% of the historic geographic extent of the Everglades and channelization of water flow has greatly reduced its filter capacity, leading to poor water quality and discharge of polluted and hypereutrophic water into the St. Lucie and Caloosahatchee estuaries. Large fluctuations in the volume of freshwater discharged into Biscayne Bay and Florida Bay have adversely affected salinities and water quality to the detriment of their marine communities. The loss of water retention has also resulted in water shortages throughout the region, and it has been predicted that conditions will continue to deteriorate unless large-scale remediation is undertaken. As a result, the Everglades are now the focus of one of the world's most ambitious restoration efforts – the Comprehensive Everglades Restoration Plan (CERP) (USACE and SFWMD 1999).

The CERP is, in many ways, a massive re-engineering project, the goal of which is to restore more natural flows of water, including sheetflow (water flow that is not constrained by channels, moving instead across the ground in a slow-moving, sheet-like mass), improved water quality, and more natural hydroperiods in the south Florida ecosystem. The remedial actions contemplated by CERP have the potential to significantly alter salinity regimes, nutrient load, and water quality of Florida Bay. Historically, it was thought that the extremely low relief of land in the region (an altitudinal gradient of ~3 cm/km) combined with a highly complex system of shallow waterways slowed flow through the system to the point that water accumulated during one season was available for use in subsequent seasons (Browder 1976, Walters et al. 1992). This slow, continuous flow through heterogeneous habitat also permitted extraction of most nutrients, resulting in oligotrophic outflow of freshwater from the
Everglades into the adjacent coastal environment. Although CERP cannot completely restore these historical conditions, the recommended plan would create 73,350 ha of surface water storage area, equal to about 1.85 billion cubic meters, and would restore more natural flow mainly to the south and southwest through Taylor Slough and Shark River Slough in the Everglades National Park (USACE and SFWMD 1999). This is expected to increase the flow of oligotrophic fresh water into northeastern Florida Bay and provide more natural seasonal variation in salinity.

Because CERP is unprecedented, and its impacts on the surrounding estuarine and marine systems uncertain, several studies were undertaken, including the Florida Bay and Florida Keys Feasibility Study (FBFKFS). The goal of the FBFKFS was to evaluate the connections between the Everglades and Florida Bay, the Gulf of Mexico, and the Florida Keys’ marine ecosystem, and determine what modifications would be needed to successfully restore the water quality and ecological conditions of the Bay while maintaining or improving these conditions in the adjacent Florida Keys’ marine ecosystem. Central to the FBFKFS was a multi-level modeling exercise to simulate how different water deliveries to Florida Bay impact the water quality and the ecology of the bay and the Florida Keys. This chapter focuses on the likely effect of CERP on Caribbean spiny lobster (*Panulirus argus*) and the hard-bottom communities on which it depends in Florida Bay and the Florida Keys, as revealed by a highly detailed, spatially-explicit, agent-based simulation model.

*Panulirus argus* was chosen as a model organism for this project because of its economic and ecological importance. Since 1986, *P. argus* has consistently ranked as the first or second most valuable commercial fishery in Florida, alternating with pink
shrimp. The dockside value of the commercial lobster fishery varies between $20 and $30 million/yr (Harper 1995, Hunt 2000), which does not include its ancillary economic benefits such as the value of the large recreational sport diving fishery for lobster. Each year, over 150,000 people purchase permits to recreationally fish for lobster in south Florida, accounting for ~20% of the total recorded catch (Sharp et al. 2005).

Ecologically, *P. argus* is an important component of the Florida Bay marine ecosystem for several reasons. It is a locally abundant, benthic predator of a variety of gastropods, bivalves, crustaceans, echinoderms, and small fishes (Andree 1988, Herrnkind et al. 1988). Its juveniles also fall prey to a variety of even larger predators, comprising a major portion of the diet in many species (e.g., nurse sharks, bonnethead sharks, rays), some of which are important to sport (e.g., permit, bonefish) and commercial fisheries (e.g., gray snapper, grouper)(Smith and Herrnkind 1992). As both predators and prey, lobsters are thus an integral component of the trophic structure in southern Florida Bay.

Southern Florida Bay contains approximately 20% of the total hard-bottom habitat of the Florida Keys, and has been a significant nursery habitat for *P. argus*, supplying the nearby barrier reef system with new recruits (Bertelsen et al. 2009). Crucial to its role as a nursery habitat for lobsters is Florida Bay's sponge community, and, in particular, the large sponge taxa, like the loggerhead sponge, *Spheciospongia vesparium*, that provide shelter for vulnerable juvenile lobster. In some areas of Florida Bay, the densities of large sponges (those > 20 cm diameter) have exceeded three individuals per m$^2$ (Field and Butler 1994, Peterson et al. 2006). The emphasis on “southern Florida Bay” as spiny lobster habitat highlights another aspect of the ecological importance of juvenile lobsters as an indicator of ecosystem transition.
Lobsters are marine, not estuarine species, and thus only persist in southwestern Florida Bay at its juncture with the adjacent Florida Keys and Southeast Gulf Shelf marine ecosystems. Their presence in the northern and eastern portions of Florida Bay is limited by salinity and perhaps by habitat structure and postlarval availability (Field and Butler 1994, Robles et al. 2005). In addition, the sustainability of the Florida Keys’ population of spiny lobsters ultimately depends on recruitment of larvae (Butler and Herrnkind 1997), most of which probably arrive from elsewhere in the Caribbean (Lyons 1981, Silberman et al. 1994). Extreme salinities and temperatures are lethal to post-settlement larvae and early stage juveniles (Field and Butler 1994, Butler 2003) and can also cause loss of the sponge habitat that juveniles require for shelter from predation (Kohout and Kolipinski 1967; Butler unpublished data). Algal blooms also cause loss of habitat structure by precipitating mass sponge die-offs (Butler et al. 1995). Water delivery restoration efforts in Florida Bay may therefore affect lobsters directly via salinity and indirectly via the impact of salinity and water quality changes on shelter-providing sponges. Juvenile lobsters are thus indicators of ecological change in Florida Bay because they are sensitive to alterations in freshwater input to the system, as well as to changes in water quality that affect benthic habitat structure (Butler et al. 1995, Butler 2003).

The objective of this portion of my research was to determine the potential effects of Everglades restoration on spiny lobster populations and their nursery habitat in Florida Bay and the Florida Keys region through model simulations. Input data provided by FBFKFS on potential salinity, temperature, and cyanobacteria blooms in the region were used in a spatially-explicit, agent-based model describing lobster
recruitment and the die-off of common large sponges and octocorals. Thus, the model incorporated a multi-trophic level assemblage of species (sponges, octocorals, and lobster), but the focus of the model was the Caribbean spiny lobster. This very applied use of a spatially-explicit, agent-based lobster recruitment model demonstrates the practical use of such models to help guide resource management, which contrasts with its use in Chapter 3 where the focus is more theoretical.

METHODS

Only a few truly agent-based, spatially-explicit models exist for motile marine species (e.g. Hinckley et al. 1996, Hermann et al. 2001), and the model described herein is the only one developed for lobsters. Earlier versions of the model have been used to investigate: (a) the potential effect of a massive sponge die-off on lobster recruitment (Butler et al. 2005), (b) the consequences of temporal and spatial variation in postlarval supply on lobster recruitment (Butler et al. 2001), (c) the effect of nursery habitat structure and its geographic specificity on lobster recruitment (Butler et al. 2001), and (d) the potential evolutionary benefits of different types of social behavior and habitat structure on lobster recruitment (Dolan and Butler 2006). The model simulated the arrival of individual postlarval Caribbean spiny lobster and their subsequent daily settlement, growth, shelter selection, mortality, and movement (Fig. 1). Each lobster was individually represented in the model with regard to its location, size, age, and physiological stress in response to local salinity. I used 50 mm carapace length (CL) as the final size for estimation of recruitment because the dynamics of lobsters longer than
Fig. 1. Model flow diagram depicting the sequence of major processes in the model. Each simulated day begins by updating the environment, by reading new values for temperature, salinity, and cyanobacteria concentration for each modeled cell. Larger juvenile lobster then have the opportunity to move to another cell if the new salinity value is outside of their tolerance. Three distinct periods are depicted (nocturnal, crepuscular, and diurnal), and mortality is calculated independently within each period.
50 mm CL are complicated by the activities of the fisheries, specifically the use of juveniles between 50 mm and 70 mm CL as "live decoys" in traps (Lyons and Kennedy 1981, Hunt et al. 1986, Forcucci et al. 1994). In addition, over 90% of the lobsters that occur in Florida Bay are <50 mm CL; larger individuals move from the nursery to the ocean side of the Florida Keys in an ontogenetic migration, and so are unlikely to be directly impacted by changes in environmental conditions in the bay.

Lobster population dynamics played out on a spatial map of 2792 square contiguous 1 km² habitat cells that corresponds to the primary nursery habitat for *P. argus* in South Florida (Herrnkind et al. 1997b). The geographic region simulated encompasses most of the Florida Keys archipelago stretching from Key Largo to the Marquesas (Fig. 2). It is bounded to the south by the northern edge of Hawk Channel and to the north by a series of bathymetric features, including a line of carbonate mud banks in Florida Bay that limit postlarval transport (Field and Butler 1994) and depths > 3 m that limit postlarval settlement (Goldstein and Butler 2009) to the north of the Middle and Lower Keys. Thus, the area covered included most of the bay- and gulf-side spiny lobster nursery habitat and a narrow 1-2 km ocean-side strip of bottom that is also suitable nursery habitat. The dominant habitat type of each model cell was designated as seagrass, hard-bottom, open (i.e., unvegetated sand or mud bottom including non-emergent banks and channels through otherwise solid banks), or land (which includes emergent banks). These cell-specific habitat designations corresponded to the actual spatial distribution of these habitats in the region, based in part on geographic data from NOAA's Benthic Habitats of the Florida Keys Project (FMRI and NOAA 2000) and on
Fig. 2. Extent of the model region showing the habitat type of each cell. There were a total of 2792 inhabitable cells, of which 846 were hard bottom, 1696 were seagrass, and 250 were open (unvegetated) sand/mud.
Fig. 3. Hard bottom survey sites. More than 300 sites were surveyed by divers to ascertain benthic habitat type. On hard bottom sites, additional data were collected regarding habitat structure, including lobster density and potential lobster shelter density.
detailed diver-based field survey data collected from more than 300 sites throughout the Florida Keys (Fig. 3; Butler, unpublished data). Each seagrass and open cell in the model was considered a single, homogeneous habitat type. However, the habitat in hard-bottom cells contained additional structural details, including unlimited macroalgae for early benthic stage lobsters and realistic densities of several types of benthic structures that are used as shelter by larger juvenile lobsters, including: loggerhead sponges (*Spheciospongia vesparium*), vase sponges (*Ircinia campana*), other sponges (mostly stinker sponges, *Ircinia strobilina*, and grass sponges, *Spongia cheiris*), solution holes, octocoral-sponge complexes, and other shelters (mainly scleractinean corals). Densities of each shelter type were measured using belt transects on 109 hard-bottom sites in 2002 (Butler unpublished data). Ordinary kriging was then used to generate density surfaces that determined the numbers of each shelter type in the model's hard-bottom cells. For each shelter (i.e., individual sponge, coral, solution hole, etc.), the maximum number of lobsters that could simultaneously use the structure (lobster capacity) was determined by a random draw from the empirical distribution of maximum group sizes specific to that shelter type as observed at over 100 field sites throughout the Florida Keys (Butler and Herrnkind 1997, Herrnkind et al. 1997b).

Although differences in habitat structure among the model's spatial cells were indicative of those in the Florida Keys region when divided into 1 km² areas, the actual numerical representations of lobster dynamics and shelter abundances in each habitat cell are on a scale approximating a 1000 m² area, which matches that at which empirical data were obtained. In essence, I modeled lobster dynamics and habitat structure in each cell at an ecologically realistic scale (1000 m²) considered representative of the larger
Fig. 4. Overview of major factor and process interactions. Arrows denote the direction of effect. Harmful algal blooms only indirectly affected lobsters through their effect on the availability of sponges and octocorals used by lobster as shelters, whereas temperature and salinity have both direct and indirect effects on lobster. Both temperature and salinity directly impacted lobster mortality at extreme values, and temperature also had an indirect effect on lobster mortality through its effect on growth rates.
region (1 km²) it was meant to depict. This approach is similar to that used in forest
succession models that simulate every tree in a specified size plot within a region of
forest, rather than the entire forest (Shugart and West 1977). Had I chosen to simulate
the true number of lobsters in 1-km² cells, I would have needed to simultaneously
model billions of individuals, which is beyond the capability of current
microcomputers. Even so, at certain times there were more than 750,000 individual
lobsters in the model (immediately following a postlarval influx event), and each single
replicate of a 10-year simulation generated tens of billions of unique individuals.

Environmental Factors and Effects

Spatio-temporal changes in salinity and temperature, and exposure to harmful
algal blooms (HABs) are the environmental factors that influence local population
dynamics (e.g., growth, survival, movement) of lobster, as well as the survival of
sponges and octocorals that are important structural features of lobster nursery habitats
(Fig. 4). Therefore, in addition to habitat structure, each habitat cell was characterized
by temperature, salinity, and an indicator of cyanobacteria concentration. Each
simulated day, the values of these variables for each model cell were read from input
files generated by the FBFKFS (see Model Input: FBFKFS Scenarios for
Environmental Conditions, below) for each of the simulations described below. The
values of these variables were then used in stochastic functions governing their effects
on lobster and sponges.
Fig. 5. Survival of early benthic phase juvenile *P. argus* over typical ranges of temperature and salinity. The surface was fitted to weekly survival data from Field and Butler (1994). Early benthic phase juveniles are intolerant of salinities below 30 (on the Practical Salinity Scale) and of temperatures above 28 °C or below 20 °C.
Effect on Lobsters:

Temperature affects lobster growth, and the combination of extreme temperature and salinity also increases the probability of mortality for early benthic juveniles. Laboratory studies using temperatures between 18°C and 32°C and salinities ranging from 25 PSU to 50 PSU indicate that early benthic juvenile spiny lobsters are intolerant of salinity change and experience high mortality, especially at high summer temperatures (Witham et al. 1968, Field and Butler 1994). Weekly survival data from Field and Butler (1994) were used to derive a function describing the relationship of survival ($P_s$) to salinity (S) and temperature (T) (Fig. 5):

$$P_s = 123.6e^{\frac{1}{2}\left(\frac{T-24.39}{5.565}\right)^2 + \left(\frac{S-35.31}{8.587}\right)^2}$$

The survival and growth of larger juvenile lobsters were unaffected within this range of salinities; however, several studies (Lellis and Russell 1990, Forcucci et al. 1994, Sharp et al. 2000) have found that higher temperatures increase growth rates by reducing the intermolt interval. Baseline molt probability ($P_m$) was calculated as a function of lobster carapace length ($l$) and time since the most recent molt ($t$):

$$P_m = 0.00256 + \frac{0.9788}{1 + \left(\frac{t}{4.4256 + 0.8567l}\right)^{-1.7 + 0.4l}}$$

To simulate the effect of temperature, one of two temperature-dependent functions was used to modify the baseline molt probability, depending on lobster size:

$$P_{m} = P_m(0.3127119 - 0.0119446T + 0.0004570T^2 - 0.0000402T^{2.5} + 0.0000009T^3)$$

for lobster ≤ 35 mm CL, or
\[ P_m = P_m(0.4040059 - 0.0085638T + 0.0003440T^2 - 0.0000301T^{2.5} + 0.0000007T^3) \]

for lobster > 35 mm CL. For each lobster, a uniform random deviate was generated, and if the value was less than or equal to its calculated probability of molting, its size was increased according to the linear function \( \Delta l = 0.464 + 0.111l \).

Salinity extremes also alter activity levels of larger juveniles under laboratory conditions (Butler unpublished data). Lobsters were held in annular mesocosms in water with a salinity of 15, 25, 35, or 45 PSU. At the extremes (15 psu and 45 psu), lobsters nearly doubled their movement during the first night of exposure as compared to movement rates at normal salinity (35 psu). However, after the first 24 hours of exposure, their movements declined to the normal rate and then ceased, presumably as a result of exhaustion due to the increased metabolic demand of osmo- and ion regulation. At the less extreme level of hyposalinity (25 psu), lobsters also nearly doubled their movement rates but in this case maintained high levels of movement for 3 days.

Although the movements measured in this experiment are not the same as movement rates, they do reflect relative levels of activity. Therefore, I assumed that they are indicative of the relative probabilities of emigration of lobsters exposed to these salinities in the field. As modeled, the probability of movement among cells \( (P_M) \) was dependent on the habitat and shelter a given lobster was able to find and its carapace length:

\[
\begin{align*}
P_M &= -0.5 + (0.0250l) & \text{for lobsters in algal or hard-bottom crevice shelters} \\
P_M &= -0.275 + (0.0137l) & \text{for lobsters in seagrass} \\
P_M &= -0.05 + (0.0025l) & \text{for lobsters in open (sub-optimal crevice shelters)}
\end{align*}
\]
Lobsters subjected to salinities above 40 PSU or below 30 PSU were only half as likely to remain in their current habitat cell as those within that range. Additionally, movement probability was set to zero for lobsters subjected to salinities above 45 PSU or below 25 PSU for more than three consecutive days. Lobsters moving in response to salinity stress in the model followed the salinity gradient toward oceanic water, so moved to the adjacent cell with salinity closest to 35 PSU. If several adjacent cells were equally good, a destination was randomly selected from among those that were tied.

