The impact of marine reserves on exploited species with complex life histories: a modeling study using the Caribbean spiny lobster in Exuma Sound, Bahamas

William T. Stockhausen

College of William and Mary - Virginia Institute of Marine Science

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UMI
THE IMPACT OF MARINE RESERVES ON EXPLOITED SPECIES WITH
COMPLEX LIFE HISTORIES: A MODELING STUDY USING THE CARIBBEAN
SPINY LOBSTER IN EXUMA SOUND, BAHAMAS

A Dissertation
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Doctor of Philosophy

by
William T. Stockhausen
2001
APPROVAL SHEET

This dissertation is submitted in partial fulfilment of

the requirements for the degree of

Doctor of Philosophy

William T. Stockhausen, Jr.

Approved: September, 2001

Romuald N. Lipcius, Ph.D.
Committee Chairman/Advisor

Mark E. Patterson, Ph.D.

Emmett Duffy, Ph.D.

Carl T. Friedrichs, Ph.D.

Michael J. Fogarty, Ph.D.
NOAA/NMFS EASC
Wood's Hole, MA
DEDICATION

To Victoria Farrington and my parents, William and Joanne Stockhausen,

for their love and support,

and to the experiences which kindled my interest in marine science:

SCUBA diving in the kelp beds off White's Point and in the Channel Islands, California
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Chapter</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>CHAPTER 1. Introduction</td>
<td>2</td>
</tr>
<tr>
<td>2</td>
<td>CHAPTER 2. Joint Effects of Larval Dispersal, Population Regulation, Marine Reserve Design and Exploitation on Production and Recruitment in the Caribbean Spiny Lobster</td>
<td>14</td>
</tr>
<tr>
<td>3</td>
<td>CHAPTER 3. A Revised Population Dynamics Model for the Caribbean Spiny Lobster in Exuma Sound, Bahamas</td>
<td>49</td>
</tr>
<tr>
<td>4</td>
<td>CHAPTER 4. Model Sensitivity Analyses</td>
<td>103</td>
</tr>
<tr>
<td>5</td>
<td>CHAPTER 5. The Influence of Fishery Aggregation and Benthic Dispersal on the Performance of Marine Reserves</td>
<td>140</td>
</tr>
<tr>
<td>6</td>
<td>CHAPTER 6. Single large or several small marine reserves for the Caribbean spiny lobster?</td>
<td>177</td>
</tr>
<tr>
<td>7</td>
<td>CHAPTER 7. SUMMARY</td>
<td>189</td>
</tr>
<tr>
<td></td>
<td>VITA</td>
<td>192</td>
</tr>
</tbody>
</table>

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LIST OF TABLES

Chapter 2

Table 1. Parameters for the Caribbean spiny lobster pelagic life-history stage model.  .................................................................................................................................................. 23
Table 2. Parameters for the Caribbean spiny lobster benthic life-history stage model. ............................................................................................................................................ 24
Table 3. Baseline parameters for the Caribbean spiny lobster reproduction submodel. ........................................................................................................................................... 27
Table 4. Total annual larval production ($L_{P_{T}}$) and settlement ($S_{T}$) rates by hydrodynamic scenario for no exploitation, no reserve. Rates are individuals yr$^{-1}$. .................. 30
Table 5. Total annual larval production ($L_{P_{T}}$) and settlement ($S_{T}$) rates by hydrodynamic scenario for exploitation ($F = 1.0$ yr$^{-1}$) with no reserve. Rates are individuals yr$^{-1}$ ......................................................... 31

Chapter 3

Table 1. Baseline parameters for the planktonic sub-model component of the Caribbean spiny lobster model ........................................................................................................ 87
Table 2. Baseline parameters for the benthic sub-model component of the Caribbean spiny lobster model .............................................................................................................. 88
Table 3. Baseline parameters for the reproductive sub-model component of the Caribbean spiny lobster model ....................................................................................... 89

Chapter 4

Table 1. Scenarios for model sensitivity studies .................................................................................................................................................................. 116
Table 2. Cross-correlations for spatial patterns of larval production among the Hydrodynamic Scenarios (row x column). .................................................................................. 117
Table 3. Cross-correlations for spatial patterns of settlement among the Hydrodynamic Scenarios (row x column). .................................................................................. 117
Table 4. Cross-correlations for spatial patterns of larval production among the Larval Duration scenarios (row x column). For the baseline, $a_{PL} = 120$ d. .................. 118
Table 5. Cross-correlations for spatial patterns of settlement among the Larval Duration scenarios (row x column). For the baseline, $a_{PL} = 120$ d. .................. 118
Table 6. Cross-correlations for spatial patterns of larval production among the Boundary Porosity scenarios (row x column). For the baseline, the porosity of deepwater boundaries to larval transport ($\omega_{LB}^{DB}$) was 50%.

Table 7. Cross-correlations for spatial patterns of settlement among the Boundary Porosity scenarios (row x column). For the baseline, the porosity of deepwater boundaries to larval transport ($\omega_{LB}^{DB}$) was 50%.

Table 8. Cross-correlations for spatial patterns of larval production among the Puerulus Dispersal scenarios (row x column). For the baseline scenario, daily swimming speeds were 0.25 km d$^{-1}$ offshore, and 1.0 km d$^{-1}$ nearshore.

Table 9. Cross-correlations for spatial patterns of settlement among the Puerulus Dispersal scenarios (row x column). For the baseline scenario, daily swimming speeds were 0.25 km d$^{-1}$ offshore, and 1.0 km d$^{-1}$ nearshore.

Table 10. Cross-correlations for spatial patterns of larval production among the Benthic Dispersal scenarios (row x column).

Table 11. Cross-correlations for spatial patterns of settlement among the Benthic Dispersal scenarios (row x column).

Table 12. Cross-correlations for spatial patterns of larval production among the Benthic Habitat Variability scenarios (row x column).

Table 13. Cross-correlations for spatial patterns of settlement among the Benthic Habitat Variability scenarios (row x column).

Chapter 5

Table 1. Nominal level of effort, resulting in $F_m = 0.40$ in year 49 with no reserve, for the three Equal Fishing Mortality Fishery Scenarios.

Table 2. Estimated variance in (relative) average population growth rate associated with Reserve Location and Equal Effort Fishery Scenario, for the largest reserve size considered (20%). Reserve Location and EE Fishery Scenario were treated as random factors in a main effects analysis of variance to obtain expected mean square estimates. Standard formulas (Underwood, 1981) were used to compute the variance ($\sigma^2$) associated with each factor. The High Aggregation Fishery Scenario was excluded from the analysis (see text).

Table 3. Estimated variance in (relative) average population growth rate associated with Reserve Location and Equal Fishing Mortality (EFM) Fishery Scenario, for the largest reserve size considered (20%). Reserve Location and EFM Fishery Scenario were treated as random factors in a main effects analysis of variance to obtain expected mean square estimates. Standard formulas (Underwood, 1981) were used to compute the variance ($\sigma^2$) associated with each factor. The High Aggregation Fishery Scenario was excluded from the analysis (see text).
Table 4. Estimated variance in (relative) average population growth rate associated with Reserve Location and Benthic Dispersal Scenario, for the largest reserve size considered (20%). Reserve Location and Benthic Dispersal Scenario were treated as random factors in a main effects analysis of variance to obtain expected mean square estimates. Standard formulas (Underwood, 1981) were used to compute the variance ($\sigma^2$) associated with each factor.
Chapter 2

Figure 1. Exuma Sound, Bahamas. ................................................................. 20

Figure 2. Near-surface geostrophic current patterns (relative to 500 db) derived from CTD data collected during cruises in Exuma Sound (Hickey, 1995): (A) November 1993, (B) June 1994 ...................................................... 21

Figure 3. Conceptualized geometry for the complex life-history model. .................. 22

Figure 4. Probability of survival vs age for larvae and postlarvae using the baseline parameters for the pelagic submodel (Table 1). .................................................. 22

Figure 5. Probability of survival and size vs age for benthic life-history stages using the baseline parameters for the benthic submodel (Table 2). ............................. 25

Figure 6. (A) Temporal spawning patterns and (B) size-specific fecundity using the baseline parameters for the adult spawning submodel. .................................. 26

Figure 7. Computational model grid for Exuma Sound ......................................... 27

Figure 8. Marine reserve configurations used in simulations: (A) SE location, (B) NE location, (C) NW location, (D) SW location. Reserve sizes are given as a percentage of the coastline. (Note: smaller sizes are shown offset from the coast; not all sizes are illustrated) .................................................. 28

Figure 9. Spatial distribution in model year 50 of annual settlement (grey fill) and larval production (solid line) for the no-exploitation, no-reserve case under each hydrodynamic scenario: (A) D1, (B) AD1, (C) AD2 .............................................. 31

Figure 10. Spatial distribution in model year 50 of annual settlement (grey fill) and larval production (solid line) for the exploitation-only, no-reserve case under each hydrodynamic scenario: (A) D1, (B) AD1, (C) AD2 ............................................. 32

Figure 11. Effect of reserve configuration (size expressed as PAC, see text) and hydrodynamic conditions on larval production for the exploitation-with-reserve cases. The change in larval production was calculated as \(\frac{LP_{MR}}{LP_E} - 1\) x 100 (%), where \(LP_{MR}\) represents the total larval production in model year 50 for the exploitation-with-reserve case and \(LP_E\) represents the total larval production in model year 50 for the corresponding exploitation, no-reserve case. Model results are plotted as functions of reserve size (PAC) for each reserve location: SE (□), NE (△), NW (▼), and SW (◇). Results for each hydrodynamic scenario are graphed separately: (A) D1, (B) AD1, (C) AD2. ........................................... 33

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Figure 12. Effect of reserve configuration (size expressed as EPC, see text) and hydrodynamic conditions on larval production for the exploitation-with-reserve cases. The change in total larval production was calculated as for Figure 11. Model results are plotted as functions of reserve size (EPC) and shaded differently for each hydrodynamic scenario (D1, no shading; AD1, grey shading; AD2, black). A linear fit to the results is also shown for each hydrodynamic scenario. Reserve location is indicated by different symbols: SE (□), NE (△), NW (▽), and SW (○). .............................................................34

Figure 13. Effect of reserve configuration on catch (size expressed as PAC, see text) for the exploitation-with-reserve cases. The change in catch was calculated as \((C_{MR}/C_E - 1) \times 100\) (%), where \(C_{MR}\) represents the total catch in model year 50 for the exploitation-with-reserve case and \(C_E\) represents the total catch in model year 50 for the corresponding exploitation, no-reserve case. Model results are plotted as functions of reserve size (PAC) for each reserve location: SE (□), NE (△), NW (▽), and SW (○). Results are graphed separately for each hydrodynamic scenario: (A) D1, (B) AD1, (C) AD2. ...............................35

Figure 14. Effect of reserve configuration on catch (size expressed as EPC, see text) for the exploitation-with-reserve cases. The change in total catch was calculated as for Figure 13. Model results are plotted as functions of reserve size (EPC) for each reserve location: SE (□), NE (△), NW (▽), and SW (○). Results are graphed separately for each hydrodynamic scenario: (A) D1, (B) AD1, (C) AD2. ...................................................................................................................36

Chapter 3

Figure 1. Conceptual relationship among sub-models comprising full population model for a benthic invertebrate species with a complex life history. .........................90

Figure 2. Schematic illustrating the conceptual physical geometry and ecological processes for the population dynamics model. The oceanic region, \(\Omega\), is a (horizontal) 2-dimensional region with a 1-dimensional boundary, \(\Omega_B\), comprising either deep water or shallow coastal regions. The “coastal coordinate”, \(\theta\), defines locations along the boundary.......................................91

Figure 3. Exuma Sound, Bahamas. .................................................................92

Figure 4. Nearsurface geostrophic currents (Hickey, in press) observed in the sound: a) November, 1993; b) June, 1994. .................................................................93

Figure 5. Conceptualized life-history stages for \textit{Panulirus argus} (Latreille), the Caribbean spiny lobster: egg (not shown), a) phyllosome larva, b) puerulus postlarva, c) algal phase benthic juvenile, d) post-algal phase benthic juvenile, e) sub-adult, and f) adult.................................................................94

Figure 6. Ontogenetic habitat shifts for the Caribbean spiny lobster (after Lipcius and Cobb, 1994). .................................................................94
Figure 7. Temporal variation in the hydrodynamic pattern multipliers, $\varepsilon_Y$ and $\varepsilon_I$, for the November, 1993 and June 1994 hydrodynamic current patterns (see Fig. 4) for the baseline model scenario.................................................................95

Figure 8. Probability of survival vs. age for larvae (age $< a_{pl}$) and postlarvae (age $> a_{pl}$) for the baseline model scenario (see Table 1).................................................................95

Figure 9. Survival and growth vs. age during the benthic life-history stages for the baseline model scenario (Table 2). Density dependent effects were ignored.................................................................96

Figure 10. A) temporal spawning and hatching patterns, and b) size-specific fecundity for the baseline model scenario (see Table 3) .................................................................96

Figure 11. Numerical grid for the Caribbean spiny lobster/Exuma Sound application. Grid cells are 2.5 km x 2.5 km. The value of the "coastal coordinate", $\theta$, is shown at various locations around the grid boundary. The boundary across the mouth of the sound, between Long Island and Cat Island, is classified as a deepwater boundary; the remaining boundary is classified as coastal habitat.................................................................97

Figure 12. Model results for the baseline scenario: time series of regional adult abundance and larval production during the 30-year simulation period. .......... 98

Figure 13. Model results for the baseline scenario—the spatial distribution (along the coast) of annual larval production (line) and settlement (shaded bars) for the final model year. The location of the deepwater boundary across the mouth of the sound is indicated by the cross-hatched zone.................................................................99