*Effect on Sponges and Octocorals:*

Although the focus of the model was lobster recruitment, it also predicted changes in the abundance of selected species of sponge and octocorals chosen because they were either: (a) the dominant structural features of hard-bottom communities (therefore important shelters for juvenile lobster); (b) species that represent important ecological guilds (e.g., fast growing, rapid colonizing “weedy” sponges vs. highly tolerant persistent species vs. slow growing, long-lived climax species); or (c) species of economic importance (i.e., commercial sponges). Changes in the sponge and octocoral components of habitat structure were driven solely by mortality associated with altered salinity, temperature, and harmful algal blooms (Fig. 4). A paucity of information on recruitment, growth, and natural mortality of the various sponge and octocoral species that occur in Florida Bay/Florida Keys hard-bottom communities precluded my modeling of the population dynamics of these species. Thus, the model was populated with realistic abundances and distributions of these species, and those populations were
assumed to be static unless exposed to salinity, temperature, or cyanobacteria
congestion regimes known, from laboratory and field studies, to be deleterious to
these species.

The salinity tolerance of five ecologically representative species of sponge
(logginghead, vase, brown branching, sheepswool, golfball) and two species of octocoral
were tested at typical summer and winter temperatures in Florida Bay (Butler
unpublished data). The patterns of mortality of sponges and octocorals was the same
whether the change in salinity was maintained for one week or altered for two days and
then returned to normal. The sponges varied in their tolerance to low salinity, although
none survived the 15 ppt treatment at winter temperatures and none survived any low
salinity during high summer temperatures. The least tolerant species was the
commercial sponge (*Hippospongia lachne*) and the most tolerant was the finger sponge
(*Ircinia sp.*). Both species of octocoral experienced 100% mortality at salinities below
35 ppt at all temperatures. Response surfaces were fitted to the data generated by these
experiments using Tablecurve 3D (Systat Software, Inc., ©2002). The best model for
each species was chosen using a combination of the coefficient of determination ($r^2$)
and visual inspection of the surfaces for continuity, smoothness, and simplicity (Fig. 6).
The weekly discrete probabilities generated by these functions were converted to
instantaneous rates, then to discrete daily probabilities. For each individual sponge or
octocoral in the model, a uniform random deviate was generated and compared to the
calculated probability. If the random number was higher than the calculated probability
of survival, the organism was removed from the model and any resident lobsters were
placed in the open habitat type.
Fig. 6. Sponge and octocoral survival versus temperature and salinity. In each case, over 37,000 models were fitted to empirical data by least squares. From those models with a coefficient of determination > 0.79, the qualitatively simplest surface lacking singularities was selected. Generally, loggerhead sponges were the most sensitive to lower salinities, and vase sponges were the least sensitive. Sponges other than loggerhead and vase were more sensitive to increased temperatures.
The effects of cyanobacteria blooms on sponges were simulated in a similar manner to the effects of temperature and salinity. Field data indicate that cyanobacteria concentrations in excess of $10^8$ cells/l are capable of killing several kinds of sponge, including loggerhead sponges, vase sponges and others, mainly *Ircinia* sp. (Butler et al. 1995, Phlips and Badyak 1996, Phlips et al. 1999). Harmful algal blooms killed loggerhead sponges at the lowest rate, whereas the vase sponge, several species of commercial sponges, and other similar-sized sponges (*Ircinia* sp.) all died quickly (Butler et al. 1995, Herrnkind et al. 1997b). The model accepts cell-state changes related to HABs similarly to the way it handles temperature and salinity in that an input file was used to define the spatial and temporal coverage of blooms. The effects of HABs on hard-bottom habitats were simulated by subjecting loggerhead sponges to a 0.0225% daily mortality rate, vase sponges to a 0.125% daily mortality rate, and by decrementing by 0.125% the abundances of other bloom-affected sponges each day and in each cell for which the cyanobacteria concentration exceeded the threshold. These rates were chosen to match die-off rates observed during the HAB that occurred in 1991–1992 (Butler et al. 1995, Herrnkind et al. 1997b). Octocorals (angular sea whip, purple sea plume) were not affected by HABs in the model because they appear to be unaffected by HABs of the type that have recently occurred in Florida Bay (Herrnkind et al. 1997b).

**Model Input: FBFKFS Scenarios for Environmental Conditions**

The South Florida Water Management District supplied ten scenarios that they deemed likely to reflect the range of conditions that might result from the proposed restoration project based on hydrodynamic modeling results using the Environmental
Table 1. Summary of simulation scenarios. The combinations of environmental input data used for each simulation scenario are shown. EFDC (Environmental Fluid Dynamics Code) is the hydrodynamic model that generated the baseline data.

<table>
<thead>
<tr>
<th>Scenario Name</th>
<th>Salinity</th>
<th>Temperature</th>
<th>Cyanobacteria Bloom</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baseline</td>
<td>EFDC</td>
<td>EFDC</td>
<td>None</td>
</tr>
<tr>
<td>Historic HABs</td>
<td>EFDC</td>
<td>EFDC</td>
<td>Fall 1990 and Fall 1991</td>
</tr>
<tr>
<td>Annual HABs</td>
<td>EFDC</td>
<td>EFDC</td>
<td>Every fall</td>
</tr>
<tr>
<td>Smoothed Salinities</td>
<td>30 day moving average of EFDC values</td>
<td>EFDC</td>
<td>None</td>
</tr>
<tr>
<td>Global Warming</td>
<td>EFDC</td>
<td>EFDC + 2°C</td>
<td>None</td>
</tr>
<tr>
<td>Small Salinity Decrease</td>
<td>EFDC–0 to 5 PSU gradient</td>
<td>EFDC</td>
<td>None</td>
</tr>
<tr>
<td>Large Salinity Decrease</td>
<td>EFDC–0 to 10 PSU gradient</td>
<td>EFDC</td>
<td>None</td>
</tr>
<tr>
<td>Large Salinity Decrease with</td>
<td>EFDC–0 to 10 PSU gradient</td>
<td>EFDC</td>
<td>Every Fall</td>
</tr>
<tr>
<td>Annual HABs</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small Salinity Increase</td>
<td>EFDC + 0 to 5 PSU gradient</td>
<td>EFDC</td>
<td>None</td>
</tr>
<tr>
<td>Large Salinity Decrease</td>
<td>30 day moving average of EFDC values–0 to 5 PSU gradient</td>
<td>EFDC</td>
<td>None</td>
</tr>
<tr>
<td>Smoothed Salinities</td>
<td>5 PSU gradient.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Fluid Dynamics Code (EFDC) (Hamrick 1996). Each of those scenarios provided a set of spatially- and temporally-explicit data (i.e., "expected conditions) for salinity, temperature, and cyanobacteria bloom that I then used as input to my model. The ten scenarios that I modeled were as follows and summarized in Table 1.

1. **Baseline**: This scenario depicted the system given no changes to hydrodynamics and no disturbances leading to HABs. The EFDC modeled temperature and salinity of the region for the period from 1/1/1990 to 12/31/1999. Cyanobacteria concentrations were set below the HAB threshold for the entire simulated period. This scenario was intended to represent the best possible outcome if no modifications to the current hydrologic regime are made. However, it should be noted that HABs did occur in Florida Bay during this period, as previously noted and modeled in the next scenario.

2. **Historic HABs**: This scenario incorporated the baseline salinity and temperature values, but cyanobacteria concentrations in the simulation were set to mimic the timing and spatial extent of the cyanobacteria blooms that occurred in Florida Bay in 1991–1992 (Fig. 7). In 1991, the bloom began November 15 and ended January 2, 1992. In 1992, the bloom began October 1 and ended January 27, 1993. After that, no more blooms were simulated and the scenario was identical to the baseline.

3. **Annual HABs**: This scenario also used the baseline salinity and temperature values, but cyanobacteria concentration was set to mimic 1991 bloom timing (November 15 – January 2) every year. This was envisioned as a possibility if restoration efforts resulted in more disturbance to sediment in Florida Bay or
higher sediment load in the water entering the bay.

(4) Smoothed Baseline Salinities: Healthy wetlands buffer the system from rapid releases by recharging soil storage and also buffer against drier periods by slowly releasing the stored water. Therefore, smoother salinity patterns should be expected with upstream wetland restoration. This scenario simulated that using a 30-day running average of the baseline salinities. The baseline temperatures were used unmodified, and cyanobacteria concentrations were kept below the bloom threshold.

(5) Global Warming: The temperatures used in the baseline simulations were increased uniformly by 2 degrees to simulate a possible regional effect of global climate change in a manner extrapolated from observed sea surface temperature increases associated with other partially enclosed water bodies that are influenced by large freshwater inputs (Belkin 2009). Baseline salinities and cyanobacteria concentrations were used unmodified.

*Decreased and Increased Salinity Scenarios:* Because the majority of the area within the model boundary is oceanic and not expected to be strongly affected by water management changes and restoration, increased freshwater flow into the system was modeled using east-west gradients superimposed on the values generated by the EFDC (McDonald personal communication). Three gradients were generated simulating (1) a large increase in freshwater flow with maximum reduction by 10 units on the practical salinity scale (PSU), (2) a small increase in flow with a maximum decrease of 5 PSU, and (3) a small increase in salinity with a maximum change of 5 PSU. To create each gradient
of salinity change, the magnitude of the change in each modeled cell ($\Delta$) was calculated as a function of the column number ($x$) of the cell from west-most ($x = 1$) to east-most ($x = 183$) and the maximum magnitude of the change ($D_{max}$), using the equation $\Delta = D_{max}(x - 55/128)^4$. In addition, because the region affected by the plume of estuarine water leaving Florida Bay is unknown, it was assumed that the water around Key West was unaffected and fluctuations in salinity in that area were assumed to be indicative of oceanic conditions. Therefore, salinity was modified only in cells in which the standard deviation of daily mean salinity exceeded that of Key West as modeled (1.16 PSU). The resulting modified gradient is shown in Figure 8.

(6) Small Salinity Decrease: Chlorophyll and temperature were set to baseline levels in this scenario. Baseline salinities were decreased following an east-west gradient with a maximum magnitude of 5 PSU.

(7) Large Salinity Decrease: This scenario was similar to the Small Salinity Decrease scenario in that cyanobacteria concentration and temperature were set to baseline levels, and salinity was adjusted downward using an east-west gradient. However, the maximum change in salinity was 10 PSU.

(8) Large Salinity Decrease with Annual HABs: For this scenario, temperatures were set to baseline levels, and salinity was handled as for the Large Salinity Decrease scenario ($D_{max} = 10$ PSU). Chlorophyll was set to mimic 1991 bloom timing every year from November 15 to January 2, as in the Annual Blooms scenario.

(9) Small Salinity Increase: Salinity was adjusted upward by a maximum of 5 PSU following the same gradient of effect used for the Large and Small Salinity Decrease scenarios. Chlorophyll and temperature were set to baseline levels.
(10) Large Salinity Decrease Smoothed: This scenario was similar to the Large Salinity Decrease Scenario, but instead of adjusting from the Baseline scenario, the adjustments were applied to the Smoothed Salinity scenario levels. As before, cyanobacteria concentrations and temperature were set to baseline levels.

Fig. 7. Extent of simulated cyanobacteria blooms. The southwestern extent of the bloom-affected region corresponds to the extent of the severe HABs that occurred in 1991–1992. Chlorophyll-α fluorescence indicated that higher concentrations of cyanobacteria occurred north of this area, but that region does not contain significant lobster habitat, so was not modeled.
Fig. 8. Salinity change gradient. The grayscale ramp represents the magnitude of the change to the baseline salinities generated by the EFDC for model scenarios that simulated small changes in salinity. For simulation of decreased salinities, the EFDC values were adjusted downward by the amount indicated. For simulation of large changes in salinity, the maximum change was 10 PSU, but declined to 0 PSU over the same extent. Apparent gaps (empty cells) within the gradient are cells occupied by land or emergent banks.
Each of the ten Everglades restoration scenarios described above were simulated in 10 replicate model runs, each of 10 years duration, beginning January 1, 1990 and ending December 31, 1999. Each set of replicate runs used a random seed value for the random number generator used by the model’s subroutines, resulting in some variability in the results among replicate simulations. The number of replicate runs needed to detect a 5% change in total lobster recruitment to the 50 mm CL size class was determined using a Visual Jackknife technique (Confalonieri et al. 2007). Briefly, the results of twenty replicate runs of a control scenario that used seasonal default temperature values, uniform oceanic salinity of 35 psu, and no HABs were analyzed. The optimal number of replicates was determined by resampling the data, systematically taking larger subsamples to find the subsample size at which the rate of change of the subsample means was negligible. For each subsample size, 500 sets of subsamples were drawn to determine the mean and variance, resulting in the Visual Jackknife optimal estimate of six replicates. The minimum number of replicates necessary to detect a 1% difference from the mean at the $\alpha = 0.05$ level was also calculated using an iterative procedure based on Student’s T, yielding an identical result to the Jackknife procedure. Because the variability of the results under other scenarios was not known, the replicate estimate was rounded up to ten to ensure sufficient replication.

Analyses

The potential output from the model is enormous, both in terms of the diversity of parameters that can be produced as well as the spatial (each cell to whole domain), temporal (per day to entire simulation period), and demographic (individual to
population) details. Therefore, I produced estimates most relevant to resource managers concerned with the potential impact of Everglades restoration measures, including: (a) the number of lobsters recruiting to >50 mm CL (the pre-recruits for the fishery), (b) the number of lobsters within each 5 mm CL size class (from 5–50 mm CL), and (c) the abundances of four structure-forming hard-bottom taxa: loggerhead sponge, vase sponge, other large sponges, and octocoral-sponge complexes. These data were produced and outputted for each cell in the model, simulation day, and replicate simulation.

The effect of the restoration effort was expected to be more strongly evident in the area immediately adjacent to the Everglades, so the data were aggregated into two regions, Florida Bay and the remainder of the Florida Keys (Fig. 9), to provide more powerful comparisons. However, the lobster populations within the two regions were not independent of each other because of the potential for movement between them. Further, the experimental treatments (FBFKFS scenarios) were not independently applied to each region. Therefore, recruitment in Florida Bay and recruitment in the remaining Florida Keys constituted multiple responses and were analyzed using MANOVA to determine if the system as a whole was affected by any of the scenarios. The applications of salinity changes, temperature changes, and HABs were not performed in an orthogonal design, but were the expected results of complex system-wide changes to hydrology within the Everglades; therefore, this was treated as a one factor design (FBFKFS Scenario) with ten levels. Habitat structure and lobster population structure were examined graphically to better understand the mechanisms that lead to significant changes in lobster recruitment.
Fig. 9. Geographic regions used for data aggregation. The area labeled Florida Bay includes a narrow strip of nearshore habitat on the ocean side of the Florida Keys that is not part of Florida Bay per se; however, this area is highly connected to Florida Bay by water and animal movement. The southwestern extent of the Florida Bay Region was chosen to encompass the southwestern extent of HABs that have occurred in the area.

**RESULTS**

Differences among the FBFKFS scenarios in simulated lobster recruitment per square kilometer in Florida Bay and in the Florida Keys were analyzed using MANOVA. The assumptions of the analysis were checked as follows. Graphical evaluation of the raw
data and analysis of Mahalanobis distances revealed no likely univariate or multivariate outliers (distances greater than $\chi^2_{2,0.99} = 9.210$). Univariate normality of the residual values was evaluated using the Shapiro-Wilk Test, which showed no significant deviations ($W=0.990$, $P=0.652$, and $W=0.996$, $P=0.992$ for Florida Bay and the Florida Keys, respectively). Because the number of replicates of each scenario was relatively small ($n=10$), the Henze-Zirkler Test, which performs well with small sample sizes (Mecklin and Mundfrom 2004), was used to test the assumption of multivariate normality, and the data also met this assumption ($t_p =0.308$, $P=0.101$). Box’s M test failed to reject homogeneity of covariance matrices ($M=39.316$, $P=0.120$); however, MANOVA is robust to this violation given equal sample sizes. Levene’s Test of homogeneity of error variances revealed marginally significant heterogeneities among variances for both dependent variables ($F_{9,90}=2.413$, $P=0.017$ and $F_{9,90}=2.111$, $P=0.036$ for Florida Bay and the Florida Keys, respectively); therefore, Pillai’s Trace was used to evaluate the significance of the MANOVA, and a more conservative alpha value ($\alpha=0.01$) was chosen for follow-up tests, as recommended by Tabachnick and Fidell (2007). The assumption of linearity was not checked because the MANOVA result was significant ($V=1.243$, $F_{18,180}=16.437$, $P<<0.0005$).

To better understand the recruitment results, Profile Analysis was used to follow up the MANOVA (Tabachnick and Fidell 2007). Using Pillai’s Trace, the profiles deviated significantly from parallelism ($V=0.436$, $F_{9,90}=7.717$, $P<<0.0005$) and flatness ($V=0.771$, $F_{9,90}=303.437$, $P<<0.0005$). The levels test (the effect of FBFKFS Scenario averaged among regions) was also significant ($F_{9,90}=33.179$, $P<<0.0005$). Taken together, these analyses indicate that the environmental changes reflected in the FBFKFS scenarios
significantly affected recruitment in both regions, but did so in different ways.

Profile plots (Fig. 10) and multiple comparisons within each geographic region (Tukey’s HSD, Table 2) were used to identify the specific differences among the scenarios. In Florida Bay, the three HAB scenarios resulted in the lowest recruitment. The combination of the large salinity decrease and HAB had the lowest of those and was significantly different from the large salinity decrease alone. All of the other scenarios were grouped together with the Baseline scenario. In the rest of the Florida Keys, the only scenario that resulted in significantly different simulated lobster recruitment was the Global Warming Scenario, with a 6% increase above baseline recruitment.

Sponges are also important components in the benthic communities simulated by this model and their survival may affect lobster survival. However, they were not the focus of this study, and their demography was only incompletely represented in the model. Therefore, I elected to analyze sponge survival separately from lobster recruitment as a means of understanding the patterns of lobster recruitment under the various FBFKFS scenarios. Additionally, because the FBFKFS scenarios applied salinity changes differently to the two regions, and because the profile analysis of lobster recruitment indicated that the two regions behaved differently, I analyzed sponge survival in each region separately, and used a Bonferroni corrected alpha (\(\alpha=0.025\)) to control Type 1 error. The results for vase sponge mortality were conservative because the equation used underestimated their mortality, but, based on vase sponge abundance, this error only resulted in a maximum 1% difference in sponge community structure, well within the error likely from field survey estimates of sponge abundance and laboratory estimates of sponge mortality.
Fig. 10. Profile plots of simulated lobster recruitment and sponge survival for each FBFKFS scenario. The scenarios are arranged in order of increasing lobster recruitment in the Florida Bay region. Within Florida Bay, HABs had the strongest effect on simulated lobster recruitment and sponge survival. Decreases in salinity also reduced lobster recruitment and sponge survival in Florida Bay. Salinity variability in the ranges modeled had no appreciable effect on simulated lobster recruitment, whereas reducing salinity variance led to higher sponge survival even at lower salinities. In the rest of the Florida Keys, only the Global Warming scenario resulted in significant differences in lobster recruitment (an increase) or sponge survival (a decrease). Means are plotted ± 1 S.E. Error bars for sponge survival are not shown because their ranges were too small.
Table 2. Multiple comparisons of lobster recruitment in Florida Bay and the Florida Keys. Scenario labels are as follows: AH=Annual HABs, B=Baseline, GW=Global Warming, HH=Historic HABs, LSD=Large Salinity Decrease, LSDH=Large Salinity Decrease with Annual HABs, SmB=Smoothed Baseline Salinities, SmLSD=Smoothed Large Salinity Increase, SSD=Small Salinity Decrease, and SSI=Small Salinity Increase. Homogeneous subsets at the $\alpha=0.01$ level were found using Tukey’s HSD within each region, and are indicated by a horizontal line beneath similar values.

Simulated lobster recruitment (1000/km$^2$) in Florida Bay

<table>
<thead>
<tr>
<th>Scenario</th>
<th>LSDH</th>
<th>AH</th>
<th>HH</th>
<th>LSD</th>
<th>SmLSD</th>
<th>SSD</th>
<th>GW</th>
<th>B</th>
<th>SSI</th>
<th>SmB</th>
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<tbody>
<tr>
<td>Mean</td>
<td>31.93</td>
<td>34.64</td>
<td>36.01</td>
<td>38.35</td>
<td>38.58</td>
<td>39.34</td>
<td>41.9</td>
<td>42.17</td>
<td>42.22</td>
<td>42.75</td>
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Simulated lobster recruitment (1000/km$^2$) in the Florida Keys

<table>
<thead>
<tr>
<th>Scenario</th>
<th>LSD</th>
<th>SmLSD</th>
<th>B</th>
<th>LSDH</th>
<th>AH</th>
<th>SSI</th>
<th>HH</th>
<th>SSD</th>
<th>SmB</th>
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</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>44.56</td>
<td>44.88</td>
<td>45.16</td>
<td>45.17</td>
<td>45.46</td>
<td>45.59</td>
<td>45.62</td>
<td>45.68</td>
<td>45.82</td>
<td>48.22</td>
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</table>

In Florida Bay, the residual distributions of the proportions of sponges surviving each ten-year replicate were significantly heteroscedastic (Levene’s Test: $F_{9,90}=10.710$, $P<<0.001$). Only one group deviated significantly from normality at the $\alpha=0.05$ level (Shapiro-Wilk Test: $W=0.797$, $df=10$, $P=0.013$), but due to the small sample sizes, the residuals were also analyzed pooled and were found to deviate significantly from normality (Kolmogorov-Smirnov Test: $K=0.106$, $df=100$, $P=0.008$). No transformation was found to sufficiently improve the fit of the data to these assumptions, so they were rank transformed, and a one-factor ANOVA was performed on the ranks. The ANOVA was highly significant at the $\alpha=0.025$ level ($F_{9,90}=483.9$, $P<<0.0005$) (Table 3). To
identify homogeneous subsets within the results, I used Tukey’s HSD (Table 4), which revealed only two groups, one at the extreme low end of the range of survival proportions, consisting of the two scenarios in which annual HABs were simulated, and one at the extreme high end of the range of survival proportions, consisting of the Smoothed Baseline Salinities Scenario (SmB) and the Small Salinity Increase Scenario (SSI). All of the other scenarios were significantly different from each other. Both smoothed salinity scenarios resulted in significantly higher sponge survival than the respective high variance scenarios. The smoothed scenarios also resulted in higher sponge survival than the Small Salinity Decrease Scenario (SSD). The salinities of the smoothed scenarios had fewer extreme events than their respective unmodified scenarios, and the salinities used in the SmB Scenario included fewer extreme values than the SSD Scenario. However, the Smoothed Large Salinity Decrease Scenario (SmLSD) consistently had more extreme values than the SSD Scenario, and nevertheless resulted in higher sponge survival. This apparent contradiction is possible because of the spatial structure of the salinity effects. That is, the extreme salinities of the smoothed scenario occurred more consistently in the same places than did the extreme salinities of the SSD Scenario. Because there was no sponge recovery, damage was cumulative and permanent in this model; so, once the sponges in a given cell were destroyed, successive salinity extremes in that cell could do no more damage. Salinity extremes in the SSD Scenario, on the other hand, were not as spatially restricted, resulting in more widespread (simulated) damage in Florida Bay, in spite of those events not being as extreme as those in the Smoothed Large Salinity Decrease Scenario.

The situation was quite different in the Florida Keys, in which sponge survival
exceeded 97% in every scenario. Both scenarios that used smoothed salinities (Smoothed Baseline Salinities and Smoothed Large Salinity Decrease) resulted in 100% survival in every replicate; therefore they were excluded from statistical analysis. The results of the remaining scenarios met the assumptions of normality whether analyzed by scenario or pooled (K=0.084, df=80, P>0.200). Likewise, the residual distributions were homoscedastic (F_{7,72}=1.124, P=0.358), therefore a model I one-factor ANOVA was performed on the raw data. The relatively small differences in the proportions of sponges surviving were nonetheless highly significant (F_{7,72}=443.401, P<0.0005). Tukey’s HSD, with α=0.025, was used to identify homogeneous subsets (Fig. 11). The Global Warming scenario was the only one that was not grouped with the Baseline scenario. It also had the lowest proportion of sponges surviving (97.01%). The remaining scenarios fell into two groups with four of the seven scenarios occurring in both groups. As previously noted, both scenarios that used 30-day moving averages to smooth salinities resulted in 100% sponge survival even though one of those also decreased salinities. Because that decrease was imposed as a gradient with larger impacts eastward (i.e. Florida Bay), the maximum magnitude of the salinity change was small, even at the eastern extreme of the Florida Keys region as defined here.
Table 3. Analysis of variance of sponge survival in Florida Bay and the Florida Keys. In both cases, there were significant differences in sponge survivorship using a Bonferroni correct alpha level of 0.025.

**Florida Bay**

<table>
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<tr>
<th>Source</th>
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<th>MS</th>
<th>F</th>
<th>P</th>
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<td>483.983</td>
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<td>error</td>
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<td>18.742</td>
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<tr>
<td>Total</td>
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**Florida Keys**

<table>
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<th>MS</th>
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<tr>
<td>error</td>
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</tr>
<tr>
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<td>79</td>
<td></td>
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</table>
Table 4. Multiple comparisons of sponge survival in Florida Bay and the Florida Keys.
Scenario labels are as follows: AH=Annual HABs, B=Baseline, GW=Global Warming, 
HH=Historic HABs, LSD=Large Salinity Decrease, LSDH=Large Salinity Decrease with 
Annual HABs, SmB=Smoothed Baseline Salinities, SmLSD=Smoothed Large Salinity 
Increase, SSD=Small Salinity Decrease, and SSI=Small Salinity Increase. Homogeneous 
subsets as indicated by Tukey’s HSD are indicated by a horizontal line beneath similar 
values. The Small Salinity Increase and Smoothed Baseline Salinities were not included in 
the analysis of sponge survival in the Florida Keys region because they resulted in 100% 
survival with no variance. They are shown separated from the other scenarios by a vertical 
bar.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>LSDH</th>
<th>AH</th>
<th>HH</th>
<th>LSD</th>
<th>SSD</th>
<th>GW</th>
<th>SmLSD</th>
<th>B</th>
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<tr>
<td><strong>Mean</strong></td>
<td>0.466</td>
<td>0.468</td>
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<td>0.821</td>
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<table>
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<th>LSDH</th>
<th>SSD</th>
<th>B</th>
<th>AH</th>
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<th>SSI</th>
<th>SmB</th>
<th>SmLSD</th>
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<tbody>
<tr>
<td><strong>Mean</strong></td>
<td>0.9701</td>
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</table>
Fig. 11. Effect of salinity variability on simulated sponge survival in Florida Bay and the Florida Keys. All scenarios resulted in significantly different survival from each other and from the Baseline scenario in Florida Bay, but there were no significant differences in survival in the rest of the Florida Keys. B = Baseline Scenario; SmB = Smoothed Baseline; LSD = Large Salinity Decrease; SmLSD = Smoothed Large Salinity Decrease. In each case, n=10. Bars are the mean percent change in sponge survival relative to Baseline sponge survival ± 1 S.E.

Harmful Algal Blooms

The scenarios that included HABs were the only ones that resulted in significantly reduced lobster recruitment relative to the Baseline Scenario (Fig. 10 and 12). In the
Fig. 12. Effect of HABs on simulated lobster recruitment in Florida Bay and the Florida Keys. B=Baseline, HH=Historic HABs, AH=Annual HABs, LSD=Large Salinity Decrease, LSDH=Large Salinity Decrease with Annual HABs. Bars are the mean percent difference in recruitment relative to baseline recruitment ± 1 S.E. Letters above each bar identify homogenous subsets (Tukey’s HSD, α=0.05 level) in Florida Bay. There were no significant differences in recruitment in the rest of the Florida Keys.

Historic HABs and Annual HABs scenarios, this was caused entirely by loss of habitat in Florida Bay, i.e., more than 50% mortality of structure-providing sponges. Lobster recruitment in the scenario that included both a large salinity decrease gradient and HABs was not significantly different from the other two, but was lower nonetheless, suggesting
a weak deleterious effect of the salinity decrease on lobsters. In the rest of the Florida Keys, these three scenarios produced slightly higher recruitment than the Baseline Scenario, though the increases were not significant at the $\alpha=0.01$ level, suggesting that movement of lobsters out of Florida Bay occurred, but did not contribute significantly to the low recruitment values.

**Global Warming**

The Global Warming Scenario was the only one that resulted in a significant increase in simulated lobster recruitment in the Florida Keys west of Florida Bay. The resulting 6.8% increase in lobster recruitment can be partially explained by increased growth rates, which reduced exposure to simulated size-selective predation. However, the same increase in recruitment did not occur in the simulation of Florida Bay, even though the 2°C temperature increase was applied uniformly over the model domain. Simulated temperatures in Florida Bay ranged from 15°C to 35°C in the Global Warming Scenario, with a mean of 27°C, whereas the rest of the Florida Keys ranged from 13°C to 33°C with a mean of 25°C. This, together with widely fluctuating salinities in Florida Bay, at times would have caused higher rates of mortality for EBJ lobster. At the same time, the Global Warming Scenario also resulted in a decline of the simulated sponge population of more than 6% in Florida Bay, but only 1% in the rest of the Keys relative to the Baseline Scenario populations. The loss of sponges may have increased the movement rates of larger, mobile juvenile lobster out of the area, increasing the population of the rest of the Keys. Thus, the combination of locally increased EBJ mortality and emigration of larger juveniles from the bay could have compensated for increased growth rates in
one region while increasing the population in the other.

**Salinity Increases**

With a small average increase in salinities, lobster recruitment was not significantly different from that of the Baseline Scenario in either Florida Bay or the rest of the Florida Keys. Sponge survival in Florida Bay was significantly higher (5.8%) with increased salinities than that of the Baseline Scenario, whereas in the rest of the Florida Keys, there was no significant difference, though survival was slightly higher. The increase in sponge survival was a direct result of the functions chosen to model sponge response to salinity and temperature, because these functions increase monotonically at high salinities. The lack of a significant increase in lobster recruitment with a significant increase in sponge survival implies that the lobster population simulated in the Baseline Scenario was not significantly limited by shelter availability.

**Salinity Decreases**

All of the scenarios for salinity decreases resulted in significantly lower simulated sponge survival in Florida Bay than in the Baseline Scenario. (The Large Salinity Decrease with HABs Scenario had the lowest sponge survival, but that result was presented with the other HAB scenarios and is omitted here.) The largest reduction in sponge survival, 17.9%, occurred in the Large Salinity Decrease Scenario (LSD), which had 87.4% of the survival in the Baseline scenario. None of these scenarios resulted in a statistically significant reduction of lobster recruitment compared to the Baseline
Fig. 13. Effect of salinity increase and decreases on simulated lobster recruitment in Florida Bay and the Florida Keys. B=Baseline, SSI=Small Salinity Increase, SSD=Small Salinity Decrease, LSD=Large Salinity Decrease. Bars are the mean change in lobster recruitment relative to baseline recruitment ± 1 S.E. None of the observed differences were statistically significant at the $\alpha=0.05$ level.

Scenario (Tukey’s HSD, $P > 0.16$ in all cases) (Fig. 13), but mean reductions in recruitment ranged from 6.7% under the Small Salinity Decrease scenario to 9.1% in the LSD Scenario. In the rest of the Florida Keys, salinity decreases produced no significant differences in sponge survival or lobster recruitment.
Salinity Variability

As previously noted, the Large Salinity Decrease (LSD) and Baseline scenarios resulted in lower sponge survival in both regions than the corresponding smoothed salinities scenarios (SmLSD and SmB, respectively). This was also true of lobster recruitment in both regions, though the differences between the smoothed scenarios and their counterparts were small (0.6% and 1.4% for the LSD and Baseline scenarios, respectively, in Florida Bay, and 0.7% and 1.5% for the LSD and Baseline scenarios, respectively, in the Florida Keys) and not statistically significant. In the rest of the Florida Keys, the scenarios with smoothed salinities resulted in 100% simulated sponge survival, which, though not amenable to statistical analysis, would certainly be biologically significant if it occurred in the real system.

DISCUSSION

The Comprehensive Everglades Restoration Plan is one of the world’s most ambitious engineering efforts, intended to restore natural ecosystem function and services to a land area of nearly 1 million hectares. To evaluate the potential impacts of proposed freshwater management scenarios in the Everglades on the marine communities within Florida Bay and the Florida Keys, I conducted simulations incorporating changes in salinity, temperature, and harmful algal blooms expected under different Everglades restoration plans, provided by the Florida Bay and Florida Keys Feasibility Study (FBFKFS).

My results suggest that returning the flow of freshwater in the Everglades to more
"natural" pre-development conditions is likely to be detrimental to truly marine taxa, such as spiny lobsters and sponges, which currently occupy the transitional region between Florida Bay and the Florida Keys. Simulated juvenile lobster abundance declined 6–24% in Florida Bay in scenarios where salinity either decreased alone or in combination with algal blooms. The most severe decline in lobster recruitment occurred when salinity was lowest in conjunction with annual HABs. Only about one-third of the decline was attributable to the salinity decrease, which directly influenced lobster mortality and movement rates and indirectly led to higher mortality through habitat destruction. Harmful algal blooms accounted for the majority of the decline in lobster recruitment, though their impact on the simulated lobster population was entirely indirect. Higher temperatures and salinities had little or no impact on lobsters in Florida Bay, but higher temperatures increased simulated juvenile lobster recruitment in the Florida Keys by 6.8%. Higher temperatures also increased simulated sponge survival; however, in most of the other scenarios, sponges were more negatively impacted than lobster. Most notably, the abundance of sponges in Florida Bay declined by 52.1–53.4% in simulations with HABs, and decreased salinities alone led to simulated sponge die-offs, ranging from 8.6–17.9%. Clearly, the most influential factor examined in these simulations with regard to both lobster and sponge survival was the presence or absence of HABs.