Figure 14. Model results for the baseline scenario—the spatial distribution (along the coast) of adult abundance (line) and settlement (shaded bars) during the final model year: a) Spring (Julian day 90), b) Summer (Julian day 180), c) Fall (Julian day 270), and d) Winter (Julian day 364). Settlement patterns were time-integrated over the previous quarter-year (thus, the settlement pattern for Winter integrates instantaneous rates over Julian days 271-364), whereas patterns of adult abundance are for the day in question (thus, the pattern for Winter is that on Julian day 364). The location of the deepwater boundary across the mouth of the sound is indicated by the cross-hatched zone. .............. 100

Figure 15. Model results for the baseline scenario—regional benthic size distributions at four different times during the final model year: a) Spring (Julian day 90), b) Summer (Julian day 180), c) Fall (Julian day 270), and d) Winter (Julian day 364)..................................................................................101

Figure 16. Comparison of baseline model predictions and observed patterns at four field sites (Lipcius et al., 1997) for a) mean adult density and b) mean settlement. Model predictions were computed by averaging over a 50 km region approximating the extent of each field site. Observed values were averaged over 3 field seasons. Predicted and observed values were log-transformed and standardized prior to comparison. Agreement between model predictions and observed values would yield a slope close to 1.................................102
Chapter 4

Figure 1. Exuma Sound, Bahamas. The righthand figure also shows the computational grid for the pelagic sub-model, as well as values of the coastal coordinate (in km) at various locations along the coastal boundary of the sound. Spatial patterns relative to the coastline (i.e., settlement, abundance in different benthic life-history stages, and larval production) are graphed as functions of the coastal coordinate (see Results). ................................................................. 123

Figure 2. Nearsurface geostrophic current patterns used in the pelagic sub-model to drive larval and postlarval transport ................................................................. 124

Figure 3. Intra-annual variation of the multipliers $\varepsilon_N$ and $\varepsilon_J$ for each Hydrodynamic Scenario ............................................................................................................ 125

Figure 4. Variation in stage-specific habitat quality (i.e., carrying capacity) for each Habitat Variation scenario. The cross-hatched area indicates the deepwater boundary across the mouth of the sound. The wavelength for large scale variation (LSVwM, LSVwMM) is ~200 km; for small scale variation (SSVwM, SSVwMM) it is ~50 km. Regional habitat quality (i.e., spatially-averaged carrying capacity) is identical for all cases. For the “matched” cases (LSVwM, SSVwM), habitat quality for later benthic stages (sub-adult, dashed line; adult, dash-dotted line) is in-phase with that for early stages (algal phase, solid line; postalgal phase, dotted line); for “mismatched” cases (LSVwM, SSVwMM), habitat quality for later benthic stages is 180° out-of-phase with that for early stages .......................................................................................... 126

Figure 5. Spatial distributions of larval production (solid line) and settlement (shading) in model year 30 under different Hydrodynamic Scenarios: a) D1, b) AD1, c) AD2, d) AD12a, e) AD12b, f) AD12c. The cross-hatched area indicates the deepwater boundary across the mouth of the sound. See text for description of individual scenarios ................................................................................................................................. 127

Figure 6. Comparison of regional larval production (a, c) and settlement (b, d) during the final model year for the Hydrodynamic Scenario cases (see text for description of individual scenarios). In graphs a) and b), results are plotted using absolute scales; in graphs c) and d), results are plotted relative to the baseline scenario (AD12b) ................................................................................................................................. 128

Figure 7. Spatial distributions of larval production (solid line) and settlement (shaded bars) in model year 30 under different Boundary Porosity Scenarios: a) Closed System (porosity = 0%), b) baseline (50%), and c) Open System (100%). The cross-hatched area indicates the deepwater boundary across the mouth of the sound ................................................................................................................ 129

Figure 8. Regional larval production (a) and settlement (b), relative to the baseline scenario (porosity = 50%), during the final model year for the Boundary Porosity scenarios: 1) Closed (porosity = 0) and 2) Open (porosity = 100%). ................................................................................................................................. 130
Figure 9. Spatial distributions of larval production (solid line) and settlement (shaded bars) in model year 30 under different Larval Duration Scenarios: a) Short Duration (60 d), b) baseline (120 d), and c) Long Duration (180 d). The cross-hatched area indicates the deepwater boundary across the mouth of the sound.

Figure 10. Regional larval production (a) and settlement (b), relative to the baseline scenario (120 d larval period), during the final model year for the Larval Duration scenarios: Short (0.5 x baseline) and 2) Long (1.5 x baseline).

Figure 11. Spatial distributions of larval production (solid line) and settlement (shaded bars) in model year 30 for the Puerulus Dispersal scenarios: a) passive settlement (i.e., no swimming), b) baseline, and c) fast swimming (2 x baseline). The cross-hatched area indicates the deepwater boundary across the mouth of the sound.

Figure 12. Regional larval production (a) and settlement (b), relative to the baseline scenario, during the final model year for the Puerulus Dispersal scenarios: 1) passive (0 x baseline) and 2) fast swimming (2 x baseline).

Figure 13. Spatial distributions of larval production (solid line) and settlement (shading) in model year 30 under different Benthic Dispersal Scenarios: a) baseline, b) Very Slow (0.1 x baseline), c) Slow (0.3 x baseline), d) Fast (3 x baseline), and e) Very Fast (10 x baseline). The cross-hatched area indicates the deepwater boundary across the mouth of the sound.

Figure 14. Regional larval production (a) and settlement (b), relative to the baseline scenario, during the final model year for the Benthic Dispersal Ability scenarios: 1) Very Slow (0.1 x baseline), 2) Slow (0.3 x baseline), 3) Fast (3 x baseline), and 4) Very Fast (10 x baseline).

Figure 15. Spatial distributions of larval production (solid line) and settlement (shaded bars) during the final model year for the Benthic Habitat Variability scenarios: a) baseline, b) in-phase (matched) large scale variations (LSVwM), c) out-of-phase, mismatched large scale variations (LSVwMM), d) in-phase, matched small scale variations (SSVwM), and e) out-of-phase, mismatched small scale variation (SSVwMM). Average habitat quality is identical for all scenarios. The spatial pattern of sub-adult and adult habitat quality is shown in the upper third of each graph; the dotted line indicates completely unfit habitat. The spatial pattern of algal and post-algal phase habitat quality is either in phase (b and d) or out of phase (c and e) with the pattern shown. The cross-hatched area indicates the deepwater boundary across the mouth of the sound.

Figure 16. Regional larval production (a) and settlement (b), relative to the baseline scenario, during the final model year for the Benthic Habitat Variability scenarios: 1) in-phase (matched) large scale variations (LSVwM), 2) out-of-phase, mismatched large scale variations (LSVwMM), 3) in-phase, matched small scale variations (SSVwM), and 4) out-of-phase, mismatched small scale variation (SSVwMM).
Figure 17. Regional larval production (a) and settlement (b), relative to the baseline scenario, during the final model year for 10% variation in stage-specific carrying capacity (positive variation, dark bars; negative variation, light bars).

Chapter 5

Figure 1. Example of spatial allocation of fishing effort under the three Fishery Scenarios: No Aggregation (e = 0; dashed line), Proportional Aggregation (e = 1; dotted line), and High Aggregation (e = 20; solid line). The dotted line also corresponds to the spatial pattern of lobster abundance used to create this example.

Figure 2. Spatial configuration for the marine reserve scenarios (the 15% reserve size is not illustrated). Smaller reserves are shown offset from the coast for clarity.

Figure 3. Final spatial patterns of adult lobster abundance (line), and annual catch (shaded area) under Exploitation (No Reserves) for the different Fishery Scenarios: a) No Aggregation, b) Proportional Aggregation, and c) High Aggregation. Fishing effort was 0.4 yr\(^{-1}\) in each case. The cross-hatched area indicates the deepwater boundary across the mouth of Exuma Sound. The coefficient of spatial variation for adult abundance in these cases was: a) 1.96, b) 0.78, and c) 0.41.

Figure 4. Final spatial patterns of settlement under Exploitation (No Reserves) for the different Fishery Scenarios: a) No Aggregation, b) Proportional Aggregation, and c) High Aggregation. Fishing effort was 0.4 yr\(^{-1}\) in each case. The cross-hatched area indicates the deepwater boundary across the mouth of Exuma Sound where settlement does not occur. The patterns were highly correlated; correlation coefficients were: a-b) 0.95, b-c) 0.99, and c-a) 0.90.

Figure 5. Effective fishing mortality in model year 49, as a function of total fishing effort, for the three Fishery Aggregation Scenarios.

Figure 6. Model results for total catch during the final year of the Exploitation-Only cases, plotted as functions of total effort (a) and effective fishing mortality (b) for the three Fishery Aggregation Scenarios: No Aggregation (e = 0, circles), Proportional Aggregation (e = 1, squares), and High Aggregation (e = 20, triangles). The righthand graphs provide a "blow-up" for the area denoted by dotted rectangle in the corresponding lefthand graph.

Figure 7. Model results for larval production during the final year of the Exploitation-Only cases, plotted as functions of total effort (a, b) and effective fishing mortality (c, d) for the three Fishery Scenarios: No Aggregation (e = 0, circles), Proportional Aggregation (e = 1, squares), and High Aggregation (e = 20, triangles). The righthand graphs (b, d) provide a "blow-up" for the area denoted by dotted rectangle in the corresponding graph to the left.
Figure 8. Model results for population growth rate during the final year of the Exploitation-Only cases, plotted as functions of total effort (a, b) and effective fishing mortality (c, d) for the three Fishery Scenarios: No Aggregation (ε = 0, circles), Proportional Aggregation (ε = 1, squares), and High Aggregation (ε = 20, triangles). The righthand graphs (b, d) provide a "blow-up" for the area denoted by dotted rectangle in the corresponding graph to the left.

Figure 9. Model results for the effect of reserves on total catch during the final year of the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Equal Effort Fishing Scenarios [No Aggregation (ε = 0, circles), Proportional Aggregation (ε = 1, squares), and High Aggregation (ε = 20, triangles)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

Figure 10. Model results for the effect of reserves on total larval production during the final year of the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Equal Effort Fishing Scenarios [No Aggregation (ε = 0, circles), Proportional Aggregation (ε = 1, squares), and High Aggregation (ε = 20, triangles)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

Figure 11. Model results for the effect of reserves on mean population growth during reserve implementation for the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Equal Effort Fishing Scenarios [No Aggregation (ε = 0, circles), Proportional Aggregation (ε = 1, squares), and High Aggregation (ε = 20, triangles)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

Figure 12. Model results for the effect of reserves on total catch during the final year of the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Equal Fishing Mortality Fishing Scenarios [No Aggregation (ε = 0, circles), Proportional Aggregation (ε = 1, squares), and High Aggregation (ε = 20, triangles)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

Figure 13. Model results for the effect of reserves on total larval production during the final year of the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Equal Fishing Mortality Fishing Scenarios [No Aggregation (ε = 0, circles), Proportional Aggregation (ε = 1, squares), and High Aggregation (ε = 20, triangles)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.
Figure 14. Model results for the effect of reserves on mean population growth during reserve implementation for the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Equal Fishing Mortality Fishing Scenarios [No Aggregation (e = 0, circles), Proportional Aggregation (e = 1, squares), and High Aggregation (e = 20, triangles)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

Figure 15. Model results for the effect of reserves on total catch during the final year of the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Dispersal Scenarios [Very Low Dispersal (circles), Baseline Dispersal (squares), and Very High Dispersal (triangles)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

Figure 16. Model results for the effect of reserves on larval production during the final year of the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Dispersal Scenarios [Very Low Dispersal (circles), Baseline Dispersal (squares), and Very High Dispersal (triangles)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

Figure 17. Model results for the effect of reserves on mean population growth during reserve implementation for the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Dispersal Scenarios [Very Low Dispersal (circles), Baseline Dispersal (squares), and Very High Dispersal (triangles)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

Chapter 6

Figure 1. Cartoon of spatially-explicit spiny lobster population model. The life history is divided into pelagic (phyllosoma larvae and puerulus postlarvae) and benthic (algal, postalgal, and older juvenile stages followed by reproductively active adult stages) phases. The density of each pelagic phase is represented as a continuous function in space (x, y) and time within the 2-dimensional (horizontal) oceanic region. Similarly, the density of each benthic phase is represented as a continuous function of the 1-dimensional coastal coordinate (θ) and time. The model represents population dynamics in both regions using sets of partial differential equations.