Since the early 1990s, hard-bottom communities in south-central Florida Bay have experienced episodes of sponge die-off tied to blooms of cyanobacteria (*Synechococcus sp.*) that blanketed the region for months at a time (Butler et al. 1995, Phlips and Badylak 1996, Herrnkind et al. 1997b, Phlips et al. 1999). The physiological mechanisms underlying the sponge die-offs are still not known (Lynch and Phlips 2000),
but the lethal effect is clear. For example, following the HABs that occurred in 1992 and 1993, no sponges remained on 27 survey sites that previously supported high densities of large sponges (Butler et al. 1995). Although the causes of the HABs in Florida Bay are not entirely known (Melesse et al. 2008, Briceño and Boyer 2010, Goleski et al. 2010), a complex picture is emerging, involving different sources of limiting nutrients, particularly phosphorus, the influence of fluctuating salinities on the interaction of the diatom and cyanobacteria populations in the plankton, and positive feedback from the continuing loss of filter-feeders, particularly loggerhead and vase sponges (Peterson et al. 2006). Circumstantial evidence suggests that blooms of the type occurring in southwestern Florida Bay may be triggered by re-suspension of sediment-bound phosphorus caused by anthropogenic or natural physical disturbances. Rudnick et al. (2006) found a strong correlation between hurricane activity preceded by road construction and mangrove removal, peak total phosphorus, and a HAB that persisted from 2005-2006 in eastern Florida Bay. The blooms that occurred in 1991-1993 were apparently precipitated by a mass die-off of seagrasses (mainly *Thalassia testudinum*) (Robblee et al. 1991, Butler et al. 1995) that was possibly caused by a combination of salinity and temperature stress (Zieman et al. 1999, Koch et al. 2007), sulfide poisoning from overcrowding (Carlson et al. 1994, Koch and Erskine 2001, Borum et al. 2005), and infection by *Labyrinthula* sp., a slime mold-like protist (Durako and Kuss 1994). Fluctuations in salinity may also play a role in shifts in microplankton dominance. Richardson (2004) found that, over the range of typical salinities in most of Florida Bay (10–50%), diatoms outcompete cyanobacteria in terms of growth of biomass. However, large hypersaline fluctuations (>61%) such as those that occur in the northern and north-
central parts of the bay (Boyer et al. 1999) result in reductions of diatom populations and a competitive release of cyanobacteria due to their greater tolerance for extreme salinities. This pattern of shifting dominance between cyanobacteria and diatoms was also directly observed in Florida Bay in the fall of 1993 (Phlips and Badylak 1996).

In addition to these bottom-up controls, there is evidence that the loss of top-down regulation may play a role in promoting cyanobacteria HABs in Florida Bay. Beyond their role as shelter for juvenile lobsters and other cryptic species, sponges also alter planktonic communities and biogeochemical cycles through their filtering activities, and their demise in Florida Bay may be responsible for changes in water chemistry, nutrient cycling, and microplanktonic assemblages. Prior to the die-off, loggerhead and vase sponges comprised 69% of the total sponge biomass in the region (Sweat and Stevely 2005), both of which are capable of removing a wide range of micro- and picoplankton from the water column, including Synechococcus sp. (Lynch and Phlips 2000, Peterson et al. 2006). Based on estimates of the sponge distribution prior to the initial die-off, field estimates of sponge filtration rates, and their own laboratory-based filtration estimates, Peterson et al. (2006) calculated that the sponge community of central Florida Bay could completely filter the water column in three days, whereas the surviving community required 15 d. Although their suggestion that no other factor is needed to explain the recurring HABs in Florida Bay is extreme, an order of magnitude difference in grazing pressure could make the region more conducive to HABs. A similar pattern of effects occurred with the removal of oyster culture racks from Tapong Bay, Taiwan. In that case, removal of the dominant filter feeder from the system, Crassostrea gigas, led to a 43% increase in mean phytoplankton biomass and 39-100% decrease in the mean biomass of
most benthic invertebrates and fishes (Lin et al. 2009). Similarly, the decline of the northern quahog, *Mercenaria mercenaria*, in the waters of Long Island, New York, is thought to have had a releasing effect on the alga *Aureococcus anophagefferens*, resulting in brown tides (Cerrato et al. 2004). Coincidentally, the estimated turnover rate of bay water by *M. mercenaria* populations prior to the advent of the brown tides (3 d; Kassner 1993) is the same as that estimated for the sponge communities of central Florida Bay before the 1991 die-off. Even if the sponge die-off is not the sole cause of HAB formation in Florida Bay, the loss of sponges appears to set up a positive feedback loop, allowing the recurrence and spread of HABs, a phenomenon that might be common to recurring HABs worldwide (Sunda et al. 2006). In addition, many of these sponges host large and diverse microbial communities (Taylor et al. 2007, Weisz et al. 2008), which are capable of a variety of metabolic processes, including photosynthesis (Cheshire and Wilkinson 1991, Usher 2008), nitrogen fixation (Wilkinson et al. 1999), and ammonia oxidation (Steger et al. 2008). Several species of sponge found in the region are also of commercial importance, so their loss due to water quality changes associated with CERP may have economic as well as ecological ramifications.

Unfortunately, the sponge community of Florida Bay and the Middle Keys has not recovered. Additional HABs occurred in 1994 and 1995, also originating in central Florida Bay, but not extending as far west as the 1992–93 bloom, and these may have suppressed sponge recruitment (Butler et al. 1995). By 1997, loggerhead sponges in the waters around Long Key had recovered to ~25% of their original abundance, apparently through regrowth from surviving basal disks that were not detectable by earlier surveys (Stevely and Sweat 2002). Surveys undertaken between 2001–2005, ten years and more
after the initial mass mortalities, still found total sponge abundances around Long Key at only 39.5% of their pre-bloom levels, and no evidence of recruitment of loggerhead or vase sponges to that area (Stevely and Sweat 2002, Butler 2007). The total abundance of sponges, including *S. vesparium*, at the periphery of the bloom near Marathon had recovered, but the mean of loggerhead sponge sizes was significantly smaller than before the die-off, and *I. campana* were completely absent (Stevely and Sweat 2002). Thus, it appears that recovery of the sponge community by natural processes may require decades without additional disturbances. Unfortunately, another HAB blanketed the region in the fall of 2007, again resulting in massive sponge die-offs (Butler unpublished data).

The effect of these HABs on the lobster population has also been significant. A shelter enhancement study begun in 1991, prior to the sponge die-off, provided Butler et al. (1995) with the opportunity to compare the distribution and shelter use of juvenile *P. argus* before and after the die-off in a natural experiment. They found that, after the sponge die-off, lobster were redistributed among the remaining shelters in each site, but more lobster were found on sites in which shelter had been artificially enhanced with artificial dens than had been on those sites before the die-off, and fewer lobster remained on sites in which shelters had not been artificially enhanced. Additional surveys throughout the Florida Keys found that the juvenile lobster population declined overall by ~5% (Herrnkind et al. 1997b). Fishery landings in 1994–1996 were no lower than landings prior to the die-off, and it is hypothesized that large cohorts of postlarvae that arrived in 1992-1994 (three times normal; Hunt unpublished data, cited in Herrnkind et al. 1997b) offset the additional mortality that had been expected due to habitat loss. Since then, postlarval supply to the Florida Keys has remained highly variable, with annual
values ranging from 60–122% of the long-term mean from 1995–2007 (J. Hunt, Florida Fish and Wildlife Conservation Commission, Marathon, FL, unpublished data). However, adult stocks declined in spite of a regulatory program that reduced the number of traps in the fishery from ~851,000 in the 1991-92 fishing season to ~550,000 in 2002 (Ehrhardt and Deleveaux 2009). So, it appears that the HABs are both a symptom and a cause of system-wide deterioration. If the CERP causes additional HABs, it seems unlikely that Florida Bay will return to being a productive nursery ground for Florida’s spiny lobster population. However, the simulation results also suggest that the system will not necessarily deteriorate much further with regard to lobster and sponges, as long as the area affected by HABs does not continue to grow. The bulk of the damage has already been done, and sponge populations may recover, albeit slowly, in the absence of HABs.

Lobster were not directly affected by the algal bloom, however, in the absence of HABs, my simulation results suggest that decreasing salinities would reduce juvenile lobster recruitment in Florida Bay by 6–9%. Postlarval and early benthic phase (EBJ) *P. argus* are stenohaline, not tolerating salinities very different from 35 PSU in combination with temperature extremes above 33°C or below 18°C (Field and Butler 1994), and some portion of the predicted increase in mortality is due to this direct effect of salinity. However, some of these scenarios also resulted in sponge mortality of up to 11.8% more than the Baseline Scenario, so even in the absence of HABs, some portion of the increase in lobster mortality may be due to habitat loss. To tease apart the direct and indirect effects of reduced salinity on *P. argus*, it is instructive to examine the results from the Large Salinity Decrease and the Smoothed Large Salinity Decrease scenarios. Both of these resulted in nearly identical lobster recruitment in Florida Bay (38,350 and 38,580
lobsters/km², respectively), but different sponge survival (82.1% and 92.4%, respectively). At the same time, there was no increase in recruitment from the Florida Keys, which might have indicated increased emigration from the affected area. This suggests that the simulated lobster population in Florida Bay was not significantly shelter-limited, in spite of the loss of sponges, therefore, the 9% reduction in lobster recruitment under these scenarios is the result of direct mortality, which may have ramifications with regard to possible recovery of the lobster population.

In the face of the decline in the Caribbean spiny lobster population of south Florida, it has been suggested that enhancement of the population might be accomplished by supplementing natural shelter with artificial structures (Eggleston et al. 1992, Herrnkind et al. 1997a, 1999), and some might lobby for this option as applied to situations arising from CERP in which shelters for juvenile lobster are lost (e.g., sponge die-offs). In habitats with low shelter densities, such as seagrass meadows, *P. argus* will aggregate in large numbers in artificial shelters (sometimes referred to as "casitas") and fishermen in some countries (e.g., Cuba, Belize, Mexico, Bahamas; the practice is illegal in Florida) use such structures to fish for lobster (Lozano-Álvarez et al. 1994, Herrnkind et al. 1997a, Briones-Fourzán and Lozano-Álvarez 2001). However, the potential for enhancement of lobster populations with artificial structures is not without ecological risks. For example, aggregations of lobster in casitas attract predators that increase mortality rates of small juvenile lobster within 30 m of the structure (Eggleston et al. 1992), as is the case near large natural dens (e.g., solution holes) that harbor large predators such as nurse sharks and grouper (Schratwieser 1999). The local increase in lobster abundance may also lead to prey depletion (Edelist and Spanier 2009), especially
for small juvenile lobster that do not forage far from shelter. Artificially aggregating lobsters may also increase the transmission of disease, the subject of the next chapter. To avoid the deleterious effects of large aggregations, the use of smaller artificial structures has been suggested (Herrnkind et al. 1997a). Such structures more closely mimic the size range of natural crevices (e.g., those under sponges) used by juvenile lobster in south Florida. These structures can enhance the local population of small juveniles, but it has not been unambiguously demonstrated that this translates to enhancement of the larger population (Butler and Herrnkind 1997, Herrnkind et al. 1999). However, if the CERP results in a large change in salinity, I hypothesize that any effort to mitigate the loss of lobsters via placement of artificial shelters in Florida Bay will have no effect on the lobster population.

The CERP’s goal is to return a more historically natural hydrology to the Everglades. If successful, it appears that this will also return much of Florida Bay to a more estuarine, brackish-water state. Unfortunately, this can also be expected to negatively impact marine species in Florida Bay, such as lobster, sponges, and some game fish (e.g., bonefish, permit). Thus, the goal of the CERP is in apparent conflict with the interests of some user groups. However, it is important to realize that any perception that the current conditions in Florida Bay are natural are likely the result of a shifting baseline (sensu Pauly 1995). Unfortunately, there is little information regarding historical ecological conditions in Florida Bay prior to the re-engineering of the Everglades (Labisky et al. 1980, Fourqurean and Robblee 1999). In the case of *P. argus*, bully net fishing occurred in Florida Bay as early as the 1940s, but the main reasons the fishery was not established earlier apparently were because the area was inaccessible and there
was little market for lobster outside of the fin-fishing industry of Key West (Labisky et al. 1980). Nonetheless, there are some indications, mainly from isotopic studies of corals, that salinities in Florida Bay are currently higher, on average, and vary more widely than they did before 1900 (Fourquean and Robblee 1999). Fortunately, although the CERP is likely to negatively affect current fisheries in Florida Bay, my results also suggest that the impact to the rest of the Florida Keys will be minimal.
CHAPTER III

THE EFFECTS OF BEHAVIOR AND HABITAT STRUCTURE ON DISEASE DYNAMICS IN A SOCIAL MARINE ORGANISM: THE CARIBBEAN SPINY LOBSTER

INTRODUCTION

Parasites can induce novel host behaviors that increase the parasite’s fitness, sometimes in spectacular ways. A parasitoid wasp, *Hymenoepimecis sp.*, induces its orb-weaving spider host to produce a unique, cocoon-like web to protect its larvae (Eberhard 2000). Crickets infected by larvae of the nematomorph *Paragordius tricuspidatus* are driven to “suicide” by entering water required by the adult hairworm (Thomas et al. 2002). Other parasites alter host behavior to enhance transmission by increasing contact rates among hosts. For instance, the presence of the rabies virus in neural tissue often instigates an immune response in its mammalian host that acts on the limbic system, increasing aggression, thus enhancing transmission by increasing bite rates (reviewed by Klein 2003, Thomas et al. 2005). Similarly, a wide range of vector-borne infectious organisms increase the vectors’ bite rates, increasing transmission among definitive hosts (reviewed by Lefèvre and Thomas 2008). Parasites that require multiple hosts to complete their life cycle often alter host behavior or morphology in ways that enhance transmission to a subsequent host (Lefèvre and Thomas 2008, Lagrue and Poulin 2010). Coral polyps infected by metacercariae of the trematode *Podocotyloides stenometra*, for example, become pink and swollen, unable to withdraw into their calcareous shelter,
rendering them more attractive to and vulnerable to predation by butterfly fish, the parasite’s definitive host (Aeby 2002).

The innate behavior of host organisms can also affect the spread of parasites. It has long been hypothesized that sociality brings with it certain costs, including increased vulnerability of the host population to diseases (Alexander 1974, Möller et al. 1993, Altizer et al. 2003). For directly transmitted diseases, it is usually assumed that the contact rate of the social host is greater than that of the asocial host. Thus, under the mass-action assumption (sensu Anderson and May 1985), the force of infection is higher in social organisms. Similarly, larger group sizes correlate with increased disease prevalence and infection intensity due to increased contact rates (Cote and Poulin 1995). However, host behavior can also act as a barrier to disease. Moribund ants of the species *Temnothorax unifasciatus* infected with *Metarhizium anisopliae*, a communicable fungal pathogen, leave their nests to die in isolation (Heinze and Walter 2010). Similarly, in the eusocial honeybee, *Apis mellifera*, sickened individuals remove themselves from the colony and do not return, resulting in altruistic suicide (Rueppell et al. 2010). Even the lethargy that accompanies many bacterial and viral infections may reduce transmission to susceptible conspecifics by reducing contact rates.

In most studies of host behavioral changes in response to parasites, the focus has been on the behavior of the infected host. There are few examples where the behavior of uninfected, susceptible hosts changes in ways that may reduce parasitism. Chronic Bee Paralytic Virus in eusocial bees (*A. mellifera*) elicits a non-stinging, but aggressive behavior in uninfected hive-mates, in which they chew the body surface of the infected individual until nearly all their setae are removed. This is hypothesized to reduce parasite
load (Waddington and Rothenbuhler 1976, Drum and Rothenbuhler 1983, 1985). Uninfected female mice increase anxiety-associated behaviors in response to the odor of males parasitized by the nematode, *Heligmosomoideps olygyrus*, or the protozoan, *Eimeria vermiformis*, which is hypothesized to elicit avoidance of parasitized males (Kavaliers et al. 1998). Even normally gregarious Caribbean spiny lobster, *Panulirus argus*, avoid cohabitation of communal dens with conspecifics infected by a lethal virus, *Panulirus argus* Virus 1 (PaV1) (Behringer et al. 2006, Butler et al. 2008, Lozano-Alvarez et al. 2008, Behringer and Butler 2010). Thus, in the evolutionary arms race between pathogens and their hosts, changes in host behavior in response to communicable parasites and pathogens act to alter the small-scale spatial organization of the host population so as to reduce host-to-host contacts. Yet, for most species other factors, such as habitat structure, may play a larger role in shaping the evolutionary trajectory of the host-parasite relationship.

It is increasingly recognized that spatial structure contributes substantially to disease dynamics and can affect disease virulence and transmissibility. At a basic level, virulence, the pathogenicity of a disease-causing agent, is tied to its within-host reproductive rate. In directly transmitted diseases, transmissibility is a function of both the contact rate of infected and susceptible hosts and the amount of the pathogen available for transmission. Thus, virulence and transmissibility of a disease can be positively related because virulence increases the amount of the pathogen available per contact. However, there is a trade-off in that increasing pathogen virulence tends to decrease contact among hosts by increasing host morbidity and death. Because spatial structure within host populations further limits dispersal and, therefore, contact among
hosts, it is a powerful selective force for reducing the virulence of transmissible pathogens. Barriers to dispersal of hosts may also be barriers to the parasite, thus a highly virulent disease that otherwise would be maintained in a large population, instead decimates the smaller, local population without further spread (Pie et al. 2004, Boots and Mealor 2007). Patchiness in host populations is intimately tied to habitat structure, which can thus be a stabilizing force in disease dynamics. Rapid changes in habitat structure, then, might lead to changes in the host population structure or host behavior that destabilize established host-parasite relationships (Hess 1996, McCallum and Dobson 2002). Such is the situation in Florida Bay and the Florida Keys (USA), where recent perturbations to the nursery habitat for juvenile Caribbean spiny lobster has diminished the availability of shelter for lobsters, potentially affecting the dynamics of a pathogenic viral disease present in this social species.

The Caribbean spiny lobster has a life cycle typical of other palinurid lobsters, and indeed similar to that of other coastal species with complex life cycles. Their planktonic larvae disperse in the open sea and after 6–8 mos (Goldstein et al. 2008), settle in shallow (< 3 m), back-reef hard-bottom habitat and reside solitarily for a few months within patches of macroalgae (Marx and Herrnkind 1985). Coinciding with a shift in shelter use from the ubiquitous macroalgae to more discrete crevice shelters, the juvenile lobsters undergo an ontogenetic shift in sociality (Childress and Herrnkind 1996). That is, they become social and aggregate in crevices provided by large sponges, corals, and rocky holes scattered in hard-bottom areas. Aggregating by day within crevices provides spiny lobsters with protection from diurnal predators via cooperative defense (Childress and Herrnkind 1997, 2001, Dolan and Butler 2006). Nevertheless, in the Florida Keys,
group sizes tend to be small, with about half of juvenile *P. argus* sheltering individually (Childress and Herrnkind 1997).