Figure 2. Exuma Sound, Bahamas with overlay showing model spatial computational grid. Numbers indicate geographic locations corresponding to values (in km) of the coastal coordinate (θ in Fig. 1), a coordinate used to describe the spatial distribution, along the coastal margins of the sound, of the benthic life history stages.
Figure 3. A) Spatial pattern of near-surface geostrophic currents, computed from CTD observations, observed during November, 1993 (Hickey 2000). The small rectangle highlights the "twin gyre" feature (TGF). B) Snapshot of stochastic current pattern, based on TGFs, used to model advective transport of pelagic life history stages. Two TGFs are evident in the current field. .......................... 181

Figure 4. Spatial distributions of total larval production (dark grey bars), which reflects local adult abundance and size structure, and catch (solid line) over the final year of simulation for model runs incorporating the a) Single Large Reserve and b) Several Small Reserves Management Scenarios under the Fast Hydrodynamic Scenario. Reserve locations are indicated by coastal regions which are shaded light grey background; lobsters are vulnerable to the fishery in unshaded coastal areas. The coastal coordinate defines the spatial location of points along the edge of the sound as the distance, following the outside edge of the model grid in a counterclockwise fashion, from the southernmost point in the sound to the location of the point in question (see Fig. 2) .......... 183

Figure 5. Model results plotted as a function of Management Scenario (SL = Single Large Reserve, SS = Several Small Reserves, RE = Reduced Effort, NMA = No Management Action) for the performance indicators: a) total catch in the final model year (log scale), b) total larval production during the final model year (log scale), and c) average population growth rate over the 20 year period in which management strategies were applied. Hydrodynamic Scenario is indicated by fill shading: black = Slow scenario, grey = Fast scenario. Vertical bars (catch, larval production) or symbols (population growth) indicate mean values. Error bars indicate 95% confidence intervals. Horizontal bars at the top of each graph denote Management Strategies with significantly different effects (based on SNK multiple comparisons, \(P < 0.001\)); factor levels connected by the same bar were not significantly different. For catch and larval production, mean values and confidence intervals were back-transformed from log10-transformed data. .............................................. 184
ABSTRACT

Most benthic invertebrates and reef-associated fish undergo a dispersive, planktonic larval stage prior to settlement and metamorphosis into the juvenile and adult stages. In some species, settlement may be decoupled from adult abundance at local spatial scales if hydrodynamic conditions or larval behavior do not promote local retention. Similarly, spatial variability in postsettlement mortality or secondary dispersal by juveniles and adults may decouple spatial patterns of adult abundance from those of settlement. As a consequence, spatial patterns of settlement and adult abundance may be functionally related in a complex fashion.

Whether biotic/environmental factors control spatial patterns of abundance may have profound implications for conservation of exploited benthic marine species, particularly when patterns of exploitation are themselves spatially structured—as they are under management by marine reserves. As part of this dissertation, a spatially-explicit population dynamics model for the Caribbean spiny lobster in Exuma Sound, Bahamas was developed. The model is stage- and age-structured, and features dispersal of larvae from hatching sites via advection by hydrodynamic currents and diffusion, active migration of postlarvae into shallow nursery habitats, density-dependent survival and dispersal of benthic life-history stages (juveniles and adults), size-specific fecundity, and spatially-explicit exploitation rates.

The population dynamics model was used heuristically to investigate the joint effects of reserve design (i.e., size, location, number), exploitation, population regulation and larval dispersal via hydrodynamic currents on population abundance and fishery yield. Principal findings were that fishery yield and larval production were idiosyncratic functions of reserve size, substantially influenced by interactions between current patterns and reserve location. Also, use of a single “large” reserve led to population growth and fishery yields that were significantly larger than, or not different from, results obtained using a network of “small” reserves, an overall reduction in effort, or no management action whatsoever. In general, results from these studies lend support to the efficacy of marine reserves as a tool for rebuilding overexploited marine populations and creating sustainable fisheries. However, they also run counter to the notion that one can just “do it” to create successful reserves. Instead, the results of this dissertation suggest that haphazard reserve creation may lead to a false sense of security when reserves are situated in an area which either protects a small fraction of the population or constitutes a “sink” habitat for the population. Designing successful marine reserves requires knowledge of local and regional patterns of hydrodynamic transport and larval dispersal, as well as other species’ life-history characteristics, in order to select optimal reserve configurations.
THE IMPACT OF MARINE RESERVES ON EXPLOITED SPECIES WITH
COMPLEX LIFE HISTORIES: A MODELING STUDY USING THE CARIBBEAN SPINY
LOBSTER IN EXUMA SOUND, BAHAMAS
Chapter 1: Introduction

Most benthic invertebrates and reef-associated fish undergo a dispersive, planktonic larval stage prior to settlement and metamorphosis into the juvenile and adult stages (Thorson, 1950; Mileikovsky, 1971; Roughgarden et al., 1988; Leis, 1991). In some species, settlement may be decoupled from adult abundance at local spatial scales if hydrodynamic conditions or larval behavior do not promote local retention (Fogarty, 1997; Lipcius et al., 1997). Similarly, spatial and temporal variability in post-settlement mortality or secondary dispersal by juveniles and adults may decouple spatial patterns of adult abundance from those of settlement (Jones, 1991). As a consequence, spatial patterns of settlement and adult abundance may be functionally related in a complex fashion.

The manner in which biotic or environmental factors control spatial patterns of abundance at different life-history stages may have profound implications for the management of exploited benthic marine species, particularly if patterns of exploitation are themselves spatially structured. The use of marine reserves (no-take areas or harvest refugia, sensu Dugan and Davis, 1993), an increasingly popular strategy for fisheries management, imposes explicit constraints on spatial patterns of exploitation. However, the effects of interactions between natural factors controlling abundance and spatially-segregated exploitation are not well understood.

Marine reserves can be viable tools for sustainable fisheries management (Roberts and Polunin, 1991; Dugan and Davis, 1993) that potentially enhance fisheries through
two mechanisms: (1) local migration—surplus adults emigrate from reserves to adjacent areas and become vulnerable to the fishery; and (2) enhanced recruitment—larval or postlarval supply, settlement, and recruitment to the fishery are increased at regional scales due to surplus reproductive output from reserves. These mechanisms involve dramatically different spatial scales (i.e., local vs. regional) and processes (e.g., density-dependent migration vs. density-independent dispersal). The effectiveness of reserves for fisheries enhancement will therefore depend on the interaction between reserve design (i.e., size, shape, and location) and the relative importance of local versus regional processes in controlling spatial patterns of population abundance.

Numerous field studies of reserve function have demonstrated enhanced fisheries production of temperate and tropical reef fish (e.g., Alcala and Russ, 1990; Russ and Alcala, 1996) and invertebrates (e.g., Davis and Dodrill, 1980; Davis and Dodrill, 1989; Gitschlag, 1986; Yamasaki and Kuwahara, 1990) through local emigration. In contrast, field tests of enhanced recruitment by reserves remain elusive due to the difficulties in experimenting with the processes that control temporal and spatial variability in larval supply and recruitment success (Doherty, 1991; Doherty and Fowler, 1994; Man et al., 1995). Hence, much of the effort dealing with the effects of reserves on recruitment and fisheries production involve modeling efforts (Polacheck, 1990; Die and Watson, 1992; DeMartini, 1993; Quinn et al., 1993; Attwood and Bennett, 1995; Man et al., 1995; Holland and Brazee, 1996; Sladek Nowlis and Roberts, 1997; Sladek Nowlis and Roberts, 1999; Lauck et al., 1998; Hastings and Botsford, 1999; see also Guenette et al., 1998).

Previous modeling studies evaluating the effectiveness of marine reserves to enhance fishery yield and recruitment reached mixed conclusions. In two-habitat
Chapter 1

(reserve or exploited) patch cohort models with reduced mortality within the reserve, increasing reserve size enhanced spawning stock biomass per recruit (SSB/R), whereas yield per recruit (Y/R) was generally reduced in temperate (Polacheck, 1990) and coral reef (DeMartini, 1993) fish. Increased transfer rates of post-settlement individuals between reserve and fished areas, as well as increased fishing pressure outside the reserve, diminished the effects of increased reserve size; however, the positive effect on SSB/R from increased reserve size generally outweighed the negative effect on Y/R when transfer rates were independent of density (Polacheck, 1990; DeMartini, 1993).

Conversely, density-dependent transfer rates negated enhancement of SSB/R; reserves were unlikely to augment SSB/R in heavily exploited species without complementary regulation of effort and size composition in exploited areas (DeMartini, 1993).

Die and Watson (1992) used a two-patch model to address the utility of inshore marine reserves for enhancing the Australian penaeid shrimp fishery. Recruitment to the population occurred only in the closed area; migration from closed to open areas made animals vulnerable to capture by the fishery. Averaged over ranges of fishing and natural mortality rates, mean changes in Y/R for the three migration rates considered were negative at all reserve sizes. Y/R declined fastest with reserve size for the slowest migration rate. Conversely, mean value per recruit (V/R) initially increased with reserve size for all three migration rates; ultimately, it decreased with reserve size for the lower two migration rates. In all cases, the mean number of eggs per recruit increased with reserve size.

In a two-patch logistic model, population collapse of the red sea urchin, Strongylocentrus franciscanus, was prevented by a marine reserve, even at high levels of exploitation when the species was also subject to Allee effects in reproduction or
recruitment (Quinn et al., 1993). A more detailed age-structured, spatially-explicit model incorporating larval dispersal through simple diffusion produced similar results. Multiple small reserves spaced closer than the average distance of larval dispersal were more effective than larger, but fewer and more distantly spaced, reserves in sustaining the exploited population (Quinn et al., 1993).

Using a spatially explicit, age-structured model, Attwood and Bennett (1995) varied recruitment and dispersal according to the life-history characteristics of three sympatric surf-zone fish species targeted by shore anglers in South Africa. Recruitment was assumed to be independent of local abundance for one species (white steenbras, *Lithognathus lithognathus*) while recruitment-spawner biomass functions were used to compute local settlement rates for the other two species (galjoen, *Dichistius capensis*, and blacktail, *Diplodus sargus capensis*). Tag returns indicated little or no post-settlement movement for blacktail; consequently, dispersal was assumed to be via passive larval drift. Transfer rates for larval blacktail between adjacent model cells were determined assuming simple turbulent diffusion. Post-settlement transfer rates between model cells for white steenbras and galjoen were estimated from tag return data. The impact of reserve size and spacing on yield-per-recruit ($Y/R$) or yield ($Y$) was evaluated differently among the species. Because recruitment was assumed constant for white steenbras, model results for this species were evaluated in terms of $Y/R$ and spawning stock biomass per recruit ($SSB/R$), whereas results for galjoen and blacktail were evaluated in terms of $Y$ alone. For white steenbras, $SSB/R$ increased with reserve size, whereas $Y/R$ decreased (Attwood and Bennett, 1995). For a given reserve size, $SSB/R$ decreased as reserve spacing increased, whereas $Y/R$ increased. For galjoen, $Y$ increased dramatically as reserve size increased (Attwood and Bennett, 1995). For blacktail, closely-spaced
reserves optimized yield (Attwood and Bennett, 1995). No results regarding spawning stock were reported for galjoen or blacktail.

In a metapopulation model for tropical reef fish, the ratio of extinction rate to colonization rate in exploited patches was the key parameter determining optimal reserve size, defined as the fraction of habitat patches protected (Man et al., 1995). When fishing pressure was low or colonization rate high, maximum sustained yield was obtained without reserves; as fishing pressure increased or colonization rate decreased, the optimal fraction of patches set aside as reserves increased asymptotically to 0.5. For a given ratio, maximum sustained yield was obtained when half of all patches (reserve + exploited) were occupied at equilibrium.

Using a two patch model, Holland and Brazee (1996) examined the utility of marine reserves for fisheries management of the Gulf of Mexico red snapper from an economic perspective. Their model incorporated a stock-recruit relationship and the concept of the present value of harvest (PVH), which utilizes discounted values of future harvests over a given time horizon, to determine optimal reserve size. Increasing discount rates resulted in smaller optimal reserves sizes. Using a 60 year PVH time horizon, no combination of reserve size and fishing effort performed better than the MSY fishing effort (0.75) with no reserve. When fishing effort was slightly larger than MSY (0.75-1.0), optimal reserve sizes were negligibly small. However, when effort was much larger than MSY (1.5-2.0), optimal reserve sizes ranged from 15-20% and resulted in increased PVHs of 4-8% when compared with no reserve (Holland and Brazee, 1996).

In a two-patch model incorporating stochastic exploitation rates, the probability that stock abundance remained > 60% of carrying capacity after 20 years of exploitation at a given mean rate was a function of the reserve area (relative to total area) and the
coefficient of variation (cv) in the harvest rate (Lauck et al., 1998). For moderate cv’s, the chance of success declined rapidly as reserve size decreased below 70%. For higher cv’s, the probability of success was < 1 even when harvested areas were very small. Reserves allowed higher mean harvest rates, with consequent higher catches, while still protecting the stock (Lauck et al., 1998).

Sladek Nowlis and Roberts (1997; 1999) used two-patch models for several exploited coral reef species to examine short- and long-term effects of reserve establishment on fishery yields. Reserves were only effective in increasing fishery yields when fisheries were overexploited in the absence of a reserve. For a fixed reserve size, greatly overexploited fisheries recovered faster than more lightly-exploited ones from initial losses associated with reserve establishment (Sladek Nowlis and Roberts, 1997). For a fixed fishing intensity, larger reserves resulted in higher catches after 30 years (Sladek Nowlis and Roberts, 1997). Optimal reserve size (that which produced the highest long-term yield for a given fishing intensity) increased with fishing intensity while yields associated with optimal reserves were similarly high over a range of fishing intensities for most of the species considered (Sladek Nowlis and Roberts, 1999).

Finally, Hastings and Botsford (1999) demonstrated that a system of optimally-sized marine reserves in a two-patch model could achieve maximum yields identical to that possible under allocation of a fixed fraction of a stock to a fishery—a more traditional management approach.

The principal mechanism determining spatial structure in these models is the spatial pattern of exploitation. A major assumption in many of these models (Polacheck, 1990; DeMartini, 1993; Attwood and Bennett, 1995; Man et al., 1995; Sladek Nowlis and Roberts, 1997; Sladek Nowlis and Roberts, 1999; Hastings and Botsford, 1999) is that
larvae are so well-mixed over the area the population occupies that relative recruitment to reserve and exploited areas is identical to the proportion of each relative to the total area. As a consequence, reserve function is evaluated in terms of reserve size and, possibly, spacing. However, hydrodynamic current patterns may play an important role in how a marine reserve functions (Carr and Reed, 1993). Through advective transport of larvae, hydrodynamic currents can impose spatial structure on settlement at regional scales for benthic species (Tremblay et al., 1994; Lipcius et al., 1997). Hydrodynamic conditions may thus modify patterns of connectivity among widely-separated sub-populations. Consequently, the interaction between hydrodynamic currents (Fogarty, 1997; Lipcius et al., 1997) and the location of spawning stock may determine the optimal design of reserves for widely dispersing marine species (Carr and Reed, 1993; Roberts, 1997).

Thus, reserve location may be equally as important as size in determining reserve performance. Because previous empirical and theoretical studies have not addressed this issue, the primary objective of my dissertation is to model the joint effects of hydrodynamic current pattern (with concomitant larval dispersal) and marine reserve configuration (location and size) on reserve function for an exploited benthic invertebrate with a widely-dispersing larval phase. Specifically, I wish to determine whether: 1) reserves of similar size but different locations function equivalently for a given pattern of larval dispersal, 2) reserves of similar size and location function equivalently under different patterns of larval dispersal, and 3) "optimal" reserve size and location are similar under different patterns of larval dispersal. The model I developed integrates the effects of reserve size and location, larval transport via oceanic currents, post-settlement dispersal and mortality, and adult spawning upon the population dynamics of a commercially exploited benthic invertebrate with a complex life history. The results
presented here are based on the Caribbean spiny lobster, *Panulirus argus*, in Exuma Sound, Bahamas as the model system.

The remainder of this dissertation is divided into five chapters. In Chapter 2, I present the results of a study which focuses principally on the joint effects of larval dispersal, hydrodynamic transport patterns, and marine reserve configuration on reserve design. This study used the "original" version of the complex life history model for the spiny lobster/Exuma Sound model system; the model is explained in the chapter and a succeeding appendix in detail. Chapter 2 was recently published as Stockhausen *et al.* (2000).

In Chapter 3, I discuss a "revised" spiny lobster/Exuma Sound model. I also compared results from the model, using a baseline set of parameters, to results from the field study reported in Lipcius *et al.* (1997). The revised model differs from the original (discussed in Chapter 2) in several important respects. Most significantly, the revised model allows for time-varying spatial patterns for hydrodynamic currents and possible aggregation of fishing effort in areas with relatively high population densities. Although somewhat redundant and perhaps rather tedious, I included a complete description of the revised model in this chapter—rather than simply detailing the changes to the original model. I believe, however, that this approach is worthwhile, as it consolidates future references to the model features.

In Chapter 4, I discuss the results from a sensitivity study of the revised model. Basically, I varied baseline model parameters and analyzed the resulting changes in regional and local abundance patterns to assess model robustness.

I considered the impact that differences in fisher and lobster behavior may have on the function of marine reserves for the study reported in Chapter 5. I used the model
to test whether the degree to which fishers target locally high densities of lobsters has a substantial effect on the function of marine reserves. I also assessed the degree to which benthic dispersal by lobsters (i.e., local migration) may impact reserve function.

Finally, I addressed the so-called SLOSS (Single Large or Several Small) issue of reserve area configuration for the study reported in Chapter 6. I used the spiny lobster/Exuma Sound model to compare differences in reserve function between equally-sized reserve areas configured as either a Single Large reserve or a network of smaller reserves. I also considered whether changes in the spatiotemporal scale of the hydrodynamic currents which influenced larval dispersal would alter the conclusions regarding SLOSS. Chapter 6 was recently accepted for publication as Stockhausen and Lipcius (in press) by Marine and Freshwater Research for its issue covering the proceedings of the 6th International Conference and Workshop on Lobster Biology and Management (September 2000, Key West FL). The first galley proofs of the version accepted for publication are reproduced here.
Chapter 1

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Chapter 1


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Chapter 2: Joint Effects of Larval Dispersal, Population Regulation, Marine Reserve Design and Exploitation on Production and Recruitment in the Caribbean Spiny Lobster

Published as:

JOINT EFFECTS OF LARVAL DISPERSAL, POPULATION REGULATION, MARINE RESERVE DESIGN, AND EXPLOITATION ON PRODUCTION AND RECRUITMENT IN THE CARIBBEAN SPINY LOBSTER

William T. Stockhausen, Romuald N. Lipcius and Barbara M. Hickey

ABSTRACT

A spatially explicit population-dynamics model for the Caribbean spiny lobster (*Panulirus argus*) in Exuma Sound, Bahamas, was used to investigate the joint effects of marine reserve design and larval dispersal via hydrodynamic currents on an exploited benthic invertebrate. The effects of three hydrodynamic scenarios (one diffusion-only and two advection-diffusion cases), one exploitation level, and 28 reserve configurations (7 sizes x 4 locations) on catch and larval production were simulated. The diffusion-only scenario represented the condition in which settlement did not vary substantially over broad spatial scales; in contrast, the advection-diffusion scenarios represented realistic hydrodynamic patterns and introduced broad spatial variation. Both advection-diffusion scenarios were based on empirical measurements of near-surface flow in Exuma Sound. Catches were sensitive to interactions between reserve configuration and pattern of larval dispersal. A given reserve configuration led to enhancement or decline in catch, depending on the hydrodynamic scenario, reserve size, and reserve location. Larval production increased linearly with reserve size, when size was expressed as the population fraction initially protected by the reserve, but when reserve size was expressed as the fraction of coastline protected, larval production decreased for some reserve configurations under the two advection-diffusion hydrodynamic scenarios. Use of a simple reserve-design rule (e.g., protect 20% of a coast) would, in the latter cases, lead to a false sense of security—thereby endangering—not protecting—exploited stocks. The optimal design of marine reserves therefore requires attention to the joint effects of larval dispersal, reserve location, and reserve size on fishery yield and recruitment.

Most benthic invertebrates and reef-associated fish undergo a dispersive, planktonic larval stage before settlement and metamorphosis into the juvenile and adult stages (Thorson, 1950; Mileikovsky, 1971; Roughgarden et al., 1988; Leis, 1991). In some species, settlement may be decoupled from adult abundance at local spatial scales if hydrodynamic conditions or larval behavior do not promote local retention (Fogarty, 1998; Lipcius et al., 1997). Similarly, spatial and temporal variability in postsettlement mortality or secondary dispersal by juveniles and adults may decouple spatial patterns of adult abundance from those of settlement (Jones, 1991). Spatial patterns of settlement and adult abundance may therefore be functionally related in a complex fashion.

The manner in which biotic or environmental factors control spatial patterns of abundance at different life-history stages may have profound implications for the management of exploited benthic marine species, particularly if patterns of exploitation are themselves spatially structured. The use of marine reserves (no-take areas or harvest refugia, sensu Dugan and Davis, 1993), an increasingly popular strategy for fisheries management, imposes explicit constraints on spatial patterns of exploitation, but the effects of interactions between natural factors controlling abundance and spatially segregated exploitation are not well understood.
Marine reserves can be viable tools for sustainable fisheries management (Roberts and Polunin, 1991; Dugan and Davis, 1993) that potentially enhance fisheries through two mechanisms: local migration (surplus adults emigrate from reserves to adjacent areas and become vulnerable to the fishery) and enhanced recruitment (larval or postlarval supply, settlement, and recruitment to the fishery are increased at regional scales by surplus reproductive output from reserves). These mechanisms involve dramatically different spatial scales (local and regional) and processes (e.g., density-dependent migration and density-independent dispersal). The effectiveness of reserves for fisheries enhancement will therefore depend on the interaction between reserve design (i.e., size, shape, and location) and the relative importance of local and regional processes in controlling spatial patterns of population abundance.

Numerous field studies of reserve function have demonstrated enhanced fisheries production of temperate and tropical reef fish (e.g., Alcala and Russ, 1990; Russ and Alcala, 1996) and invertebrates (e.g., Davis and Dodrill, 1980, 1989; Gitschlag, 1986; Yamasaki and Kuwahara, 1990) through local emigration. In contrast, field demonstration of enhancement of recruitment by reserves remains elusive because of the difficulties in experimenting with the processes that control temporal and spatial variability in larval supply and recruitment success (Doherty, 1991; Doherty and Fowler, 1994; Man et al., 1995). Much of the effort dealing with the effects of reserves on recruitment and fisheries production therefore involves modeling efforts (Polacheck, 1990; Die and Watson, 1992; DeMartini, 1993; Quinn et al., 1993; Attwood and Bennett, 1995; Man et al., 1995; Holland and Brazee, 1996; Sladek Nowlis and Roberts, 1997, 1999; Lauck et al., 1998; Hastings and Botsford, 1999; see also Guénette et al., 1998).

Previous modeling studies evaluating the effectiveness of marine reserves in enhancing fishery yield and recruitment reached mixed conclusions. In two-habitat (reserve and exploited) patch cohort models with reduced mortality within the reserve, increasing reserve size increased spawning-stock biomass per recruit (SSB/R), whereas yield per recruit (Y/R) was generally reduced in temperate (Polacheck, 1990) and coral-reef (DeMartini, 1993) fish. Increasing transfer rates of postsettlement individuals between reserve and fished areas, as well as increasing fishing pressure outside the reserve, diminished the effects of increased reserve size, but the positive effect on SSB/R from increased reserve size generally outweighed the negative effect on Y/R when transfer rates were independent of density (Polacheck, 1990; DeMartini, 1993). Conversely, density-dependent transfer rates negated enhancement of SSB/R; reserves were unlikely to augment SSB/R in heavily exploited species without complementary regulation of effort and size composition in exploited areas (DeMartini, 1993).

Die and Watson (1992) used a two-patch model to address the utility of inshore marine reserves for enhancing the Australian penaeid shrimp fishery. Recruitment to the population occurred only in the closed area; migration from closed to open areas made animals vulnerable to capture by the fishery. Averaged over ranges of fishing and natural mortality rates, mean changes in Y/R for the three migration rates considered were negative at all reserve sizes. Y/R declined fastest with reserve size for the slowest migration rate. Conversely, mean value per recruit (V/R) initially increased with reserve size for the lowest two migration rates; ultimately, it decreased with reserve size for the lower two migration rates. In all cases, the mean number of eggs per recruit increased with reserve size.

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In a metapopulation model for tropical reef fish, the ratio of extinction rate to colonization rate in exploited patches was the key parameter determining optimal reserve size, defined as the fraction of habitat patches protected (Man et al., 1995). When fishing pressure was low or colonization rate high, maximum sustained yield (MSY) was obtained without reserves; as fishing pressure increased or colonization rate decreased, the optimal fraction of patches set aside as reserves increased asymptotically to 0.5. For a given ratio, MSY was obtained when half of all patches (reserve + exploited) were occupied at equilibrium.

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In a two-patch model incorporating stochastic exploitation rates, the probability that stock abundance remained >60% of carrying capacity after 20 yrs of exploitation at a
given mean rate was a function of the reserve area (relative to total area) and the coefficient of variation (cv) in the harvest rate (Lauck et al., 1998). For moderate cv's, the chance of success declined rapidly as reserve size decreased below 70%. For higher cv's, the probability of success was <1 even when harvested areas were very small. Reserves allowed higher mean harvest rates, with consequent higher catches, while still protecting the stock.

Sladek Nowlis and Roberts (1997, 1999) used two-patch models for several exploited coral-reef species to examine short- and long-term effects of reserve establishment on fishery yields. Reserves were only effective in increasing fishery yields when fisheries were overexploited in the absence of a reserve. For a fixed reserve size, greatly overexploited fisheries recovered faster than more lightly exploited ones from initial losses associated with reserve establishment (Sladek Nowlis and Roberts, 1997). For a fixed fishing intensity, larger reserves resulted in higher catches after 30 yrs (Sladek Nowlis and Roberts, 1997). Optimal reserve size (the size that produced the highest long-term yield for a given fishing intensity) increased with fishing intensity, and yields associated with optimal reserves were similarly high over a range of fishing intensities for most of the species considered (Sladek Nowlis and Roberts, 1999).

Finally, Hastings and Botsford (1999) demonstrated that a system of optimally sized marine reserves in a two-patch model could achieve maximum yields identical to that possible under allocation of a fixed fraction of a stock to a fishery—a more traditional management approach.

The principal mechanism determining spatial structure in these models is the spatial pattern of exploitation. A major assumption in many of these models (Polacheck, 1990; DeMartini, 1993; Attwood and Bennett, 1995; Man et al., 1995; Sladek Nowlis and Roberts 1997, 1999; Hastings and Botsford, 1999) is that larvae are so well mixed over the area the population occupies that relative recruitment to reserve and exploited areas is identical to the proportion of each relative to the total area. As a consequence, reserve function is evaluated in terms of reserve size and, possibly, spacing. However, hydrodynamic current patterns may play an important role in how a marine reserve functions (Carr and Reed, 1993). Through advective transport of larvae, hydrodynamic currents can impose spatial structure on settlement at regional scales for benthic species (Tremblay et al., 1994; Lipcius et al., 1997). Hydrodynamic conditions may thus modify patterns of connectivity among widely separated subpopulations. Consequently, the interaction between hydrodynamic currents (Lipcius et al., 1997; Fogarty, 1998) and the location of spawning stock may determine the optimal design of reserves for widely dispersing marine species (Carr and Reed, 1993; Roberts, 1997).