*Panulirus argus* is also the only known host of PaV1, the first-known viral pathogen for any species of lobster (Shields and Behringer 2004). The virus mainly affects juveniles, generally with a low prevalence of ~5–7%, but focal outbreaks have been observed with local prevalence exceeding 30% (Shields and Behringer 2004, Lozano-Álvarez et al. 2008). It is lethal to juvenile lobsters, with mortality of infected juveniles >90%, although infected adults appear asymptomatic (Behringer et al. 2010). Juvenile lobsters become infectious 6–8 weeks post-infection, and death typically occurs within 8–11 weeks (Behringer et al. 2006, Butler et al. 2008). The virus is highly contagious among early benthic phase juveniles, but susceptibility to infection decreases with lobster size (Butler et al. 2008). As previously stated, juvenile *P. argus* avoid infected conspecifics by refusing to enter crevices occupied by infected lobster, excluding infected lobster from already occupied crevices, or by abandoning the shelter when an infected conspecific enters (Behringer and Butler 2010). The specific olfactory cue used by susceptible lobster is unknown, but the onset of avoidance appears to precede infectiousness by approximately two weeks (Behringer et al. 2006).

In nature, co-occupancy of dens by infected and uninfected juvenile lobsters occurs rarely if ever (Behringer et al. 2006), and the high proportion of solitary individuals may be, in part, a consequence of disease avoidance. However, environmental changes that reconfigure nursery habitats may also alter the spatial structure of the lobster population in ways that may diminish the effectiveness of social aversion in retarding the spread of PaV1. For example, in the fall of 2007, a dense bloom of cyanobacteria
(Synechococcus sp.) swept over an area of ~ 500 km² in Florida Bay, decimating the sponge community in an important lobster nursery, similar to an event last recorded in 1990-1991 (Butler et al. 1995). Following the sponge die-off, the only shelters for lobsters that remained were small coral heads and solution holes, into which all of the juvenile lobsters then aggregated in this now shelter-limited environment. Consequently, mean group size increased from 1.74 (±1.48 sd) lobsters per shelter before the sponge die-off to 7.25 (±4.68 sd) lobsters per shelter after the sponge die-off (Butler, unpublished data). Fishing activities too can change the spatial structure of lobster populations in ways that may affect disease dynamics. In many areas of the Caribbean, especially Mexico, Cuba, and the Bahamas, large artificial structures (referred to as "casitas") are deployed on the seafloor by fishermen to aggregate lobsters for ease of capture, and infected individuals have been found with susceptible lobsters in casitas (Lozano-Álvarez et al. 2008). These and other kinds of disturbances or activities that change habitat structure and thus the spatial structure of animal populations may also alter the dynamics of disease transmission.

In this study, I reconfigured an individual-based ecological model of the juvenile P. argus population of the Florida Keys (Butler et al. 2001, Butler 2003, Butler et al. 2005, Dolan and Butler 2006) to explicitly incorporate changes to nursery habitat, PaV1 disease processes, and lobster behaviors to investigate their respective importance for the spread of the PaV1 disease in nature. I systematically varied the timing of the onset of avoidance of infected lobsters relative to their conversion to the infectious state and contrasted those results with the behavior of the system in the absence of the avoidance behavior. I also examined the effects of a degrading nursery habitat on the P. argus-PaV1
system by comparing disease dynamics in an environment with an intact habitat structure to that in a depauperate landscape corresponding to that now present in portions of Florida Bay impacted by the sponge die-off. Lastly, I investigated the effects of two hypothesized density-independent processes that may contribute to higher incidence and prevalence rates in the asocial early benthic juvenile phase of *P. argus*. The first, is a "black box" model that produces infections in algal phase juveniles at a constant daily rate, representative of an alternate host that may be a prey item, waterborne transmission to algal phase juveniles, or simply another unknown source for transmission. The second scenario was one in which postlarvae were infected on their arrival to the coastal system, as might be expected if PaV1 is vertically transmitted (i.e., there is transmission of PaV1 from adult lobsters to their progeny) or if larvae are infected while in the plankton.

**METHODS**

The model I used was an extension of one previously developed to explore the effects of habitat disturbance (Butler et al. 2005) and spatial variation in postlarval supply (Butler et al. 2001) on recruitment of *Panulirus argus*, the Caribbean spiny lobster. Detailed descriptions of the original model are presented in Butler et al. (2001), Butler (2003), and Butler et al. (2005). Minor modifications were made to the habitat structure algorithm and to the lobster growth, migration, and postlarvae distribution algorithms, which are described in detail in the appendix. The model is object-oriented and has been developed in C++ using Microsoft Visual Studio 2005 and the associated MFC Libraries. The random number generator used is the Mersenne Twister from the Boost Libraries version 1.35. The model currently runs on personal computers using the Microsoft
Windows 2000, XP, Vista, and Windows 7 operating systems. Here I briefly describe the model’s general structure, then provide a detailed description of the elements that were altered for these simulations, specifically habitat structure, lobster growth, shelter selection, and movement, disease susceptibility and transmission, and the time course of the disease and its effects on lobsters.

The model simulated the arrival of individual postlarval Caribbean spiny lobsters and their subsequent daily settlement, growth, shelter selection, mortality, and movement until they reached 50 mm carapace length (CL). Each lobster was individually represented in the model with regard to its location, size, age, and physiological stress in response to local salinity. I used 50 mm CL as the final size for estimation of recruitment because the dynamics of lobsters longer than 50 mm CL are complicated by the activities of the fisheries, specifically the use of juveniles between 50 mm and 70 mm CL as "live decoys" in traps (Lyons and Kennedy 1981, Hunt et al. 1986, Forcucci et al. 1994). In addition, over 90% of the lobsters that occur in Florida Bay are <50 mm CL; larger individuals move from the nursery to the ocean side of the Florida Keys in an ontogenetic migration, and so are unlikely to be directly impacted by changes in environmental conditions in the bay.

**Habitat Structure**

The spatial structure used for these simulations was the same as that used to investigate the effects of Everglades Restoration in Chapter 2 (see Figures 2 and 3). More specifically, lobster population dynamics played out on a spatial map of 2792 square contiguous 1 km² habitat cells that corresponded to the primary nursery habitat for $P$. 
argus in South Florida (Herrnkind et al. 1997b). The geographic region simulated encompassed most of the Florida Keys archipelago stretching from Key Largo to the Marquesas (Fig. 2). It was bounded to the south by the northern edge of Hawk Channel and to the north by a series of bathymetric features, including a line of carbonate mud banks in Florida Bay that limit postlarval transport (Field and Butler 1994) and depths >3 m that limit postlarval settlement (Goldstein and Butler 2009) to the north of the Middle and Lower Keys. Thus, the area covered included most of the bay- and gulf-side spiny lobster nursery habitat and a narrow 1-2 km ocean-side strip of bottom that is also suitable nursery habitat. The dominant habitat type of each model cell was designated as seagrass, hard-bottom, open (i.e., unvegetated sand or mud bottom including non-emergent banks and channels through otherwise solid banks), or land (which included emergent banks). These cell-specific habitat designations correspond to the actual spatial distribution of these habitats in the region, based in part on geographic data from NOAA's Benthic Habitats of the Florida Keys Project (FMRI and NOAA 2000) and on detailed diver-based field survey data collected from more than 300 sites throughout the Florida Keys (Fig. 3; Butler, unpublished data).

Each seagrass and open cell in the model was considered a single, homogeneous habitat type. However, the habitat in hard-bottom cells contained additional structural details, including unlimited macroalgae for early benthic stage lobsters and realistic densities of several types of benthic structures that are used as shelter by larger juvenile lobsters, including: loggerhead sponges (*Spheciospongia vesparium*), vase sponges (*Ircinia campana*), other sponges (mostly stinker sponges, *Ircinia strobilina*, and grass sponges *Spongia cheiris*), solution holes, octocoral-sponge complexes, and other shelters
(mainly scleractinean corals). Densities of each shelter type were measured using belt transects on 109 hard-bottom sites in 2002 (Butler unpublished data). Ordinary kriging was then used to generate density surfaces that determined the numbers of each shelter type in the model's hard-bottom cells. For each shelter (i.e., individual sponge, coral, solution hole, etc.), the maximum number of lobsters that could simultaneously use the structure (lobster capacity) was determined by a random draw from the empirical distribution of maximum group sizes specific to that shelter type as observed at over 100 field sites throughout the Florida Keys (Butler and Herrnkind 1997, Herrnkind et al. 1997b).

Although differences in habitat structure among the model's spatial cells were indicative of those in the Florida Keys region when divided into 1 km² areas, the actual numerical representations of lobster dynamics and shelter abundances in each habitat cell were on a scale approximating a 1000 m² area, which matches that at which empirical data were obtained. In essence, I modeled lobster dynamics and habitat structure in each cell at an ecologically realistic scale (1000 m²) considered representative of the larger region (1 km²) it was meant to depict. This approach is similar to that used in forest succession models that simulate every tree in a specified size plot within a region of forest, rather than the entire forest (Shugart and West 1977).

However, an important change was made to the way the model handled lobster use of shelters to accommodate the observed changes in group structure that followed the sponge die-off in 2007. To allow lobster aggregation sizes following sponge die-off in the model to approach observed values, the holding capacities of any undamaged structures remaining after bloom damage occurred were systematically increased. The increased
capacity was calculated based on the total loss of shelter capacity, the number of lobsters that would be unable to find shelter as a result, and the maximum allowable group size, as follows. On each day that sponge mortality occurred in a cell, any unused shelter capacity in the surviving structures was subtracted from the amount of loss. The lower value of that result or the number of lobsters in the cell in excess of the current unused capacity was taken as the additional shelter capacity needed. This capacity was then added by iteratively selecting a shelter at random and increasing its capacity by one lobster, until the total capacity needed was reached, subject to the limit that no shelter could have a post sponge die-off capacity that was more than four times its original capacity. If all of the remaining shelters reached their maximum capacity, no additional capacity was added.

Lobster Biological Processes and Behavior

The model of lobster biology and behavior took place within a daily time step that was composed of a sequence of processes that mimicked daily activity patterns of real lobster (Fig. 14). The details of processes not affected by disease, including influx and settlement, and the algorithms governing the simulation in the absence of disease are presented in Appendix A. Here I have focused on the ways the model was modified to simulate disease effects on growth, movement, and shelter selection and detailed the modes of PaV1 transmission and the time course of the disease.
Fig. 14. Conceptual diagram of the *P. argus*-PaV1 model. Solid arrows indicate the flow of control. Dashed arrows indicate processes affected by disease. Polygons drawn with a heavy border are processes that were added or modified for these simulations.
Growth

Growth was modeled as a true arthropod process in the sense that both an intermolt interval and growth increment were simulated, resulting in discrete, stepwise size increases. Probability of molting varied with lobster size, time since the previous molt, and temperature. In the late stages of PaV1 infection, lobsters typically become moribund, fail to groom themselves, and cease molting; therefore, I modified the growth algorithm such that infected lobster ceased molting during the course of the disease. The exact timing between exposure and cessation of molting is unknown, therefore I made the simplifying assumption that molting ceases when the lobster becomes infectious (defined below).

Shelter Selection and Movement

The algorithm for shelter selection assigned a probability value to each available structure that was weighted by the rank order of preference of the focal lobster for the shelter type and the biomass of lobsters in it. The weighted values were scaled such that their sum is 100%, and a uniform random draw then determined which shelter the lobster chose. Thus, the algorithm accounted for the lobster’s size-specific preferences for certain shelter types (Butler et al. 2005) and the attraction to conspecifics. Here, the biomass of resident lobsters was assumed to be proportional to the strength of the conspecific odor plume (Ratchford and Eggleston 1998, Nevitt et al. 2000). If there were no available shelters, the lobster was assigned to the “open” shelter type, which
corresponded to diel observations of lobsters attempting to hide by pressing against structures or clinging to bits of macroalgae.

Laboratory-based movement assays suggest that newly infected lobsters move at similar rates as uninfected lobsters, but as the disease progresses, infected lobsters become increasingly sedentary (Behringer et al. 2008). Although these simple assays gauged relative activity levels, not rates of emigration or shelter switching, I assumed that they qualitatively reflect these rates. I made a further simplifying assumption that movement rates remain unchanged until an infected lobster becomes infectious. After this state change, the probability of emigration was set to zero and the lobster no longer changed shelter unless forced out by another lobster. This is consistent with our anecdotal observations of the behavior of lightly and severely infected lobsters, but potentially introduced a bias in that simulated infected lobsters initially emigrated at higher rates than they would if a smooth function had been used to decrease their movement throughout the course of the disease.

Additionally, if the susceptible residents of the den chosen by an infected lobster detected the infection, they excluded the infected lobster with a probability of

\[ P = 1 - (1 - P_{\text{excl}})^n, \]

where \( P_{\text{excl}} \) is a constant uniform probability of exclusion by an individual resident, and \( n \) is the number of susceptible residents whose sizes are within 20 mm CL of the focal lobster’s size. This is consistent with behaviors observed during laboratory-based den competition experiments between healthy and diseased individuals (Behringer and Butler 2009). If the infected lobster was excluded from its chosen shelter, it was allowed to initiate another shelter search, subject to the limitation that no lobster could initiate a
shelter search more than three times on any given day. The search limit was required both to restrict the amount of time a lobster could spend searching before sunrise and to prevent an infinite loop of search and exclusion. On the other hand, if a detectably infected lobster successfully occupied a den containing susceptible conspecifics, or if an infected lobster became detectable while sharing a den with susceptible conspecifics, each susceptible lobster had a constant probability, $P_{esc}$, of abandoning the shelter and initiating a shelter search.

The general shelter search algorithm was further modified if a susceptible lobster attempted to occupy a den but detected a PaV1 infected lobster within it. In this case, the focal lobster had a constant uniform probability, $P_{avoid}$, that it would reject the shelter and continue searching. The rejected shelter was removed from the available shelters, and the indices of attractiveness of the remaining shelters were re-scaled to 100%. The searching lobster was allowed to proceed until either an acceptable shelter was found or all available shelters were rejected. If the search did not result in an acceptable shelter, the lobster was placed in the “open” shelter category.

The Epizootiological Model

In this agent-based model, disease transmission occurred based on specific interactions between unique individuals. To accomplish this, stochastic functions were developed, determining individual susceptibility to infection, the amount of virus to which a susceptible lobster was exposed during an interaction, and the time course of the disease in each individual. Three additional mechanisms for infecting lobsters independent of individual interactions were also developed. First, initial disease
prevalences in each cell were achieved by infecting randomly chosen individuals until user-supplied target prevalences were met. Initial PaV1 prevalence for each habitat cell were randomly drawn from a discrete probability distribution function constructed from prevalences observed at 66 sites from June-August 2002 (Butler, unpublished data).

Second, early benthic juveniles residing in macroalgae could be infected with a constant daily probability, simulating an unknown density independent mechanism. Third, individual postlarvae in newly arriving monthly cohorts could be infected to reach a targeted prevalence, simulating possible exogenous infection either by vertical transmission or planktonic infection of larvae. The details of these mechanisms follow.

**Susceptibility and Transmission**

Little is known about how susceptibility to PaV1 changes with lobster size or age, although transmission studies have demonstrated that transmission diminishes markedly with lobster size (Butler et al. 2008). Early benthic juveniles are extremely susceptible, whereas adults, here defined as those lobsters ≥65 mm CL, rarely if ever display symptoms of infection although recent results indicate that 11% of adult lobsters in the Florida Keys test positive for PaV1 infection (Behringer et al. 2010). Therefore, relative size-dependent susceptibility (S) was modeled by a linear function passing through the point 99% at 5 mm CL and decreasing to 0% at 65 mm CL. Lengths were converted to the equivalent biomass (m), resulting in

\[ S = -0.0041m + 0.99 \]  

I assumed that the amount of virus shed by any given lobster is dependent on its infectious state and is directly proportional to its size. Because actual numbers of virions
produced by infectious lobsters have not been measured quantitatively, I used the biomass of the lobster as a relative measure of the dose it would produce. Likewise, I assumed that the effective dose required to infect a susceptible lobster is dependent on its size. To date, quantification of the dose-response curve has not been possible; therefore, I modeled dose-response as a simple size-dependent threshold effect. If the dose of virions produced by a lobster of any given size is equal to the effective dose required to infect a lobster of the same size, then the probability of infection from any given exposure to one or more infectious lobsters is

\[ P = 1 - (1 - S) \frac{\sum m_i}{m_s} \] (2)

where \( S \) is the size-based susceptibility from equation 1, \( m_i \) is the mass of an infectious lobster to which the focal susceptible lobster is exposed, and \( m_s \) is the mass of the focal lobster. This relationship was generalized to allow an asymmetrical relationship between dose produced and the effective dose for a given size of lobster by inclusion of a constant of proportionality, here denoted as \( \kappa \):

\[ P = 1 - (1 - S) \frac{\sum m_i}{\kappa m_s} \] (3)

The resulting response surface is shown in Figure 15.