Reserve location may therefore be as important as size in determining reserve performance. Because previous empirical and theoretical studies have not addressed this issue, our primary objective is to model the joint effects of hydrodynamic current pattern (with concomitant larval dispersal) and marine reserve configuration (location and size) on reserve function for an exploited benthic invertebrate with a widely dispersing larval phase. Specifically, we wish to determine (1) whether reserves of similar size but different locations function equivalently for a given pattern of larval dispersal, (2) whether reserves of similar size and location function equivalently under different patterns of larval dispersal, and (3) whether 'optimal' reserve size and location are similar under different patterns of larval dispersal. The model we use integrates the effects of reserve size and location, larval transport via oceanic currents, postsettlement dispersal and mor-
tality, and adult spawning on the population dynamics of an exploited benthic invertebrate with a complex life history. Model parameters are based on the life history of the Caribbean spiny lobster, *Panulirus argus*, in Exuma Sound, Bahamas. The use of marine reserves to enhance spiny lobster fisheries is a topic of interest (see, e.g., Davis and Dodrill, 1980; Childress, 1997; Acosta, 1999), so our choice of model system is applicable as a heuristic examination for both spiny lobster and other exploited species with complex life histories.

**Methods**

In this study, we focus on interactions between patterns of larval dispersal (and subsequent juvenile recruitment) and reserve configuration (i.e., size and location). As part of recent (Lipcius et al., 1997) and continuing work with Caribbean spiny lobster, *P. argus*, in Exuma Sound, Bahamas, we have developed a preliminary population-dynamics model for this system that encompasses demographic processes during all life-history stages and 'closes the larval loop', coupling postsettlement benthic population dynamics, adult spawning, and planktonic larval dispersal (Gaines and Lafferty, 1995; Eckman, 1996). The model is preliminary, however; we use it here as a heuristic tool to explore the impact of hypothetical reserves on a hypothetical population described by the model. Our model extends the two-dimensional spatially structured, coupled planktonic/benthic population model of Possingham and Roughgarden (1990) to include multiple pelagic and benthic life-history stages, curvilinear coastal geometry and complex current patterns, and postsettlement dispersal. For this study, we also incorporated spatial variation in fishing mortality to accommodate reserve-exploited area distinctions. We used the model to simulate the population dynamics of spiny lobster in Exuma Sound, with concomitant fishery yields, for a combination of different hydrodynamic current patterns, exploitation rates, and marine-reserve configurations.

**Life History of *Panulirus argus***.—The Caribbean spiny lobster is a macrobenthic invertebrate with widely dispersing larvae and supports commercially valuable fisheries in Florida and the Caribbean (Bohnsack et al., 1994). Like other spiny lobster species, *P. argus* exhibits five distinct life-history stages: egg, phyllosoma larva, puerulus postlarva, benthic juvenile, and adult (Phillips et al., 1980; Lipcius and Cobb, 1994; Lipcius and Eggleston, in press). The larval and postlarval stages constitute the pelagic phase of the spiny lobster life history. Phyllosome larvae are released from eggs hatched on the seaward fringes of coral reefs. Subsequently, the larvae lead an oceanic planktonic existence during which they progress through approximately 11 larval stages, while growing from less than 1 mm to 12 mm carapace length (CL; Lewis, 1951; Lyons, 1980). After 4–9 mo in the plankton, surviving larvae undergo radical metamorphosis to the transparent, nonfeeding puerulus postlarval stage, which is about 6 mm CL (Lewis, 1951; Lewis et al., 1952). Pueruli are vigorous swimmers and actively migrate into coastal waters, where they subsequently invade shallow inshore areas during nighttime flood tides associated with the new moon (Little, 1977; Calinski and Lyons, 1983; Herrkind and Butler, 1986; Eggleston et al., 1998). The pueruli settle to the benthos in structurally complex habitats such as clumps of red macroalgae (*Laurencia* spp.) or among mangrove roots (Marx and Herrkind, 1985; Butler and Herrkind, 1992). Within several days of settlement, surviving postlarvae acquire pigmentation and metamorphose into the first juvenile benthic instar.

On the basis of ontogenetic habitat shifts during the benthic juvenile stage, investigators agree in dividing this stage into three substages: algal phase, postalgal phase, and subadult (Marx and Herrkind, 1985; Herrkind and Butler, 1986; Eggleston et al., 1998). Algal-phase juveniles use the structurally complex settlement habitat for both shelter and foraging (Marx and Herrkind, 1985). They undergo a solitary existence, increasing in size through a series of molts from 6 to 25 mm CL over a period of several months. After reaching 15 mm CL, algal-phase lobsters begin to use crevices, tube sponges, and octocorals for shelter (Marx and Herrkind, 1985; Smith and Herrkind, 1992; Forcucci et al.,...
Postalgal-phase juveniles (15–45 mm CL) are fairly site-attached, staying within several meters of their daytime shelter (Hermkind and Butler, 1986). At night they emerge from these daytime shelters to forage for small molluscs and crustaceans in neighboring habitats (Andree, 1981; Hermkind et al., 1994). The gregarious behavior typical of older juveniles and adults is first exhibited during this stage (Berrill, 1975).

Subadults (>45 mm CL) are nomadic and forage widely in hard-bottom habitats and sea-grass/algae meadows (Hermkind, 1980, 1983). As they approach sexual maturity (~75 mm CL), larger juveniles migrate seaward toward offshore reefs (Hermkind and Lipcius, 1989).

Adults (>75–80 mm CL) are gregarious as well, dwelling in dens of 20 or more lobsters (Hermkind and Lipcius, 1989). Adult sex ratios are size dependent; males tend to be larger than females, reflecting greater female reproductive investment and differences in molting patterns (Lipcius and Hermkind, 1987; Hermkind and Lipcius, 1989). In Exuma Sound, peak reproductive activity occurs in spring (Hermkind and Lipcius, 1989).

Site.—Exuma Sound is a deep (>1000 m), semienclosed basin in the central Bahamas, surrounded by the Exuma Cays and the Great Bahama Bank to the north and west, by Eleuthera and Cat Island to the east, and by Long Island to the south (Fig. 1). Approximately 200 km northwest to southeast and 75 km at its widest, the sound has two connections to the Atlantic Ocean: a deep (2000 m depth) gap 50 km wide between Long and Cat islands and a shallow sill (15–30 m depth) 27 km wide between Eleuthera and Cat Island. Except for these openings, Exuma Sound is bordered by either low islands or shallow carbonate bank. Exuma Sound provides habitats for spiny lobster on all sides, making the system particularly well suited for analyses of the relationships between meteorology, oceanography, recruitment, and population dynamics.

Circulation in Exuma Sound appears to be dominated by large-scale, vigorous gyres extending to depths as great as 200 m (Fig. 2; Hickey, 1995). Water exchange with the open ocean occurs regularly, and exchange with the shallow banks also occurs through dense, high-salinity intrusions. Wind forcing plays an important role in the circulation by influencing the current structure in the

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Figure 1. Exuma Sound, Bahamas.
Figure 2. Near-surface geostrophic current patterns (relative to 500 db) derived from CTD data collected during cruises in Exuma Sound (Hickey, 1995): (A) November 1993, (B) June 1994.

upper 15 m of the water column. Mesoscale features with associated fronts are superimposed on a general northwestward drift and cause convergence and preferred pathways through the sound (Colin, 1993; Hickey, 1995). Although the gyres appear to be semipermanent features in the sound, they may oscillate seasonally (Fig. 2); substantial variability in near-surface currents exists at 10–30-d time scales (Hickey, 1995).

MODEL DESCRIPTION.—The full spiny lobster population dynamics model is composed of three coupled submodels: the pelagic model, the benthic model, and the reproduction model. The spatial
domain for the model consists of a two-dimensional (horizontal), oceanic region with its one-di­

dimensional boundary, the latter encompassing both shallow coastal regions, where settlement can

coccur, and deep-water regions, where it cannot (Fig. 3).

The pelagic model tracks changes in age-specific, spatially structured density of larvae, \( L_\text{pl} \), and 
postlarvae, \( L_p \), within the oceanic region due to (1) hatching of larvae following adult reproduction 
along the coast, (2) aging, (3) mortality, (4) horizontal dispersal via two-dimensional advective 
currents and turbulent diffusion, (5) metamorphosis from larval stage to postlarval stage, and (6) 
settlement in shallow coastal regions on the spatial boundary. We regard the pelagic densities as 
continuous functions of space (x, y), time (t), and age within stage (a), so we developed a set of 
coupled reaction-advection-diffusion partial differential equations (PDEs) with associated boundary 
conditions to describe the temporal and spatial dynamics of the planktonic stages (see Appen­
dix for details). Seasonal spawning and subsequent larval production within the shallow coastal 

Figure 3. Conceptualized geometry for the complex life-history model.

Figure 4. Probability of survival vs age for larvae and postlarvae using the baseline parameters for 
the pelagic submodel (Table 1).
Table 1. Parameters for the Caribbean spiny lobster pelagic life-history stage model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age at metamorphosis to postlarva, (a_{m})</td>
<td>120</td>
<td>d</td>
</tr>
<tr>
<td>Maximum postlarval age</td>
<td>60</td>
<td>d</td>
</tr>
<tr>
<td>Mortality coefficients</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(\mu_0)</td>
<td>0.08</td>
<td>d(^{-1})</td>
</tr>
<tr>
<td>(\mu_1)</td>
<td>0.05</td>
<td>d(^{-1})</td>
</tr>
<tr>
<td>Postlarval swimming speed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>offshore</td>
<td>0.5</td>
<td>km d(^{-1})</td>
</tr>
<tr>
<td>coastal</td>
<td>2.0</td>
<td>km d(^{-1})</td>
</tr>
<tr>
<td>Turbulent diffusivity, (K)</td>
<td>0.864</td>
<td>km(^{1}) d(^{-1})</td>
</tr>
<tr>
<td>Boundary leakage function</td>
<td></td>
<td></td>
</tr>
<tr>
<td>coastal, larval stage</td>
<td>0.0</td>
<td>(none)</td>
</tr>
<tr>
<td>deep-water, larval stage</td>
<td>0.5</td>
<td>(none)</td>
</tr>
<tr>
<td>coastal, postlarval stage</td>
<td>1.0</td>
<td>(none)</td>
</tr>
<tr>
<td>deep-water, postlarval stage</td>
<td>0.0</td>
<td>(none)</td>
</tr>
</tbody>
</table>

regions on the spatial boundary determine the local influx of age-0 planktonic larvae into the oceanic region; larvae are subsequently transported from their hatching grounds by spatially variable advective currents and dispersed through turbulent diffusion. For this study, larvae were subjected to a constant mortality rate, independent of density, location, age, and time of year (Table 1). Metamorphosis from the larval to the postlarval stage occurs as an instantaneous process at an age of 120 d. This value represents the lower end of probable larval duration (4-6 mo in Exuma Sound, up to 9 mo at extremes of the geographic range; Lipcius and Eggleston, in press), but the combination of mortality rate and stage duration means that less than 0.01% of larvae hatched survive until metamorphosis to postlarvae (Fig. 4).

Postlarvae are strong swimmers and actively migrate to settlement areas (Little, 1977; Calinski and Lyons, 1983; Herrnkind and Butler, 1986). In shallow areas, postlarvae attach to structures or bury themselves in sand (Calinski and Lyons, 1983), a behavior that may enhance onshore transport near the coast if synchronized with adverse tidal flows. We therefore added an active, deterministic component to postlarval dispersal in addition to advection by mean currents and dispersal through turbulent diffusion. We also assumed that postlarvae orient toward the nearest coastline (by means of some unspecified environmental cue, possibly chemical) so that the local direction of active migration was toward the nearest coastal region, while the effective speed of migration was higher near the coast than further offshore. The local age-integrated flux of postlarvae across the coastal boundary determines local settlement rates. Prior to settlement, postlarvae are subjected to a constant mortality rate (Table 1) such that approximately 10% survive after 30 d in the pelagic zone (Fig. 4). Postlarvae are a nonfeeding stage with an estimated duration of a few weeks (Booth and Phillips, 1994; Butler and Herrnkind, 1997); postlarvae that had not settled within 60 d of larval metamorphosis were therefore regarded as dead.

The benthic model tracks changes in the size-specific, spatially structured density along the coast for algal phase \(s_1\), postalgal phase \(s_2\), subadult \(s_3\), and adult (male, \(s_4\); female, \(s_5\)) life-history stages due to (1) settlement, (2) mortality, (3) growth within a life-history stage, (4) transition between successive life-history stages, and (5) alongshore dispersal. Like pelagic densities, the stage-specific benthic densities are continuous functions—but of size \(z\), rather than age; of space \(0, position along the one-dimensional spatial boundary which includes shallow, coastal and unsuitable, deep-water benthic habitats); and of time \(t\). Again, we used a set of coupled PDEs with associated boundary conditions to describe the population dynamics of the benthic life-history stages (see Appendix for details). Local settlement provides the population 'source' term for the benthic model. 'Settled' postlarvae metamorphose into algal-phase benthic juveniles in the 6–7–
Table 2. Parameters for the Caribbean spiny lobster benthic life-history stage model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Algal phase</th>
<th>Postalgal phase</th>
<th>Subadult</th>
<th>Adult male</th>
<th>Adult female</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat index, $\Psi_i$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$c_i$</td>
<td>5,000</td>
<td>5,000</td>
<td>2,500</td>
<td>1,000</td>
<td>1,000</td>
<td>No. km$^{-1}$</td>
</tr>
<tr>
<td>Stage size limits $z_i - z_{i-1}$</td>
<td>6–25</td>
<td>20–45</td>
<td>40–80</td>
<td>75–150</td>
<td>75–150</td>
<td>mm CL</td>
</tr>
<tr>
<td>Growth, $g_i$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\alpha_i$</td>
<td>0.009</td>
<td>0.002</td>
<td>0.002</td>
<td>0.0009</td>
<td>0.0009</td>
<td>d$^{-1}$</td>
</tr>
<tr>
<td>$\beta_i$</td>
<td>50</td>
<td>150</td>
<td>150</td>
<td>150</td>
<td>150</td>
<td>mm CL</td>
</tr>
<tr>
<td>Natural mortality, $\mu_i$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\epsilon_n$</td>
<td>0.01</td>
<td>0.005</td>
<td>0.0025</td>
<td>0.0009</td>
<td>0.0009</td>
<td>d$^{-1}$</td>
</tr>
<tr>
<td>$\epsilon_n$</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>(none)</td>
</tr>
<tr>
<td>$\epsilon_n$</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>(none)</td>
</tr>
<tr>
<td>Dispersal, $J_i$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$c_n^a$</td>
<td>0</td>
<td>0</td>
<td>0.05</td>
<td>0.01</td>
<td>0.01</td>
<td>km$^2$ d$^{-1}$</td>
</tr>
<tr>
<td>$c_n^a$</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>(none)</td>
</tr>
<tr>
<td>$c_n$</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>(none)</td>
</tr>
<tr>
<td>Life-history stage transition rates, $\tau_y$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$j \rightarrow i$</td>
<td>1 $\rightarrow$ 2</td>
<td>2 $\rightarrow$ 3</td>
<td>3 $\rightarrow$ 4</td>
<td>3 $\rightarrow$ 5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$c_{m}$</td>
<td>0.05</td>
<td>0.025</td>
<td>0.02</td>
<td>0.02</td>
<td></td>
<td>d$^{-1}$</td>
</tr>
<tr>
<td>$c_{m}$</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td></td>
<td>mm$^{-1}$</td>
</tr>
</tbody>
</table>
mm CL size range, typical of first benthic instars in Exuma Sound (Eggleston et al., 1998). We
decomposed total mortality rates into a sum of 'natural' and fishing mortalities. For this study,
natural mortality rates were functions of local stage-specific densities but did not otherwise depend
on size, location, or time. Availability of appropriately sized shelter appears to be a key factor in
regulating local abundance of benthic life-history stages (Butler and Herrkind, 1997; Lipcius and
Eggleston, in press) and probably results in density-vague (Strong, 1984) mortality rates. We used
piece-wise linear functions to describe density-dependent mortality rates—constant at low densi­
ties but increasing at high densities—for all benthic life-history stages (Table 2). When density is
low, approximately 4% of settlers survive 2 yrs (Fig. 5). Local fishing mortality rates were stage-
specific, size-structured, seasonal, and spatially explicit (see below). Although individual spiny
lobsters increase in size through discrete molting events, we described growth as a continuous
process because molting is not synchronous and the model deals with distributions rather than
individuals (Botsford, 1985). We used a simple Gompertz-type growth function (see Appendix)
with density-independent parameters to describe growth rates within a stage. Selected parameter
values (Table 2) result in reasonable postsettlement growth histories (Fig. 5). Size ranges for subse­
quent life-history stages overlap, and transition from one benthic stage to the next sometimes oc­
curs without growth; transition rates from the earlier stage increase with size within this range of
overlap. After reaching maturity, males exhibit higher size-specific growth rates than females, re­
flecting the greater metabolic investment in reproduction by females (Lipcius, 1985), so the model
includes both male and female adult stages. For this study, however, males and females are treated
deceptively. Although subadult spiny lobsters in other areas of the Caribbean engage in (sometimes
spectacular) seasonal migrations (Kanciruk and Herrkind, 1978; Herrkind, 1980, 1983), such
activity has not been observed in Exuma Sound, where alongshore movements are nomadic
(Herrkind and Lipcius, 1989). We therefore described postsettlement dispersal along the coast as
a density-dependent diffusion process; we did not include deterministic movement (i.e., an advect­
tive component) such as seasonal migrations.

The reproduction model tracks temporal and spatial variation in spawning and subsequent larval
production along the coast, incorporating spawning seasons, size-specific fecundity, and size-spe­
cific adult female density (see Appendix for details). Larval production (i.e., spawning and hatch­
ing) begins in the late winter, peaks in the spring, and ends in the summer. We used a truncated
normal distribution to approximate seasonal spawning rates (Table 3, Fig. 6A). We assumed fe­
cmales mature at 75 mm CL (Herrkind and Lipcius, 1989; Lipcius et al., 1997). Because Lipcius et
al. (1997) found no difference in spatial variation in fecundity in Exuma Sound, we describe
individual fecundity as an exponential function of adult size, but independent of local density,
spatial location, and season (Fig. 6B). Parameters were based on a previous analysis of the fecun-

Figure 5. Probability of survival and size vs age for benthic life-history stages using the baseline
parameters for the benthic submodel (Table 2). Density dependence is ignored.
Figure 6. (A) Temporal spawning patterns and (B) size-specific fecundity using the baseline parameters for the adult spawning submodel (Table 3).

dity data used by Lipcius et al. (1997, see Table 3). The instantaneous rate of local larval production is the size-integrated product of size-specific fecundity and local adult density, weighted by the seasonally varying spawning rate. Coming full circle and “closing the larval loop” (Eckman, 1996), the local rate of larval production in coastal regions along the spatial boundary determines the flux of age-0 planktonic larvae into the oceanic region in the pelagic model.

Given the complexity of the model, it is not feasible to obtain analytical solutions to problems we wish to address, so we developed a numerical representation of the model based on standard techniques for integrating spatially structured, coupled PDEs. We also constructed a grid representation of Exuma Sound using 2.5- x 2.5-km² cells from a digitized map of Exuma Sound (Fig. 7). The grid consists of 1872 interior cells and 254 boundary sections. Of the 254 boundary sections, 21 contiguous sections constitute a deep-water boundary (52.5 km) representing the primary connection between Exuma Sound and the Atlantic at the southeast corner of the sound; the remaining sections constitute coastline available for settlement (582.5 km). Because there is no evidence for larval transport across the shallow sill between Cat Island and Eleuthera (Colin, 1995), we modeled this region as coastal habitat across which larvae do not disperse. We used a 1-d time step to integrate the model numerically for up to 50 model yrs.
Table 3. Baseline parameters for the Caribbean spiny lobster reproduction submodel.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maturity, $m_0$</td>
<td></td>
<td>(none)</td>
</tr>
<tr>
<td>$c_1$</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>$c_2$</td>
<td>80</td>
<td>mm CL</td>
</tr>
<tr>
<td>Spawning rate, $r_1$</td>
<td>90-180</td>
<td>Julian day</td>
</tr>
<tr>
<td>$c_1$</td>
<td>0.0115</td>
<td>d$^{-1}$</td>
</tr>
<tr>
<td>$c_2$</td>
<td>135</td>
<td>d</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>d</td>
</tr>
<tr>
<td>Fecundity, $F_1$</td>
<td>$3.69 \times 10^3$</td>
<td>No. eggs</td>
</tr>
<tr>
<td>$c_1$</td>
<td>0.0203</td>
<td>mm$^{-1}$</td>
</tr>
<tr>
<td>$c_2$</td>
<td>75</td>
<td>mm CL</td>
</tr>
</tbody>
</table>

**Model Cases.** To examine several different patterns of connectivity (via larval dispersal) in the study, we defined three hydrodynamic scenarios, consisting of two advection-diffusion cases (AD1 and AD2) and one diffusion-only case (D1), to incorporate the potential for differing patterns of spatial structure through larval dispersal. The diffusion-only scenario represented the condition in which settlement did not vary substantially over broad spatial scales, in contrast to the advection-diffusion scenarios, which represented realistic hydrodynamic transport conditions and broad spatial variation in the field. The advective currents for AD1 and AD2 were based on near-surface (5 m...
Figure 8. Marine reserve configurations used in simulations: (A) SE location, (B) NE location, (C) NW location, (D) SW location. Reserve sizes are given as percentage of the coastline. (Note: smaller sizes are shown offset from the coast; not all sizes used are illustrated.)
depth) geostrophic currents in Exuma Sound derived from physical oceanographic data collected during November 1993 and June 1994 (Fig. 2), respectively. For both cases, the current pattern was fixed temporally. For D1, the advective currents were set to zero. Eddy-diffusion coefficients were identical for all three scenarios.

Model scenarios with no exploitation were created for each hydrodynamic current pattern; subsequently, the model was numerically integrated similarly for each case. Parameters reflecting mortality, growth, dispersal, and reproduction were identical for all three scenarios. Initial abundance patterns for each life-history stage were set to zero. Each model was started when larvae were 'injected' into the pelagic submodel at constant rates along the model boundary during the first three spawning seasons. After year 3, injection was discontinued, and the population continued to grow under its own dynamics, typically reaching a steady state after 25 model yrs. The numerical model was integrated for 50 model yrs. The complete model state was saved at the beginning of model year 30 and used to initialize subsequent model runs for scenarios including exploitation. Abundance patterns for each postsettlement stage, larval production, and postlarval settlement were saved at quarterly intervals during the final 10 model yrs.

We created a "heavily exploited" case corresponding to each unexploited case using a nominal fishery mortality rate \( F \) of 1.0 yr\(^{-1}\). We adjusted the instantaneous rate of fishing mortality for a fishing season that ran from Julian day 181 to Julian day 365. Effort was uniformly distributed along the coast, and only adults larger than 75 mm CL were vulnerable to the fishery. For each case, the model state from the corresponding unexploited case at the beginning of model year 30 was used to initialize the simulation run. The model was subsequently integrated numerically for 20 yrs. The complete model state was saved at the beginning of model year 40 and used to initialize subsequent model runs for marine reserve scenarios. Spatially explicit, instantaneous catch rates, \( c(0,r) \), were calculated from the spatially explicit, stage-classified, size-specific densities \( s(z,0,t) \) and associated fishing-mortality rates. The spatial distribution of annual catch, \( C(0) \), was computed by integration of \( c(0,r) \) in time over each year. Total annual catch, \( C \), was then computed by integration of \( C(0) \) over the one-dimensional boundary.

Finally, we created 28 marine-reserve configurations (Fig. 8) using a multifactorial combination of four locations and seven sizes. The four reserve locations were chosen to be evenly distributed around the sound (roughly in its SE, NE, NW, and SW quadrants). We considered seven reserve sizes covering 5–40% of available coastal habitat. At the 40% size, adjacent reserves at different locations partially overlapped. Fishing effort displaced by the reserve was assumed to be evenly redistributed over the remaining coastal boundary region. We modified fishing-mortality rates to reflect the displaced effort by assuming that local rates of fishing mortality were proportional to local rates of effort (see, e.g., Polacheck, 1990). Thus, the nominal rate of fishing mortality in the exploited region, \( F_{m} \), after creation of a marine reserve with length \( L_{m} \), was

\[
F_{m} = \frac{F}{1 - \frac{L_{m}}{L}}
\]

where \( F \) is the rate with no reserve (1.0 yr\(^{-1}\) here) and \( L \) is the total length of habitable coastline. For each case, the model state from the corresponding exploited case at the beginning of model year 40 was used to initialize the model run. The model was subsequently numerically integrated for 10 yrs. As with all model runs, abundance patterns for each postsettlement stage, larval production, and postlarval settlement were saved at quarterly intervals. As with the exploited cases, total catch was recorded annually.

For each hydrodynamic scenario, we thus generated a no-exploitation/no-reserve case, an exploitation/no-reserve case, and 28 exploitation-with-reserve cases. Starting from identical conditions (model year 30), the no-exploitation/no-reserve case reflects the state of the population under

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pristine conditions, the exploitation/no-reserve case reflects the state of the population and fishery after 20 yrs of heavy exploitation, and the exploitation-with-reserve cases reflect the state of the population and fishery after 10 yrs of heavy exploitation followed by 10 yrs of continued heavy exploitation but with a refuge area. We evaluate reserve function by comparing annual larval production and catch rates for the final year of each simulation.

RESULTS

NO EXPLOITATION, NO RESERVE.—Despite our use of identical parameter values for natural mortality, growth, dispersal, and reproduction, each hydrodynamic scenario imposed a dramatically different spatial pattern of settlement and larval production along the coastline (Fig. 9). When larvae were dispersed through turbulent diffusion alone (D1), settlement along the coastline was approximately constant for spatial scales greater than 10 km (Fig. 9A). When advection by hydrodynamic currents was included (AD1 and AD2), settlement was spatially segregated and variable: AD1 exhibited three to five principal peaks in settlement ~50–150 km apart (Fig. 9B), and AD2 showed a single peak ~50 km from the mouth of Exuma Sound (Fig. 9C). The spatial pattern of larval production reflected, to a large degree, the spatial pattern of settlement for each hydrodynamic scenario (Fig. 9), but density-dependent mortality in the early benthic stages and dispersal in the later stages modified the pattern of larval production from that of settlement, smearing out the pattern at settlement and reducing variability. For the advective current scenarios in which settlement was focused, postsettlement dispersal allowed larval production to occur over a somewhat larger expanse of the coastline than that at which settlement occurred (Fig. 9B,C).

Annual rates of total larval production ($L_P$) and settlement ($S_T$) varied by an order of magnitude among the three hydrodynamic scenarios (Table 4). Total settlement was highest for D1, lowest for AD2, and intermediate for AD1; the ordering was identical for larval production. The ratio $L_P/S_T$, however, differed among the hydrodynamic scenarios (Table 4), reflecting higher postsettlement mortality due to density dependence in the hydrodynamic cases where advection focused settlement patterns in particular regions (i.e., Fig. 9C for AD2).

EXPLOITATION, NO RESERVES.—The relative effect of exploitation on larval production and settlement depended on hydrodynamic scenario. The high exploitation rate ($F = 1.0 \text{ yr}^{-1}$) considered in this study led to dramatically lower total settlement and larval production than in the unexploited cases, for all three hydrodynamic scenarios (Table 5). The largest differences occurred for D1 (~3 orders of magnitude), the smallest for AD2 (~2 orders of magnitude). Exploitation increased total mortality rates, but relative changes in larval production and settlement were smaller under the advection-diffusion scenarios than under the diffusion-only scenario because relative increases in mortality rates were smaller under the advection-diffusion scenarios, reflecting higher local density-dependence.