Although it might seem reasonable that susceptibility also depends on the condition of the lobster (e.g. stress level, nutritional state, etc.), the only study to date of these effects failed to show any significant contribution of lobster "condition" on its susceptibility to PaV1 infection (Behringer et al. 2008). Therefore, lobster condition had no effect on viral transmission in the model. In all cases the minimum exposure time required for successful infection by contact was modeled as one day of co-occupancy. This exposure time may be shorter than the time actually required, given that the shortest
Fig. 15. Probability of PaV1 transmission by infectious lobster size and susceptible lobster size. Generally, susceptibility to PaV1 is higher for smaller lobster. The dose of virions received by the susceptible lobster is based on the cumulative mass of all infectious lobsters to which it is exposed. The “equivalent infectious lobster carapace length” is the size of an individual lobster that would produce the same dose of virions as that same mass composed of one or more smaller lobster. Also, note that, although lobsters less than 15 mm CL are shown on the graph, very few lobsters of those sizes would be in crevice shelters, thus would neither be exposed nor contribute to the exposure of other lobsters by this mechanism.
exposure time tested in laboratory-based studies was three days (Butler unpublished data). If so, the bias introduced would enable the disease to spread more easily in the model than it would in reality.

**Time Course of the Disease**

For each individual lobster the time course of development of the disease was characterized by three quantities: the time between infection and conversion to the infectious state, production of a detectable infected cue, and death. The functions governing time to death and time to infectiousness were determined by parametric survival analyses using two-parameter exponential distributions of the form $P = 1 - e^{-(t-\delta)\lambda}$ (Lee and Wang 2003), where $\lambda$ is the shape parameter and $\delta$ is the threshold value below which it can be guaranteed an event will not occur. This particular model was chosen because it is one of the simplest and most commonly used parametric distributions for survival analysis; it fit the data sufficiently well in both cases; and is easily manipulated in a program, unlike nonparametric methods like Kaplan-Meier. The models were fitted to data from Butler et al. (2008) (Table 5, Fig. 16). To be certain

<table>
<thead>
<tr>
<th>Function</th>
<th>$\lambda$</th>
<th>$\delta$</th>
<th>$r^2$</th>
<th>df</th>
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<td>25</td>
<td>0.94</td>
<td>39</td>
</tr>
<tr>
<td>Time to Death</td>
<td>0.01242</td>
<td>41</td>
<td>0.88</td>
<td>39</td>
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</table>
Fig. 16. Cumulative probability of becoming infectious and of disease-induced mortality with time. Lines are calculated cumulative probabilities based on two-parameter exponential survival functions. Plotted points are the observed cumulative proportions of individuals that became symptomatic of PaV1 infection (open circles) and those that died (filled circles) of a group of 40 experimentally infected individuals. The observations also include censored observations (withdrawn from the study before a state change was observed).

that time to death was not biased from inclusion of uninfected lobsters, only those that exhibited disease symptoms or in which infection was later detected by PCR were included in that analysis.

To model lobster response to the avoidance cue, I assumed that production of the
cue, presumably some chemical product of cellular breakdown in the infected lobster, is independent of emission of the virus, although it seems to occur up to four weeks prior to a lobster becoming infectious (Behringer et al. 2006). Therefore, the time at which an infected lobster became detectable was determined by an exponential cumulative density function with the same shape parameter as that determining the time to infectiousness, and the threshold value was manipulated to change the mean time between detectability and infectiousness for our sensitivity analysis. The consequences of this choice were not only to increase the variance in timing of detectable infection, but also to skew the resulting distribution such that some infections were not detectable until after the infected individual became infectious. Thus, the effectiveness of the avoidance behavior was reduced relative to a model using a fixed time difference or otherwise directly manipulating the time between events.

*Density-Independent Mechanisms*

Disease dynamics among algal phase juvenile *P. argus* are unknown in the wild because they are small, camouflaged, and sparsely distributed deep within bushy stands of macroalgae. PaV1 transmission by contact is thus unlikely, though waterborne transmission is possible over short distances (Butler et al. 2008). Experiments using early benthic juveniles caged in macroalgae-covered hard bottom found that transmission occurred to isolated lobsters, but infection rates appeared independent of lobster density (Butler, unpublished data). Therefore, I incorporated a constant uniform probability of infection as a background transmission process that represented an unknown density-independent process, such as transmission through the water or by ingestion of infected
Fig. 17. Examples of possible disease development scenarios for individual lobsters. Lobster A became infected approximately two weeks prior to becoming infectious and died 120 days after being infected. Lobster B became detectable 35 days after becoming infectious and died 45 days later. Lobster C became detectable 35 days before becoming infectious and also died before becoming infectious.

prey. I tested the effect of three levels of background infection: (a) no background infection rate, (b) a low 0.1% daily incidence equivalent to a 2.5% per month incidence rate, and (c) a high 0.4% daily incidence equivalent to a 10% monthly incidence rate.

Numbers of postlarvae entering the model each month were derived from empirical data from a long-term monitoring program conducted in the Florida Keys, FL
by the Florida Wildlife Conservation Commission. The details of how those numbers were derived and postlarvae were distributed over the simulated landscape are presented in Appendix A. In addition to the infection mechanisms already described, PCR analysis of a preliminary sample of postlarvae collected from Witham collectors placed at Long Key in 2007 revealed that postlarvae may be entering the system already infected with PaV1 (Moss et al. unpublished data). Therefore, I also simulated this exogenous infection of postlarvae using the prevalences observed in their samples (Table 6).

Table 6. Proportion of newly arriving postlarvae infected by PaV1 at Long Key, Florida. Each month 25 individuals, newly settled on artificial substrate, were collected and tested for PaV1 infection using PCR analysis. Because the swimming stage is non-feeding, and the possible exposure to the virus after arrival is slight, this is the first evidence that postlarvae arrive in the benthic nursery habitat already infected.

<table>
<thead>
<tr>
<th>Month</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>April</th>
<th>May</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>25</td>
<td>25</td>
<td>25</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td>Proportion Infected</td>
<td>0.00</td>
<td>0.30</td>
<td>0.05</td>
<td>0.00</td>
<td>0.20</td>
</tr>
</tbody>
</table>

Simulations

To determine the initial lobster population structure, 30 replicate runs of ten years were performed, with no initial population and no disease. The model was populated by simulating monthly influxes of postlarvae, which were distributed over the region and juvenile lobsters then allowed to grow, move, and die using the algorithms described.
herein. Annual recruitment was measured to find the year at which recruitment stabilized, which was considered the minimum “spin-up” time necessary to produce a stable population. The cell-by-cell population structure of the model on January 1 of a randomly selected year after the spin-up period was used as the initial lobster population for all of the subsequent simulations. After determining the initial lobster population for each cell, initial PaV1 prevalences were set to mimic observed prevalences. The initial prevalence for each habitat cell was randomly drawn from a discrete probability distribution function constructed from prevalences observed from June-August 2002 (Fig 3.4). Although the data set used was larger (Butler unpublished data), data from sites with fewer than ten observations were excluded to avoid small sample size issues, such as 100% prevalence observed because only one lobster was caught and it happened to be infected.

Each simulation consisted of ten simulated years to ensure that long-term trends could be observed. The number of replicate runs needed to detect a 5% change in total lobster recruitment to the 50 mm CL size class was determined using a Visual Jackknife technique (Confalonieri et al. 2007). The results of twenty replicate runs that simulated no disease effects and which used the default temperature function, uniform oceanic salinity of 35 psu, and no cyanobacteria blooms, were analyzed. The optimal sample size was determined by resampling the data, systematically taking larger subsamples to find
Fig. 18. Frequency distribution of 150 observed PaV1 prevalences in the Florida Keys from June-August 2002. Observed percent prevalences have been combined in five percent intervals except for 0% and > 35%. The values shown on the x-axis are the midpoints of the intervals. In the model the actual (randomly selected) observed prevalence value was applied to each cohort of newly arriving lobster.

the subsample size at which the rate of change of the subsample means was negligible.

For each subsample size, 500 sets of subsamples were drawn to determine the mean and variance, resulting in the Visual Jackknife optimal sample size of six replicates. The minimum sample size necessary to detect a 1% difference from the mean at the $\alpha=0.05$ level was also calculated using an iterative procedure based on Student’s T, with identical result. Because the variability of the system under other scenarios was not known, the
sample size estimate was rounded upward to the nearest ten to ensure sufficient replication.

Modes of PaV1 Transmission: I used a three-way crossed design in the simulations by varying: (1) the number of days after infection of a lobster that others could detect and thus avoid it (avoidance onset), (2) daily rates of density-independent background infection of early benthic phase lobster, and (3) the proportion of postlarvae entering the system infected by PaV1, which I refer to as “exogenous infection of postlarvae” (Table 7). Onset of avoidance of PaV1-infected lobster by susceptible conspecifics was treated as a fixed factor from which four levels were tested: never, coincident with infectiousness, two weeks before infectiousness, and four weeks before infectiousness. The density-independent infection rate of early benthic phase lobster was also treated as a fixed factor with three levels: none, low (0.1% daily), and high (0.4% daily). Exogenous infection of postlarvae was treated as a fixed factor with two levels: none and empirical rates. The response variables monitored for each simulation were the number of lobster recruiting to 50 mm carapace length (CL), prevalences in each 5 mm CL lobster size class, the number of new infections in each size class, and incidences, expressed as the proportion of susceptible lobsters newly infected in each lobster size class. The values of each response variable were recorded for each model cell for each simulated day and summed over the entire simulated region. Significant differences in recruitment were detected using Analysis of Variance (SPSS version 17). Appropriate denominator mean squares for the mixed model were constructed using the simplified procedure described by Zar (1996). Prevalence and incidence were examined graphically.
Table 7. Summary of simulations comparing the effects of disease avoidance timing, density-independent infection of EBJs, and exogenous infection of postlarvae. A factorial design was followed, using four levels for the timing of onset of disease avoidance, three density-independent incidence rates in EBJs, and two levels of PL infection.

<table>
<thead>
<tr>
<th>Timing of the Onset of Disease Avoidance Relative to Becoming Infectious</th>
<th>Never</th>
<th>Coincident</th>
<th>2 Weeks Before</th>
<th>4 Weeks Before</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Density-Independent Incidence Rate in EBJs</strong></td>
<td>0.0% per day</td>
<td>No PL Infection</td>
<td>No PL Infection</td>
<td>No PL Infection</td>
</tr>
<tr>
<td></td>
<td>0.1% per day</td>
<td>No PL Infection</td>
<td>No PL Infection</td>
<td>No PL Infection</td>
</tr>
<tr>
<td><strong>Rate in EBJs</strong></td>
<td>0.4% per day</td>
<td>No PL Infection</td>
<td>No PL Infection</td>
<td>No PL Infection</td>
</tr>
</tbody>
</table>
**Effect of Habitat Loss on Disease Dynamics:** I also examined the likely effects of habitat loss (i.e., sponge die-off caused by HAB) and thus increased lobster aggregation within remaining shelters on disease prevalence. Sponge-die offs were simulated in the area of the model corresponding to those areas of Florida Bay that have experienced die-offs in recent years (Butler et al. 1995, and additional unpublished data), with approximately the same coverage as observed during the most recent HAB in 2007. For these simulations, HAB was treated as a fixed factor with two levels, present and absent. These were crossed with two levels of disease avoidance onset: two and four weeks prior to infection. The density-independent infection rate for EBJs was held constant at 0.1% per day and exogenous infection of newly arriving postlarvae was not simulated. Although the entire Florida Keys region was simulated, the response variables were aggregated and compared only within the HAB-impacted region (see Figure 9).

**RESULTS**

Effect of Disease Avoidance, Density-Independent Processes, and Exogenous Disease Sources

* Determination of Density-Independent Incidence Rates for Early Benthic Phase Lobster

Density-independent disease dynamics of early benthic phase lobster living in macroalgae were simulated using a constant daily probability of infection. Because the true value (if such can be said to exist) is unknown, a low value, 0.1% per day, and a high value, 0.4% per day, were first tested to find a reasonable value for use in subsequent
simulations, and the resulting prevalence values among early benthic juveniles residing in algae (i.e. EBJs between 5 mm CL and 15 mm CL) were compared to empirical values measured in field surveys in mid- to late-summer. In a preliminary study, observed prevalence in early benthic phase juveniles was as high as 60% on a site, but prevalence on most sites ranged from 0% to 31.25% (Butler, unpublished data). The low density-independent incidence resulted in annual spikes in simulated prevalence, with maxima ranging from 17.6% to 54.5%, only one of which exceeded 35% (Fig. 18). Each simulated year, the maximum prevalence occurred in late summer or early fall. The high density-independent incidence applied to early benthic phase P. argus, 0.4% per day, produced annual spikes in prevalence ranging from 44.3% to 83.8%. These are far in excess of the observed prevalences, therefore this rate was not used for any other tests.

**Interaction of Disease Avoidance, Density-Independent Processes, and Exogenous Disease Sources**

In all, 16 scenarios were simulated in a factorial design with four levels of disease avoidance (no avoidance and avoidance with onset coincident with, two weeks prior to, and four weeks prior to infectiousness), two density-independent incidences for EBJs (0.0% per day and 0.1% per day, and two levels of exogenous infection of newly arriving postlarvae (present and absent) (Table 7). These simulations produced data on recruitment whose residuals were significantly non-normal and heteroscedastic. No transformation could be found that substantially improved the fit of the data to parametric assumptions; therefore, the data were ranked and ANOVA was performed on the rank
Fig. 19. Prevalence of simulated PaV1 infection in early benthic phase *Panulirus argus* at two density-independent incidences. The 0.1% daily incidence resulted in peak prevalences that approximated empirical values. The high daily incidence (0.4% per day) resulted in values that were consistently too high. The timing of peak prevalence each year is indicated by a dated circle. Black lines indicate the mean prevalence across replicate runs on each day, gray horizontal lines indicate ±1 standard deviation.
Table 8. Three-factor model I ANOVA testing the effects of Disease Avoidance Timing $\times$ Density-Independent Infection of Early Benthic Phase Lobster $\times$ Presence of Exogenous Infection of Postlarvae on the simulated lobster recruitment. Here, recruitment is the number of lobsters surviving to 50 mm CL. There is a significant three-way interaction among the factors.

<table>
<thead>
<tr>
<th>Source</th>
<th>Df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density-Independent EBJ Infection (EBJs Infected)</td>
<td>1</td>
<td>165379.60</td>
<td>185.83</td>
<td>0.0009</td>
</tr>
<tr>
<td>Exogenous Infection of Postlarvae (PLs Infected)</td>
<td>1</td>
<td>39187.60</td>
<td>7.21</td>
<td>0.3441</td>
</tr>
<tr>
<td>Disease Avoidance (Avoidance)</td>
<td>3</td>
<td>37705.62</td>
<td>42.37</td>
<td>0.0059</td>
</tr>
<tr>
<td>EBJs Infected $\times$ PLs Infected</td>
<td>1</td>
<td>6916.90</td>
<td>3.11</td>
<td>0.1759</td>
</tr>
<tr>
<td>EBJs Infected $\times$ Avoidance</td>
<td>6</td>
<td>889.95</td>
<td>24.84</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>PLs Infected $\times$ Avoidance</td>
<td>3</td>
<td>741.75</td>
<td>0.33</td>
<td>0.8041</td>
</tr>
<tr>
<td>EBJs Infected $\times$ PLs Infected $\times$ Avoidance</td>
<td>3</td>
<td>2221.92</td>
<td>62.03</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Error</td>
<td>144</td>
<td>35.82</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>162</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

values (Table 8). There was a significant three-way interaction of PaV1 avoidance timing, density-independent infection rate of early benthic phase juveniles, and exogenous postlarval infection ($F_{3,144}=62.03$, $P<0.0001$). Plots of mean simulated annual recruitment (Fig. 19) show that, in the absence of infection in early benthic juveniles (i.e., no density-independent infection mechanism and no exogenous infection of postlarvae), the avoidance behavior maximized recruitment at approximately 4200 recruits·km$^{-2}$·y$^{-1}$ regardless of the precise timing of the onset of the behavior relative to
Fig. 20. Interaction plots of simulated annual recruitment per km² for different infection mechanisms and timings of disease avoidance. Simulations were run with different combinations of infection mechanisms: transmission by contact among crevice-dwelling juveniles (Contact); constant, density-independent infection of early benthic phase juveniles at a rate of 0.1% per day (Density-Independent Infection of EBJs); and exogenous infection of newly arrived postlarvae at empirically observed rates (Exogenous Infection of PLs). Each combination of infection mechanisms was run with one of four different timings for the onset of disease avoidance: no avoidance behavior (No Avoidance); avoidance onset coincident with onset of infectiousness (Coincident); avoidance onset two weeks before the onset of infectiousness (2 Weeks Prior); and avoidance onset four weeks before the onset of infectiousness (4 Weeks Prior).
Fig. 21. The effect of disease avoidance on PaV1 persistence in simulated populations of social, crevice dwellers. In the absence of disease avoidance, direct transmission among crevice-dwelling juvenile *P. argus* was sufficient to maintain the disease in the population and produce periodic outbreaks. With disease avoidance, PaV1 became extinct within five simulated years. Note the differences in scales of the prevalence axes. The black line is the daily mean and gray bars are ±1 standard deviation.
infectiousness. Scenarios that included either density-independent infection of EBJs or an exogenous source of infection of newly arriving postlarvae did not reach this maximum, but increasing the amount of time before infectiousness during which diseased lobster could be detected also increased recruitment.