<table>
<thead>
<tr>
<th>Hydrodynamic scenario</th>
<th>$L_P$</th>
<th>$S_T$</th>
<th>$L_P/S_T$</th>
</tr>
</thead>
<tbody>
<tr>
<td>D1</td>
<td>$2.1 \times 10^1$</td>
<td>$8.8 \times 10^0$</td>
<td>$2.3 \times 10^4$</td>
</tr>
<tr>
<td>AD1</td>
<td>$7.6 \times 10^0$</td>
<td>$4.7 \times 10^4$</td>
<td>$1.6 \times 10^4$</td>
</tr>
<tr>
<td>AD2</td>
<td>$8.9 \times 10^0$</td>
<td>$6.1 \times 10^3$</td>
<td>$1.5 \times 10^4$</td>
</tr>
</tbody>
</table>

Table 4. Total annual larval production ($L_P$) and settlement ($S_T$) rates by hydrodynamic scenario for no exploitation, no reserve. Rates are individuals yr$^{-1}$. Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
Figure 9. Spatial distribution in model year 30 of annual settlement (grey fill) and larval production (solid line) for the no-exploitation, no-reserve case under each hydrodynamic scenario: (A) D1, (B) AD1, (C) AD2.

Table 5. Total annual larval production ($LP_T$) and settlement ($S_r$) rates by hydrodynamic scenario for exploitation ($F = 1.0 \text{yr}^{-1}$) with no reserve. Rates are individuals yr$^{-1}$.

<table>
<thead>
<tr>
<th>Hydrodynamic scenario</th>
<th>$LP_T$</th>
<th>$S_r$</th>
<th>$LP_T/S_r$</th>
</tr>
</thead>
<tbody>
<tr>
<td>D1</td>
<td>$2.5 \times 10^4$</td>
<td>$1.1 \times 10^4$</td>
<td>$2.3 \times 10^6$</td>
</tr>
<tr>
<td>AD1</td>
<td>$6.2 \times 10^4$</td>
<td>$4.4 \times 10^4$</td>
<td>$1.4 \times 10^5$</td>
</tr>
<tr>
<td>AD2</td>
<td>$1.3 \times 10^4$</td>
<td>$9.9 \times 10^3$</td>
<td>$1.3 \times 10^4$</td>
</tr>
</tbody>
</table>
dent mortality, as a result of advection-focused settlement patterns, in the corresponding unexploited cases.

In addition, the spatial patterns of larval production and settlement were substantially altered under two hydrodynamic scenarios (D1, AD1; Fig. 10A,B) but not under the third (AD2; Fig. 10C). For all hydrodynamic scenarios, the spatial concordance among settlement, adult density, and larval production increased over the unexploited cases. Under diffusion alone (D1), the constriction and termination of the sound at its northwestern end (Fig. 1), coupled with vastly reduced larval production, actually increased relative local retention and led to higher settlement and subsequent adult abundance there than in other coastal regions. Under AD1, survival rates were spatially structured in the unexploited case because of density-dependent mortality during the early benthic stages—survival rates were lowest where settlement was highest, higher where settlement was low—but
high exploitation rates resulted in reduced settlement rates overall. Consequently, the effect of spatially heterogeneous, density-dependent mortality was reduced, and the pattern of local abundance more closely reflected that of settlement. For all three scenarios, high exploitation rates reduced postsettlement dispersal, potentially altering connectivity among regions within the sound.

**Exploitation with Reserves.**—When reserve size was expressed in terms of the fraction of the coastline covered by the reserve (the protected area coverage, PAC), the response of larval production to reserve configuration was not a function of reserve size alone but was also sensitive to reserve location and hydrodynamic scenario (Fig. 11). In D1, larval production increased rapidly with reserve size at all locations (Fig. 11A). In

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Figure 11. Effect of reserve configuration (size expressed as PAC, see text) and hydrodynamic conditions on larval production for the exploitation-with-reserve cases. The change in larval production was calculated as \((L_{PM}/L_{P_R}) \times 100\%)\), where \(L_{PM}\) represents the total larval production in model year 50 for the exploitation-with-reserve case and \(L_{P_R}\) represents the total larval production in model year 50 for the corresponding exploitation, no-reserve case. Model results are plotted as functions of reserve size (PAC) for each reserve location: SE (□), NE (△), NW (▽), and SW (●). Results for each hydrodynamic scenario are graphed separately: (A) D1, (B) AD1, (C) AD2.
Figure 12. Effect of reserve configuration (size expressed as EPC, see text) and hydrodynamic conditions on larval production for the exploitation-with-reserve cases. The change in total larval production was calculated as for Figure 11. Model results are plotted as functions of reserve size (EPC) and shaded differently for each hydrodynamic scenario (D1, no shading; AD1, grey shading; AD2, black). A linear fit to the results is also shown for each hydrodynamic scenario. Reserve location is indicated by different symbols: SE (□), NE (△), NW (▽), and SW (◇).

contrast, larval production under AD1 was reduced from that of the no-reserve case for several reserve locations when reserve size was small. When reserves were larger than 20%, however, larval production increased rapidly with size for all locations, as under D1 (Fig. 11B). In addition, variation in response among reserve locations at the same reserve size was greater for AD1 than for D1. In AD2, larval production responded positively to reserve size at only one location (SE), where larval production increased rapidly with reserve size, reaching an asymptote at a reserve size near 10% (Fig. 11C). For the other three reserve locations, larval production decreased with reserve size under AD2.

The dependence of the larval-production response on reserve location for a given hydrodynamic scenario disappears if reserve size is expressed in terms of the exploited population coverage (EPC) rather than PAC. We define EPC as the fraction of the exploited population (prior to reserve creation) that settled in the reserve area and would be protected under a given reserve configuration. Thus, EPC incorporates actual settlement rates in a reserve location, whereas PAC does not. Because the exploited populations, particularly under AD1 and AD2, exhibit substantial spatial heterogeneity (Fig. 10B,C), PAC and EPC are not equivalent. For all three hydrodynamic scenarios, EPC provides a simpler description than PAC for the response of larval production to reserve creation when EPC is larger than 1–2% (Fig. 12). When EPC is smaller than 1%, larval production is reduced from that in the case with no reserve. In contrast, when EPC is greater than 2%, larval production increases linearly with EPC for each hydrodynamic scenario. The effect of reserve location, independent of EPC, on larval production is relatively small, but using EPC does not remove the effect of hydrodynamic scenario. The slopes for linear regressions of larval production against EPC are substantially different for the three scenarios: the slope for D1 is more than twice that for AD1 (Fig. 12).
Figure 13. Effect of reserve configuration on catch (size expressed as PAC, see text) for the exploitation-with-reserve cases. The change in catch was calculated as \((C_{\text{RES}}/C_e - 1) \times 100\%\), where \(C_{\text{RES}}\) represents the total catch in model year 50 for the exploitation-with-reserve case and \(C_e\) represents the total catch in model year 50 for the corresponding exploitation, no-reserve case. Model results are plotted as functions of reserve size (PAC) for each reserve location: SE (□), NE (△), NW (▽), and SW (■). Results are graphed separately for each hydrodynamic scenario: (A) D1, (B) AD1, (C) AD2.

Total annual catch varied dramatically with reserve size (PAC), location, and hydrodynamic scenario (Fig. 13), indicative of a strong three-way interaction among these factors. Optimal combinations of reserve site and size increased catch rates by 75–200%, whereas some suboptimal combinations decreased catch in some cases. For each hydrodynamic scenario, at least one combination of reserve size and location increased catch, but the optimal reserve size and location differed for each hydrodynamic scenario. Furthermore, any apparent functional dependence (e.g., parabolic, Fig. 13) of catch on reserve size varied with reserve location both within and between hydrodynamic scenarios.
Figure 14. Effect of reserve configuration on catch (size expressed as EPC, see text) for the exploitation-with-reserve cases. The change in total catch was calculated as for Figure 13. Model results are plotted as functions of reserve size (EPC) for each reserve location: SE (□), NE (△), NW (▽), and SW (○). Results are graphed separately for each hydrodynamic scenario: (A) D1, (B) AD1, (C) AD2.

Expressing catch in terms of EPC did not remove the effect of reserve location (Fig. 14). At small EPC (<1%), catch was lower than that in the case with no reserve. For the two advection-diffusion scenarios, catch rate exhibited a somewhat parabolic dependence on EPC for each reserve location—first increasing to a maximum positive value then decreasing and turning negative—as EPC increased (Fig. 14B,C), but the shape of the parabola (e.g., location of the maximum) varied with reserve location. In the diffusion-only scenario, using EPC did not reduce the complexity of the response for catch (Fig. 14A); catch remained a function of reserve size, location, and hydrodynamic scenario even when reserve size was expressed as EPC.
Chapter 2

STOCKHAUSEN ET AL: FACTORS SHAPING RESERVE DESIGN

Discussion

Our model results indicate that marine reserves can be effective tools for management of heavily exploited, benthic marine species like the Caribbean spiny lobster, though their efficacy is determined by spatial aspects of population dynamics. Many configurations of reserve size and location yielded both higher catch and higher larval production than cases with no reserve, illustrating that enhancement of yield and the spawning stock can be achieved simultaneously. In contrast, certain reserve configurations caused simultaneously decreased catches and decreased larval production. For each of the three hydrodynamic scenarios considered, one 'optimal' reserve configuration simultaneously maximized catch and increased larval production, but both the size and location of optimal reserves were unique to each hydrodynamic scenario. In our model, each hydrodynamic scenario altered the pattern of connectivity among coastal sites via larval dispersal and postlarval settlement. Our results therefore further suggest that reserve effects are not functions of size alone but also depend on reserve location and the pattern of connectivity among sites. Although not surprising (Carr and Reed, 1993), this aspect of determining 'optimal' marine reserves has not been addressed.

Catch rates (i.e., yield), in particular, responded to reserve size, location, and hydrodynamic scenario in a complex fashion, indicating that the interaction between reserve features and pattern of connectivity is critical. In addition, although larval production responded linearly to the relative fraction of the exploited population protected by a reserve (i.e., EPC) regardless of reserve location, the slope of this relationship differed substantially among hydrodynamic scenarios. Our model results suggest that, (1) under a particular hydrodynamic condition, reserves of similar size (measured as EPC but not as PAC) but at different locations function similarly to increase larval production but do not increase catch rates equivalently; (2) under different hydrodynamic conditions, identical reserve configurations do not function equivalently; and (3) both size and location of 'optimal' reserves differ with hydrodynamic conditions.

Previous theoretical studies of marine reserves (Polacheck, 1990; DeMartini, 1993; Quinn et al., 1993; Attwood and Bennett, 1995; Man et al., 1995) used models based on simple connections among sites. Consequently, reserve performance was characterized by reserve size alone (Polacheck, 1990; DeMartini, 1993; Man et al., 1995) or by reserve size and spacing (Quinn et al., 1993; Attwood and Bennett, 1995). In contrast, our results indicate that the interaction between reserve location and hydrodynamic current pattern, or other factors affecting connectivity among sites, can be complex. It is therefore unlikely that successful designs from one area will 'translate' directly into successful designs for another. Furthermore, no simple 'rule' of reserve design (e.g., 20% of a region) can be generalized across all marine species and ecosystems. For example, significant increases in larval production occurred at reserve sizes of 10-40% in most cases considered here, depending on hydrodynamic scenario. In a few cases, however, reserves decreased larval production at all reserve sizes. Use of a 20% rule would, in some cases, lead to a false sense of security, thereby endangering—not protecting—exploited stocks.

Predicting the consequences of the interaction between reserve configuration and connectivity pattern is critical to the design of optimally functioning reserves, but prediction requires detailed information not only on life-history characteristics and abundance patterns for the target species but also on hydrodynamic current patterns. For a small number of well-studied species, the requisite information may be available, and spatially explicit
models of the type used here, which integrate life-history characteristics, hydrodynamic patterns for larval dispersal, and spatial patterns of exploitation, may be useful in comparing alternative reserve designs. For most species, however, funding levels and time constraints are unlikely to allow fishery managers to incorporate the required level of detail about connectivity. In addition, the stochastic nature of hydrodynamic patterns and other environmental effects, population processes like recruitment success and interspecific interactions, and the human component of fisheries dictate taking a bet-hedging approach (Lauck et al., 1998) that spreads the risk associated with incomplete information (Lauck et al., 1998; Sladek Nowlis and Roberts, 1999).

We therefore recommend, to paraphrase Dante, abandoning all hope of designing optimal marine reserves—at least in the deterministic sense. An alternative approach to 'optimal' reserve design is to create relatively dense networks of small reserves (Roberts, 1997, 1998) at randomly selected locations such that a substantial fraction of the population (e.g., EPC > 5%) is protected. Multiple small reserves may function more effectively than a single large reserve in a deterministic fashion, particularly for species with sedentary adults and planktonic larvae (Quinn et al., 1993; Attwood and Bennett, 1995), and this strategy also allows one to 'spread the risks' associated with a single reserve. Because edge effects mean that smaller reserves can permit high transfer rates between reserve and exploited areas, and concomitant loss of spawning stock as motile individuals disperse beyond reserve boundaries, the trade-off between reserve size and postsettlement dispersal rates will be an important issue. Finally, the use of traditional conservation tactics (e.g., effort reduction to reduce exploitation rates) may be effective as a supplement or substitute for marine reserves where the efficacy of reserves remains questionable (Lipcius and Crowder, unpubl.).