In the absence of an infection mechanism for early benthic juvenile *P. argus* (EBJs), the disease avoidance behavior drove PaV1 to extinction in the simulated population within five years, regardless of the timing of disease detectability (Fig. 20). In the absence of the disease avoidance behavior, not only did the disease persist, but simulated prevalence values were maintained above 5% in social, crevice-dwelling juveniles. Peaks in incidence closely followed peaks in lobster abundance within size class, regardless of avoidance (Fig. 21), and incidence also tracked with the abundance of susceptible lobsters, indicating that transmission is density dependent. However, the density-dependent signal is much weaker in simulations that included avoidance. In all scenarios, simulated PaV1 prevalence cycled annually with population level in crevice-dwelling juvenile lobsters, with peak values occurring between August and October, lagging behind the annual, early spring peak in postlarval recruitment (Acosta et al. 1997) by four to six months (Fig. 22). However, there were pronounced increases in prevalence corresponding to reductions in lobster abundance in each size class due to growth and recruitment to larger size classes. This suggests that the cessation of growth of lobster in late stages of the disease may retain them in the smaller size class while allowing susceptible lobsters to move on (Fig. 23).
Fig. 22. Abundance and PaV1 prevalence in lobsters > 25 mm CL. Dashed lines are lobster abundances (right Y-axis of each graph). Solid lines are mean daily PaV1 prevalences for ten simulations with gray whiskers showing ±1 standard error. The number of lobsters is shown at the same scale for all cases, but values for PaV1 prevalence are shown at different scales due to the order of magnitude differences in the ranges for prevalence. In each case, annual peaks in prevalence corresponded with peaks in lobster abundance.
Fig. 23. Decomposition by size class for prevalence in lobsters > 25 mm CL. Dashed lines are lobster abundances (right y-axis of each graph). Solid lines are mean daily values for prevalence for ten simulations with gray whiskers showing ±1 standard error. Annual peak values in prevalence occur as the number of lobster in each size class decreases due to growth of healthy lobster.
Fig. 24. PaV1 Incidences and lobster abundances in two size classes for three levels of disease avoidance. Gray bars are mean monthly incidences of new infections with whiskers showing +1 SE. Solid lines are mean daily numbers of lobster in the size class.
Both density-independent infection of EBJs and exogenous infection of newly arriving post-larvae were sufficient at the levels simulated to produce infections in the largest lobster size classes simulated (Fig. 24). This was true even when the timing of disease avoidance was set to an unrealistically high level, that is, healthy lobsters detected and avoided diseased lobsters four weeks (on average) before diseased lobsters became infectious. Although the pulsed introduction of infection via newly arriving postlarvae was reflected in similar pulses of prevalence in subsequent lobster size classes, incidence rates changed smoothly among size classes, suggesting that increases in prevalence with population size were partially due to the growth of pre-infectious lobster to larger size classes.

**Effects of Disease Avoidance and Changes in Habitat Structure on Disease Dynamics**

Recruitment of lobsters in simulations combining changes in habitat structure (i.e., loss of sponge shelters due to harmful algal blooms; HABs) and the timing of disease avoidance (i.e., healthy lobsters avoid diseased lobsters never, 2, or 4 weeks prior to infectiousness) was examined in a two-factor, fixed effects design. For these simulations, only recruitment within Florida Bay (the area impacted by HABs) was compared. The simulation results for lobster recruitment were significantly heteroscedastic, so ANOVA was performed on natural log transformed values (Table 9). There was no significant interaction between HABs and disease avoidance ($F_{2,54}=1.07$, $P=0.35$). Both disease avoidance onset and HABs were significant ($F_{2,54}=47.81$, $P<<0.0005$, and $F_{1,54}=1664.32$, $P<<0.0005$, respectively). The lack of interaction
Fig. 25. Effect of density-independent infection of EBJs and exogenous infection of PLs on PaV1 prevalence in social juvenile P. argus 45 mm to 50 mm CL. Abundance of juvenile lobster is represented by the dashed line. The solid lines represent mean daily prevalences of PaV1 infection ±1 S. E. (gray whiskers).
Table 9. Two-factor model I ANOVA testing the effects of disease avoidance (Avoid) and HABs (HAB) on lobster recruitment in Florida Bay. There were three levels of disease avoidance, based on the timing of the onset of the behavior relative to when exposed conspecifics become infectious: never, two weeks before, and four weeks before. There were two levels of HAB, present and absent. Multiple comparisons (REGWF Test) were performed following the significant ANOVA. Homogenous subsets are indicated by a solid line beneath the mean values.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avoid</td>
<td>2</td>
<td>0.297</td>
<td>46.673</td>
<td>&lt;0.0005</td>
</tr>
<tr>
<td>HAB</td>
<td>1</td>
<td>10.810</td>
<td>1701</td>
<td>&lt;0.0005</td>
</tr>
<tr>
<td>Avoid × HAB</td>
<td>2</td>
<td>0.005</td>
<td>0.0776</td>
<td>0.463</td>
</tr>
<tr>
<td>Error</td>
<td>84</td>
<td>0.006</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>89</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

R-E-G-W-F Test on disease avoidance:

<table>
<thead>
<tr>
<th>Treatment</th>
<th>No Avoidance</th>
<th>Two Weeks</th>
<th>Four Weeks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Recruitment</td>
<td>13898</td>
<td>16889</td>
<td>16951</td>
</tr>
</tbody>
</table>
Fig. 26. Effect of HABs and disease avoidance on PaV1 prevalence in lobsters > 25 mm CL. The black lines are mean incidences with gray whiskers depicting one standard error of the mean. The dashed lines are mean numbers of lobsters. Harmful algal blooms did not affect persistence of the disease in the population.
Fig. 27. Effect of HABs and disease avoidance on PaV1 incidence in lobsters > 25 mm CL. In graphs A and B, the white line is mean incidence smoothed using a 30-day running average. In all graphs, the black lines are mean incidences with gray whiskers depicting one standard error of the mean. The dashed lines are mean numbers of susceptible lobsters. Density-dependent transmission is demonstrated when incidence increases with increasing population size, which is the case only in the absence of HABs and avoidance of disease.
suggests that HABs increased lobster mortality, so shelter limitation did occur; however, disease avoidance operated as effectively regardless of the level of shelter limitation. Avoidance was equally effective in increasing recruitment whether the onset was two or four weeks prior to infectiousness (Ryan-Einot-Gabriel-Welsch Test, P=0.82). All scenarios began with the same prevalence, and examination of prevalence and incidence in juveniles > 25 mm CL with time (Fig. 25 and Fig. 26) shows that the avoidance behavior reduced prevalence from 1% to 0% within three years, and prevalences never approached their initial level. In the absence of avoidance, prevalence oscillated with abundance, at times exceeding 5%.

**DISCUSSION**

Using spatially-explicit, agent-based modeling I explored PaV1 disease dynamics within juvenile spiny lobster populations in the Florida Keys as influenced by host behavior, background sources of infection, and nursery habitat structure. The first part of this study examined the population-level effects of disease avoidance behaviors exhibited by motile social animals among which a disease is transmitted by contact. The system was complicated by two additional mechanisms that independently introduced disease to the population. First, a density-independent infection mechanism, such as an alternate host or background waterborne transmission that operated exclusively on the very young, in this case on asocial early benthic phase lobsters. Second, the arrival of the disease with new cohorts (e.g., postlarvae) from outside the local population, a potential consequence of the openness that characterizes many marine populations. I found that in the absence of host disease avoidance behavior, outbreaks of PaV1 infection occurred rapidly,
growing in intensity and duration until, by the end of the 10 year simulation, PaV1 was maintained continuously at high levels in the older, social, crevice-dwelling juvenile lobster. When simulations included host avoidance of diseased conspecifics, PaV1 outbreak intensity and duration diminished and, in the absence of other sources of PaV1 infection, resulted in extinction of the disease within five years. However, when density-independent infection of early benthic phase *P. argus* or the arrival of infected cohorts of postlarvae were included in the model along with host disease avoidance, the disease persisted in the population at levels consistent with empirical observations. Combining the two density-independent sources of PaV1 in the model resulted in peaks in per capita prevalence exceeding all observed values. The second part of this study examined the effects of changes in nursery habitat structure on PaV1-lobster disease dynamics, specifically how the loss of shelter for juvenile lobsters and consequently larger aggregations of lobster in the remaining shelters impacted disease prevalence. The results of these simulations were counterintuitive, because the impact of disease on the lobster population appears to have been reduced because the lobster population was simultaneously reduced by higher predation. However, disease avoidance under these circumstances still resulted in significant increases in recruitment and extinction of the disease in the local population.

The *P. argus*-PaV1 system is complex in that it includes a stage-structured and spatially-structured host population, the members of which have different social behaviors at different ontogenetic stages, along with a pathogen with the potential for multiple modes of transmission. These features have important evolutionary ramifications for the evolution of the pathogen, particularly with regard to virulence, here defined as
the ability of the pathogen to damage host tissues, resulting in death of the host. Thus, case mortality (the proportion of infected individuals that die) is used as a measure of virulence. Virulence is also often tied to the reproductive rate of the pathogen in the host because a rapidly growing pathogen population damages the host more quickly, and leads to more rapid death. For many pathogens, then, maximizing lifetime reproductive success within the host can be achieved along a continuum between a maximized intrinsic rate of growth, which reduces host lifetime, and reduced reproduction rate with increased host lifetime. The pathogen population also depends on transmission among hosts, thus is constrained by the structure of the host population. In the most general terms, spread of the parasite depends on the probability of contact between parasite propagules and host organisms. The rate of transmission of parasites spread by contact, as PaV1 is spread among crevice-dwelling juvenile _P. argus_, is proportional to the rate of contact among hosts. Thus contact transmission is typically dependent on host population density. However, this aspect of transmission is also dependent on host behavior. For example, the spread of sexually-transmitted diseases in vertebrates depends more strongly on the mating system and the proportion of infected hosts than on host density (Altizer et al. 2003). For microparasites (e.g., bacteria and viruses), the probability of a successful infection for any given contact, called the transmissibility coefficient or force of infection, $\beta$, is often dependent on the intensity of the infection (the abundance of parasites in the host’s tissues) because this determines the potential number of propagules available for transfer during the contact. Thus, the fitness of a directly transmitted parasite, expressed as the basic reproductive ratio ($R_0$), the number of secondary infections arising from a single primary infection, is determined by the number of
contacts that infected hosts have with conspecifics and the probability of a successful infection, which is determined by the intensity of the infection. Clearly, then, there is a trade-off between maximizing the likelihood of infection during each contact and maximizing the potential number of contacts over the lifetime of the infection. This trade-off is central to understanding why maximum virulence is not always favored by natural selection (Anderson and May 1979). In particular, reduced virulence may be favored in populations that have low intraspecific contact rates due to lower density; thus infected hosts live longer so as to interact with more conspecifics (reviewed by Frank 1996).

*Panulirus argus* Virus 1 in crevice-dwelling juvenile *P. argus* exhibits high levels of case mortality which may have played a role in the evolution of the avoidance behavior explored in this work. However, it appears that the avoidance behavior greatly reduces contact rates between infectious and susceptible hosts, which, according to theory, should exert a selective force against high virulence. This contradiction suggests that other aspects of the system, such as other potential modes of transmission, may also be important in shaping this particular parasite-host relationship.

In addition to contact transmission among social juveniles, the *P. argus-PaV 1* system includes the potential for indirect transmission among EBJs and for vertical transmission of the virus. The *P. argus* population also has a high degree of spatial structure at multiple scales that can also affect disease dynamics. Indirect disease transmission includes environmental exposure (e.g., water- or air-borne transmission) and infection through alternate/intermediate hosts, including vectors. The dynamics of multispecies infections can be extremely complex, and there is no clear generalized theory regarding the evolution of virulence in these systems (see reviews in Bull 1994,
Woolhouse et al. 2001). A review of this subject is beyond the scope of this discussion, but there is some evidence that alternate hosts are unlikely in the P. argus-PaV1 system in that PaV1 does not infect Panulirus guttatus (Butler et al. 2008), a closely-related sympatric congener that often cohabits crevices on reefs with adult P. argus. Likewise, inoculation trials were unable to cause disease in Mithrax spinosissimus and Menippe mercenaria, which are also sympatric, crevice-dwelling crustaceans associated with P. argus dens (Butler et al. 2008). Therefore, I consider here only on the possible consequences of environmental exposure of P. argus EBJs to PaV1 with the caveat that the case against alternate hosts is far from proven.

Generally, environmental transmission favors increased virulence because the infective propagules can survive independently of their host for some period of time (Ewald 1991). Thus, rapid population growth within the host leads to rapid release to the environment, increasing the density of infective particles and the likelihood of infection of any susceptible hosts in the area. If the susceptible host population falls below the threshold necessary to sustain the epizootic, the parasite persists endemically until the host population recovers, resulting in cyclic epizootics (May and Anderson 1979). However, it appears unlikely that this is the precise mechanism operating in the P. argus-PaV1 system. First, waterborne transmission of the virus has only been demonstrated over short distances (< 2 m) through dedicated unidirectional plumbing (Butler et al. 2008). Second, laboratory studies suggest that in artificial seawater, the virus only remains capable of infecting cell cultures and EBJs for a few days (Li and Shields, unpublished data). Instead, although PaV1 has a high virulence as measured by case mortality, its development within the host is relatively slow, and the > 1 month time lag
between exposure and infectiousness may have the same function. That is, new cohorts of postlarvae arrive monthly, providing a pulsed supply of new uninfected lobster. The long lag period also allows some lobsters infected as EBJs to enter the crevice-dwelling juvenile population, maintaining a low level of prevalence in spite of the effectiveness of the avoidance behavior.

PaV1 infection of newly arriving cohorts of postlarvae suggests the potential for vertical transmission, though the evidence for this is so far only circumstantial and infection of larvae during the many months that that spend within the water column remains a possibility as well. PaV1 DNA has been detected in adult *P. argus*, apparently without any associated pathology (Huchin-Mian et al. 2009, Behringer et al. 2010). It has also been detected in nonfeeding *P. argus* postlarvae newly settled on artificial medium (J. Moss, D. Behringer, M. Butler, and J. Shields; unpublished data). Vertical transmission is generally assumed to favor reduced virulence, as demonstrated in experimentally manipulated transmission of bacteriophage virus F1 and bacteria (Messenger et al. 1999) and microsporidian infections of *Daphnia* (Vizoso and Ebert 2004). The reason for this is that the vertically-transmitted parasite is dependent on host reproductive success for its own propagation. This is consistent with the apparent low pathogenicity of PaV1 in adults, but at odds with the high virulence in juvenile *P. argus*. However, spatial structure in host populations that lead to metapopulation dynamics may promote pathogen virulence (Ferdy 2009). This occurs because local interactions that in isolation would lead to extinction can be compensated for by exogenous inputs. As is typical of many marine species, the *P. argus* population of the Florida Keys is relatively “open,” meaning that at the spatial scale at which most ecological studies of populations
take place (10-100s of km) the population has a high degree of exchange with other similar populations (Butler et al. in press).

The study of disease processes in marine systems is complicated by some of the fundamental differences between marine systems and many terrestrial systems. Foremost among those is that the marine environment is strongly advective. Many marine organisms have complex life histories that include a relatively long-lived planktonic larval stage. Dispersal of larvae, if driven primarily by large-scale circulation features, may occur over distances on the order of hundreds of kilometers, across which larvae from multiple subpopulations may be freely mixed. Thus, otherwise geographically isolated populations may exhibit high degrees of connectivity due to the exchange of larvae (Scheltema 1971, 1988). In a host-disease system, the consequences of highly connected subpopulations are the potential for the rapid spread of the disease over large geographic areas (McCallum et al. 2003) and the apparent density-independent maintenance of the disease in local populations (Gurarie and Seto 2009). Relatively few vector-borne diseases are known in marine systems (reviewed by McCallum et al. 2004), and this may also be partly due to the strongly advective environment in which viscous forces and currents can take the place of insect wings. The P. argus-PaV1 system is exemplary of many of these features and serves to highlight the urgent need for more research in marine epizootiology.
CHAPTER IV

CONCLUSIONS

Agent-based models apply interactions and mechanisms at the individual level, just as in the real world, and they explicitly incorporate variation at the individual level. As a result, agent-based models are realistic, intuitive, and generally less complex mathematically than their analytical counterparts. Their primary disadvantage is the amount of detailed data required to properly construct and parameterize them. Although the use of agent-based simulation is increasing in ecology, they continue to be regarded as highly specific, so are rarely used for development of theory. However, I have presented two very different applications of a spatially-explicit, agent-based model of the population dynamics of juvenile Caribbean spiny lobster (*Panulirus argus*) in the Florida Keys, Florida (USA), and a significant portion of the biotic and abiotic environment on which it depends.

The first application was the investigation of the likely effects of The Comprehensive Everglades Restoration Plan on the downstream communities in Florida Bay and the Florida Keys. My results suggest that returning the flow of freshwater in the Everglades to pre-development conditions is likely to be detrimental to truly marine taxa, such as spiny lobsters and sponges in the transitional region between Florida Bay and the Florida Keys. Simulated juvenile lobster abundance declined 6–24% in Florida Bay in scenarios where salinity either decreased alone or in combination with algal blooms. The most severe decline in lobsters occurred when salinity was lowest and algal blooms occurred annually. Only about one-third of the decline was attributable to the salinity
decrease, which directly influenced lobster mortality and movement rates and indirectly led to higher mortality through habitat destruction. Harmful algal blooms accounted for the majority of the decline in lobster, though their impact on the lobster population was entirely indirect. Higher temperatures and salinities had little or no impact on lobsters in Florida Bay, but higher temperatures increased simulated juvenile lobster recruitment in the Florida Keys by 6.8%. Higher temperatures also increased simulated sponge survival; however, in most of the other scenarios, sponges were more negatively impacted than lobster. Most notably, the abundance of sponges in Florida Bay declined by ~ 50% in simulations with HABs, whereas decreased salinities alone led to simulated sponge die-offs, ranging from 9–18%. Unfortunately, it has not been possible to directly link effluent water quality, salinity, and HABs in the region, so it remains unclear whether the restoration efforts will exacerbate or alleviate HABs in Florida Bay.

In Chapter III, I examined social aggregation and the tradeoff between reduction of the risk of predation and the risk of disease transmission. In addition, I examined the population level effects of behaviors that reduce gregariousness of uninfected hosts in response to disease, a behavioral change exhibited by *P. argus*. To the model developed in Chapter 2, I added appropriate disease states, transmission functions, and a set of behaviors whereby susceptible lobster may avoid exposure to the virus by avoiding contact with diseased conspecifics. Because the disease also occurs in asocial, early benthic phase juveniles through an unknown mechanism, I also included a density-independent infection mechanism, which might represent an alternate host or some other environmental exposure. As an alternative mechanism for infecting EBJs, I also simulated the arrival of the disease with new cohorts of postlarvae, a consequence of the
openness of this population that is also a characteristic of many other marine systems. Last, I was able to examine the effects of increasing host aggregation on disease transmission, because the loss of sponges due to HABs changes the pattern of cohabitation of lobster in the region. I found that in the absence of the disease avoidance behavior, outbreaks occurred rapidly, growing in intensity and duration until, by the end of the 10 year simulation, PaV1 was maintained continuously at high levels. However, the disease avoidance behavior reduced simulated outbreak intensities and durations, and in the absence of other sources of PaV1, resulted in extinction of the disease within five years. On the other hand, both the density-independent infection of EBJs and the simulated arrival of infected cohorts of postlarvae were capable of maintaining the disease in the larger population, even at the highest level of disease avoidance, probably as a consequence of the long period between exposure and death.

Disease outbreaks with far reaching ecological and economic consequences have recently occurred in marine systems. For example, in the late 1990s, Australia's Pilchard fisheries were devastated by a herpesvirus that is estimated to have reduced the stock by 70%, causing $12 million in damage to the fishery (reviewed by Murray et al. 2001). In 1983, a waterborne pathogen caused mass mortality of the herbivorous urchin, *Diadema antillarum*. Within 13 months, populations were reduced by more than 93% throughout its geographic range in the Western Atlantic Ocean (Lessios 1988). The die-off of this once-prominent grazer has been implicated as a major factor in the current loss of coral reefs throughout the Caribbean Sea due to overgrowth of macroalgae (Hughes 1994). On a larger scale, White Spot Syndrome Virus is thought to have caused $20–$30 billion in losses worldwide to the shrimp aquaculture industry since its discovery in 1992 (Lightner
1996, 1999, Witteveldt 2006). More alarmingly, it appears that there has been a general increase in marine diseases over the past 30 years (Harvell et al. 2004, Ward and Lafferty 2004), and there is some concern that the main body of epidemiological theory, developed in terrestrial systems, may not be applicable to many marine diseases (McCallum et al. 2004).

The cases presented here, the first concerned with a specific, applied goal and the second a more theoretical exploration of disease dynamics and host behavior, demonstrate the broad applicability of this agent-based model. As with most agent-based simulations, development of this model required extensive long-term datasets regarding the ecology and life history of the lobster and other organisms on which the lobster depends. However, the complexity of the model allowed investigation of interactions among organisms and the explicit separation of direct and indirect effects of environmental change on these major components of the benthic communities of this region. Likewise, in the P. argus-PaV1 system, the agent-based approach allowed the explicit simulation of behaviors involved in disease transmission and changes in social behavior exhibited by the organism while retaining a highly realistic environmental simulation. My results support the contention, expressed by others in reviews on new approaches in ecological modeling, that the explicit representation of individual organisms and the effects on them provides a more intuitively understandable result than equivalent but more abstract population-based modeling and thus should see greater use in the future as computing capabilities continue to improve.


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Habitat Structure

The dominant habitat type of each cell is designated as hard-bottom, seagrass, open (including non-emergent banks and channels through otherwise solid banks), or land (which includes emergent banks), corresponding to the actual spatial distribution of these habitats in the region, based on geographic data from NOAA's Benthic Habitats of the Florida Keys Project (Rohmann 1998) and on field survey data collected from more than 300 sites throughout the Florida Keys. I used field data and diver observations of shelter utilization by lobsters (Butler and Herrnkind 1997, Herrnkind et al. 1997b, Butler unpublished data) to further define hard-bottom habitat with regard to the availability of different types of crevice structures used by lobsters: loggerhead sponges (*Spheciospongia vesparia*), vase sponges (*Ircinia campana*), other sponges, octocoral-sponge complexes, solution holes, and other shelters (mainly scleractinean corals). Lobster sheltering capacities for each of these six shelter types were determined by measuring shelter-specific group sizes at 128 field sites (Herrnkind et al. 1997) and the densities of the shelters at 133 sites (Butler, unpublished data) throughout the Florida Keys. The observed capacities were assigned to the spatially corresponding modeled habitat cells. Capacities were assigned to the remaining hard-bottom cells using a kriging function that was generated for each species modeled. Seagrass and open cells are modeled as uniform habitats with no explicitly defined sheltering structures. Both hard-bottom and seagrass cells are assumed to provide unlimited shelter space for algal-stage lobsters and unlimited, but suboptimal shelter for crevice-dwelling lobsters unable to find appropriate shelters. Open habitat is assumed to provide only suboptimal shelter.

The field surveys also included a variety of hard-bottom dwelling organisms that are not used as sheltering structures by lobsters, but are important community members and are known to be affected by cyanobacteria blooms. Thus, the model includes state variables for the abundances of three additional sponge species: brown branching (*Ircinia* sp.), golfball (*Cinechyra* sp.), and sheepswool (*Hippospongia lachne*) sponges, and two octocoral species: the purple sea plume (*Pseudopterogorgia* sp.) and angular seawhip (*Pterogorgia anceps*). We will also include the increased mortality on seawhip-sponge complexes at the same rate as used for “other sponges.”

Lobster Growth

Growth of individual lobsters was simulated in discrete steps, reflecting the molting process of arthropods. Individuals were evaluated daily to determine whether they molted, and if molting occurred, then growth in length was determined. The probability of molting ($P_m$) was determined for each individual based on its size ($S$, mm CL) and the number of days since its last molt ($x$):
These equations were based on laboratory growth experiments (Lellis and Russell 1990). The probability that a juvenile lobster will molt within 10 days of its last molt is zero. However, the probability rises quickly to 1.0 after 34 days post-molt for small individuals (≤ 25 mm CL), and rises somewhat less steeply to 1.0 after 55 days for larger juveniles (>25 mm CL). If a generated uniform random number was ≤ P_m, then the individual molted and x (the number of days since its last molt) was reset to zero. If an individual is designated to molt, the incremental increase in length (G; mm CL) was then determined from the individual's current length (S) as:

\[ G = 0.463 + 0.111 S \]

This relationship was also based on laboratory and field determinations of molt increments (Lellis and Russell 1990, Forcucci et al. 1994).

### Lobster Mortality

searching for shelter or migrating. The probability of mortality for each lobster was calculated during each of those activities, with the exception being that algal-phase lobsters and those in seagrass cells did not search for shelter. The model assumed a diurnal period of 12 hrs, during which lobsters were quiescent in their shelters, and a two-hour crepuscular (dawn) period during which lobsters searched for a different shelter than that used during the previous day. The hourly probability of mortality (P_D) was computed as a function of lobster size (S) and shelter type:

\[ P_D = P_O = 0.373 / 24 (0.305 + S) \text{ for lobsters in the open} \]
\[ P_D = P_S = 0.15 / 24 (-0.409 + S) \text{ for lobsters in macroalgae or crevice shelters} \]
\[ P_D = P_g = 0.228 / 24 (-0.766 + S) \text{ for lobsters in seagrass} \]

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

The calculation was more complicated for postalgal-stage lobsters and for transitional lobsters in hard-bottom cells. Transitional and postalgal-stage juveniles were either in shelters (if available) or in sub-optimal shelters, assumed to have the same sheltering value as seagrass during the day (either P_S or P_g). Lobsters ≤ 25 mm CL spend only one-third of the night foraging in the algae close to their dens, so P_g was applied for 3.3 hours of their nightly activity, and P_S for the balance of the night and for the two hours of crepuscular time. Larger juveniles spent variable amounts of twilight time in the
open searching for shelter ($P_0$), and were in the seagrass at night ($P_g$). The fraction of
twilight hours spent searching ($T_p$) was assumed to be inversely proportional to the
availability of all appropriate shelters in that cell:

$$T_p = (K_T - N_t)/K_T$$

where $K_T$ is the total lobster carrying capacity of the cell (summed over shelter types that
might be used by the lobster) and $N_t$ is the current number of lobsters in those shelters.
For these lobsters, $P_0$ was applied over $2T_p$ hours and $P_g$ for the remaining $2 - 2T_p$ hours.
For each lobster searching for shelter, if a generated random deviate was less than $P_D$
multiplied by the appropriate amount of time, the lobster was assumed to have died and
was removed from the simulation.

Mortality probabilities were determined through least-squares fitting of equations
to size-specific and shelter-specific mortality data derived from tethering studies (Smith
and Herrnkind 1992). However, tethering data only yielded relative estimates of
mortality among sizes and shelters, thus the appropriate intercepts for these functions
were unknown. I estimated the intercept terms in the equations using model simulations.
Mark-recapture studies of microwire tagged first benthic stage juveniles out-planted in
macroalgae indicate that only 1 to 4% survive to 35 mm CL (Butler et al. 1997, Sharp et
al 2000). Therefore, I iteratively altered the intercept in equation (6) and ran a single
cohort of juveniles through the growth, shelter selection, and mortality routines with the
constraint being lobsters only accessed hard-bottom habitat where they could move
between macroalgae and hard-bottom structures of unlimited lobster carrying capacities.
From these simulations, I chose a mortality function for lobsters dwelling in hard-bottom
cells that resulted in 1 to 4% of the model individuals surviving to 35 mm CL. Based on
tethering results, I then assumed that survival of lobsters in open water was one-half that
of those in hard-bottom cells, and so selected an intercept for $P_0$ that resulted in 0.5 to 2%
survival to 35 mm CL. Tethering studies also suggest that survival of juveniles in
seagrass falls midway between that measured in the open and in hard-bottom structures
or macroalgae (Herrnkind and Butler 1986). I therefore chose an intercept for $P_g$ (lobsters
in seagrass) that resulted in survival intermediate to the survival in the open and in hard-
bottom cells. In addition, early benthic juveniles ($< 10$ mm CL) were subject to mortality
as a function of salinity ($S_L$) and temperature ($T$). Weekly survivorship ($L$) was given by
the function:

$$L = 1.236 \times \exp \left\{-0.5 \left[ \left( \frac{T - 24.39}{5.565} \right)^2 + \left( \frac{S_L - 35.31}{8.587} \right)^2 \right] \right\}$$

(9)

The daily probability of mortality was then given by $P_D = 1 - e^{L/7}$. 
The probability of movement of lobsters among habitat cells was a function of lobster size, the availability of shelter in their current cell, and salinity stress. The functions below that describe the size-specific probability of movement for lobsters in different types of shelter are based on mark-recapture records for over 500 individual lobsters in 24 2500-m$^2$ (50 x 50 m) field sites within hard-bottom habitat (Schratwieser 1999; Butler, unpublished data). Movement of lobsters in the open was based on my intuitive expectation that the likelihood of cell departure of large juvenile lobsters (e.g., 50 mm CL) with no shelter would be 10 times that of similar-sized individuals with access to shelter.

Movement from seagrass was derived by assigning probabilities of moving that were intermediate between those with shelter and those without. Small juvenile lobsters that have found shelter rarely move to other shelters, and typically forage at night within a meter or two of their daytime shelter (Andree 1981, Schratwieser 1999). Thus, individuals < 30 mm CL that occupied a shelter were assumed to remain in their cell. For all other individuals, I determined the probability of leaving their current cell ($P_M$) based on their size and current shelter type (seagrass, open, macroalgae, or one of the five hard-bottom shelter types):

$$P_M = -0.5 + (0.0250 \times S) \quad \text{for lobsters in algal or hard-bottom crevice shelters}$$

$$P_M = -0.275 + (0.0137 \times S) \quad \text{for lobsters in seagrass}$$

$$P_M = -0.05 + (0.0025 \times S) \quad \text{for lobsters in open (sub-optimal crevice shelters)}$$

If a uniform random number generated by the program was less than $P_M$, then the individual moved to a randomly selected cell from among the neighboring cells, following the movement rules described in detail below. Individuals could move only one cell per day, which is consistent with the distances between cells.

Based on laboratory studies of the effect of salinity change on lobster movement, daily movement probabilities in the model were altered when salinity within a spatial cell changed by 5 psu or more. At extreme salinities (15 psu and 45 psu), lobsters nearly double their movement during the first night of exposure as compared to movement rates at normal salinity (35 psu). However, movement at extreme salinities after the first 24 hours of exposure declines to ambient movement and then ceases. At less extreme hyposalinity levels (25 psu), lobsters again nearly double their movement rates but in this case maintain those high levels of movement for 5 days.

Non-directional movement appears to be the norm for post-algal-stage juvenile lobsters (Butler unpub. data), although large juveniles and adults often participate in nightly and seasonal migrations requiring directional movement (Herrnkind 1980, Cox et al. 1997, Boles and Lohman 2003). Thus, in interior model cells with no obstructions, the direction an emigrating individual took (N, S, E, or W) was randomly chosen with equal probability for each. Previous versions of the model treated the northern and southern domain boundaries as closed, and assigned equal probabilities to the remaining,
open directions of travel. In addition, movement was “wrapped” between the eastern and western boundaries (i.e., a lobster moving east from the eastern boundary reentered the model on the western boundary) as a convenient means of simulating immigration from nursery habitat beyond the modeled domain. The new model recognized reflecting, deflecting, and absorbing boundary types which were explicitly defined in the habitat input file. Lobsters attempting to move across a reflecting boundary were retained in their original cell, but were treated as immigrants. Lobsters attempting to move across a deflecting boundary were redirected in a randomly chosen direction perpendicular to the incidental movement. Lobsters moving across an absorbing boundary were removed from the model. For example, a lobster at a western deflecting boundary attempting to emigrate westward instead moved into an adjacent habitat cell either north or south of its current position, but not east or west. If the redirected lobster encountered another boundary in this direction (e.g., a lobster in the north-western corner that initially attempted to move west, but was redirected to a northern deflecting boundary), the effect of the second boundary was determined independently (Fig. A1). This allowed much more flexibility for defining the habitat area and testing the effects of the different boundary types on lobster distribution and recruitment. The simulations described in this dissertation treated all closed edges of the model domain, that is, boundaries beyond which no significant nursery habitat exists, as deflecting boundaries, and all open boundaries as reflecting.

The model also incorporated land as a cell type that included both permanently dry land and banks that emerge during low tides, and did not allow movement into or across it. The presence of a land cell resulted in a deflecting boundary in adjacent cells, mimicking lobster movement along shorelines. In addition, large, shallow banks were treated as semi-permeable regions, having a low probability of immigration and a high probability of emigration, because they generally have small channels that allow passage and in which lobsters are found, but are otherwise not used by lobsters.

Individuals designated to move from a cell are only permitted to move into an adjacent habitat cell, thus can traverse one cell per day. As discussed in the section on the spatial structure of the model (see above) the habitat structure (i.e., type and proportion of each shelter available) of each cell is constructed to be indicative of a 1-km² area in the Florida Keys and in a position in the array of habitat cells that corresponds with its real position in nature. However, the actual number of shelters, number of lobsters, and dynamics of lobsters (e.g., rates of movement) are scaled to match those typical in a 1000-m² area (the scale at which we have good empirical data). Therefore, the movement probabilities that we use should not be viewed as the probability of movement of an individual from the center of one 1-km² area to the next. Instead, the distance the juvenile lobster traverse in one night if they change cells in the model is roughly equivalent to 30-50 m. Conceptually, this is no different than lobsters moving from a 1000-m² area at the edge of one large 1-km² habitat cell into the adjacent 1000-m² area in the next 1-km² habitat cell. Portraying movement among habitats (i.e., emigration/immigration) in this way is a necessary consequence of an individual-based formulation and the way in which the spatial structure of the model is conceptualized to avoid having to model billions of individuals at a time. It is an abstraction of reality, but we believe it to be a reasonable one that conceptually has a long history (Shugart and West 1977).
Fig. A1. Movement destination transition matrices for lobsters residing in the highlighted cell. In each case, boundaries are denoted by heavy lines. The value in each cell is the probability that an individual will arrive in that cell given that it attempts to emigrate from the focal cell. (A) Unrestricted movement. (B) Movement at an edge in the original model. (C) Movement at a reflecting boundary. (D) Movement at a deflecting boundary. (E) Movement where two reflecting boundaries meet. (F) Movement in the new model where two deflecting boundaries meet.
APPENDIX B: DATA SOURCES


Temperature function: Tablecurve fit to KML long term temperature records.

Postlarval Influx cohort size: Florida Fish and Wildlife Conservation Commission Long Key Postlarvae Collectors.


Postlarval Settlement habitat preference: Herrnkind and Butler 1986


Probability of transition between algal and crevice-dwelling: Childress dissertation?


Lobster movement rates: Schratwieser 1999; M. J. Butler, unpublished data


Temperature & Salinity effect on postlarval survival: Field and Butler 1994.

Salinity effect on juvenile movement: Butler unpublished data (raceway data)

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