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LITERATURE CITED


ADDRESS: (W.T.S., R.N.L) Virginia Institute of Marine Science, College of William & Mary, P.O. Box 1346, Gloucester Point, Virginia 23062; Email <buck@vims.edu>; (B.M.H) School of Oceanography, WB-10, University of Washington, Seattle, Washington 98195.

APPENDIX: MODEL DETAILS

PELAGIC MODEL.—The number of individuals in stage $i$ at time $t$ in the age interval $[a,a+da]$ in a small rectangle with area $dxdy$ centered at $(x,y)$ is $L(x,y,t,a)dxdyda$.

The equation describing the dynamics of larvae ($i=0$) or postlarvae ($i=1$) within the oceanic region is

$$\frac{\partial}{\partial t} L_i = -\frac{\partial}{\partial x} L_i - \mu_i L_i - \left\{ \frac{\partial}{\partial x} J_i^x + \frac{\partial}{\partial y} J_i^y \right\}$$

Eq. 2

where $\mu_i$ is the local rate of mortality and $J_i^x, J_i^y$ are the $x, y$ components of larval/postlarval flux. The first term on the right represents the local change in density due to aging, the second the loss due to mortality, and the term in braces the net change in local density due to emigration/immigration via active migration, hydrodynamic currents, and turbulent diffusion.

Mortality rates for Caribbean spiny lobster phyllosomata and postlarvae have not been measured, although they are presumably high (Booth and Phillips, 1994). For this study, we set the $\mu_i$ to constants—indeed of location, time, and age within each stage (Table 1).

The flux components $J_i^x, J_i^y$ are related to density by

$$J_i^x(x,y,t,a) = \left\{ u_x - K \frac{\partial}{\partial x} \right\} L_i$$

$$J_i^y(x,y,t,a) = \left\{ v_y - K \frac{\partial}{\partial y} \right\} L_i$$

Eq. 3

where $u_x, v_y$ are the $x, y$ components of advective velocity and $K$ is the coefficient of eddy diffusion. Spiny lobster phyllosomata have little capacity for horizontal movement (Booth
and Phillips, 1994), so larval dispersal is probably primarily passive (although phyllosomata are capable of vertical movement and may be able to use the differences in current structure at different depths to influence dispersal patterns; Phillips, 1981; Yeung and McGowan, 1991). For this study, we assumed larvae to be passively dispersed; thus, $u_0$ and $v_0$ are equal to the local hydrodynamic current components $u$ and $v$. Because postlarvae, in contrast, actively migrate to settlement areas (Calinski and Lyons, 1983; Booth and Phillips, 1994), we expressed the deterministic part of postlarval dispersal as the sum of hydrodynamic current velocity and an active dispersal velocity, $u_0 = u + u'_a$ and $v_0 = v + v'_a$, where $u'_a$, $v'_a$ represent the local components of active migration. We assumed that postlarvae sense and orient to the closest suitable settlement habitat and that the effective migration rate (i.e., that over a tidal cycle) was higher near the coast, where postlarvae can sink and attach to the bottom during adverse currents (Calinski and Lyons, 1983), than further offshore (Table 1).

The pelagic model is completed by two sets of mathematical boundary conditions. The first set is at age 0 for each pelagic stage. Larvae are produced only along the coastal portion of the spatial boundary, so $L_0(x,y,t,a = 0) = 0$ for all $x,y$ not on the boundary. The local rate of production on the boundary is determined in the reproduction model (see below). If we let $R(x,y,t)$ represent the local rate of larval production (per unit distance along the coastline) at $x,y$ on the spatial boundary and let $\eta^x, \eta^y$ represent the direction cosines of a vector pointing directly offshore at the same location, the components of the local flux of age-0 larvae into the offshore region are given by

$$J_0(x,y,t,a = 0) = R(x,y,t) \eta^x(x,y)$$

Eq. 4

Metamorphosis to the postlarval stage may be environmentally cued in late-stage phyllosomata by contact with the seafloor or lower-salinity water over the continental shelf (Booth and Phillips, 1994). However, because it results in a major simplification to the model structure, we assume that the duration of the larval stage is fixed ($a_0$, Table 1) and that metamorphosis to the postlarval stage occurs wherever $a_0$ is reached. As a result, the age-0 boundary condition for the postlarval stage is simply that the local density of age-0 postlarvae equals the local density of age $a_0$ larvae.

The second set of mathematical boundary conditions concerns behavior at the spatial boundary. Because we do not consider immigration from beyond the modeled geographic region, the flux of $a > 0$ larvae, and all postlarvae, across the spatial boundary can only be directed 'outside' the oceanic region, i.e., onto the coast or beyond the deep-water boundaries. Further, actual transport across the boundary may be less than the potential maximum flux because of the stage-specific 'leakiness', $\omega(a,y)$, of the boundary. For this study, we assumed that larvae were not swept into coastal areas ($\omega_0 = 0$ along the coastal portion of the boundary) and that transport across deep-water boundaries occurred at 50% of the maximum possible rate ($\omega_0 = 0.5$). Conversely, postlarvae were not lost at deep-water boundaries ($\omega_0 = 0$) but invaded coastal habitats at the maximum possible rate ($\omega_0 = 1$).

Larval and postlarval fluxes across the spatial boundary result in corresponding decreases in density within the pelagic model, but the age-integrated postlarval flux across
coastal portions of the boundary determines the local rate of settlement, $S_{\text{coastal}}$. Consequently, postlarvae that cross the coastal boundary represent a loss within the pelagic model but a gain within the benthic model.

**Benthic Model.**—We characterize within-stage density by size rather than age because demographic rates for spiny lobster are more typically characterized by size than age (Cobb and Caddy, 1989). For small increments $dz$ in size and distance $d\theta$ along the coast, $S_i(z,\theta,t)d\theta dz$ is the number of benthic individuals in stage $i$ in the size range $[z, z+dz]$ occupying the coastline from $[\theta, \theta + d\theta]$ at time $t$.

The dynamics of $N$ postsettlement life-history stages along the coast are described by the following set of $N$ coupled partial differential equations:

$$\frac{\partial S_i}{\partial t} = -\mu_i s_i + \sum_{j=1}^{N} \tau_{ij} s_j - \sum_{j=1}^{N} \tau_{ji} s_i - \frac{\partial}{\partial z} \left\{ g_i s_i + \frac{\partial}{\partial \theta} J_i s_i \right\} + S_i$$  \hspace{1cm} i = 1 \ldots N \hspace{1cm} \text{Eq. 5}

where $\mu_i$ is the instantaneous rate of mortality, $\tau_{ij}$ is the rate at which individuals progress from stage $j$ to $i$, $g_i$ is the instantaneous rate of growth, $J_i$ is the flux of individuals dispersing along the coastline, and $S_i$ is a source term representing influx from outside the model (e.g., settlement). The functions $\mu_i$, $\tau_{ij}$, $g_i$, and $J_i$ are stage-specific and may also be functions of $z$, $\theta$, and $t$. The terms on the right-hand side of Eq. 5 represent (1) losses due to mortality, (2) gains from individuals progressing from the $j$th to the $i$th stage, (3) losses from individuals progressing from the $i$th to the $j$th stage, (4) losses and gains due to growth of individuals within a stage, (5) losses and gains due to movement of individuals along the coast, and (6) gains from settlement.

Boundary conditions for Eq. 5 take different forms depending on whether the boundary is in space ($\theta$) or in size ($z$). We do not consider dispersal through deep-water sections of the one-dimensional boundary, so the dispersal flux $J_i$ is required to be zero at intersections of coastal and deep-water portions of the boundary. Similarly, we set zero flux conditions on growth at the minimum and maximum sizes within each life-history stage

$$\left\{ g_i(z,\theta,t)s_i(z,\theta,t) \right\}_{z=\text{min}} = \left\{ g_i(z,\theta,t)s_i(z,\theta,t) \right\}_{z=\text{max}} = 0 \hspace{1cm} \text{Eq. 6}$$

because the transition from one stage to the next occurs over a range of sizes. Individuals reaching the maximum size in each life-history stage cease growth until they undergo transition to the next life-history stage.

To incorporate density-dependent processes into the model formulation in a consistent fashion, we use a nondimensional normalized life-history-stage density $\zeta_i(\theta,t)$, expressed as

$$\zeta_i(\theta,t) = \frac{\sum_{j} \epsilon_{ij} \left\{ dz s_j(z,\theta,t) \right\}}{\Psi_i(\theta,t)} \hspace{1cm} \text{Eq. 7}$$
where the $c_j$ are coefficients which characterize the additional effect of life-history stage $j$ on $i$ and $\Psi(\theta,t)$ is an auxiliary measure of habitat quality or suitability, the stage-classified index of habitat suitability. Essentially, $\Psi(\theta,t)$ represents a measure of the carrying capacity of the local environment for animals in stage $i$ and is an input to the model. In developing Eq. 7, we assume that density-dependent effects are independent of the size structure within each stage and depend only on local stage densities.

For the Caribbean spiny lobster, the benthic model encompasses five postsettlement life-history divisions: algal-phase juvenile, postalgal-phase juvenile, subadult juvenile, adult male, and adult female. Each constitutes a life-history stage within the context of the benthic model. We divided the adult stage into sex-specific components because both adult growth rates (see, e.g., Herrnkind and Lipcius, 1989) and exploitation patterns may be sex-specific, but we chose to use identical life-history parameters for the two sexes in this study.

Within the context of the model, size refers to carapace length (CL). Modeled life-history stages range in size from 6 to 150 mm carapace length (CL, Table 2), although a small fraction of lobsters reach greater size in Exuma Sound (Herrnkind and Lipcius, 1989; Lipcius and Stockhausen, unpubl.).

Different postsettlement life-history stages use different benthic habitats (Herrnkind and Lipcius, 1989; Butler and Herrnkind, 1997), so except for the adult stages, we assumed that density effects within each model stage were independent of the local density of the other stages (in Eq. 7, $c_y = 0$ if $i \neq j$; $c_y = 1$ otherwise). For the two adult stages, we assumed the effective density was the sum of the two densities (in Eq. 7, $c_y = 1$ if $i = 4, 5$ and $j = 4, 5$; $c_y = 0$ otherwise).

For this study, we also chose to ignore explicit spatial and temporal variability in demographic rates (other than fishing mortality) and in habitat suitability. Demographic rates could vary in space and time because of local changes in density but were otherwise homogeneous in space and time. In addition, we used a set of constants for the habitat index, $\Psi(\theta,t)$. The selected values (Table 2) reflect an apparent limitation of settlement habitat in portions of Exuma Sound (Lipcius et al., 1997) as well as an assumed decrease in habitat availability with size.

We decomposed the total rate of mortality, $\mu(z,\theta,t)$, into additive components associated with fishing ($\mu_F(z,\theta,t)$, 'fishing mortality') and other sources ($\mu_N(z,\theta,t)$, 'natural mortality'). We expressed the instantaneous rate of fishing mortality as

$$\mu_F(z,\theta,t) = \begin{cases} \frac{F \varphi(\theta)}{z_f} & \text{for } z_f \leq z \\ 0 & \text{otherwise} \end{cases}$$

where the parameter $F$ specifies the nominal level of fishing mortality, $z_f$ is the minimum size vulnerable to the fishery, and $r_{\text{m}}$ and $r_{\text{e}}$ specify the beginning and ending of the fishing season, respectively. The function $\varphi(\theta)$ controls the spatial pattern of effort and determines the configuration of different reserve scenarios. In this formulation, the spatial allocation of fishing effort is independent of patterns of abundance.

Several studies have determined relative mortality of Caribbean spiny lobster in experimental treatments in the field (e.g., Eggleston et al., 1990, 1992; Butler and Herrnkind, 1997), but few studies have estimated absolute rates (e.g., Munro, 1974) and none has done so within Exuma Sound. In Exuma Sound, lack of appropriately scaled shelter may
be an important factor in density-dependent mortality rates (Lipcius et al., 1997), but
density dependence is likely only at high densities, after most available shelters are occu­
pied. We therefore modeled the instantaneous rate of natural mortality using the piece­
wise linear expression

$$\mu^i(z, \theta, t) = \mu^a(z, \zeta_i) = \begin{cases} c_n \zeta_i & \text{if } \zeta_i < c_0 \\ c_n + c_{11} \left[ \zeta_i - c_0 \right] & \text{if } \zeta_i \geq c_0 \end{cases}$$

Eq. 9

where the $c_n$ are stage-specific model parameters (Table 2) and $\zeta_i(\theta, t)$ is the normalized stage-specific local density. Local rates of natural mortality are density independent when
density is low ($\zeta_i < c_0$) but increase linearly with density when density is high. Because
absolute rates have not been measured, we chose parameter values (Table 2) that gave
reasonable survival probabilities (Fig. 5; see Butler and Herrnkind, 1997).

We selected a simple, but otherwise arbitrary, functional form for the rate of transition
between life-history stages, $\tau_{ij}(z, \theta, t)$. The rate at which individuals change from stage $j$ to
stage $i$ is

$$\tau_{ij}(z, \theta, t) = \begin{cases} 0 & \text{if } z < z_{ij}^{min} \\ c_{ij} \left[ 1 - e^{-\eta_i(z - z_{ij}^{min})} \right] & \text{if } z \geq z_{ij}^{min} \end{cases}$$

Eq. 10

where the $c_{ij}$ are stage-specific model coefficients and $z_{ij}^{min}$ is the minimum size at which
transitions to later stages occur. In this formulation, the rate of transition is density inde­
pendent. The coefficients $c_{ij}$ represent the asymptotic transition rate from stage $j$ to stage $i$. The coefficient $c_{ij}$ governs the rate of increase of $\tau_{ij}(z, \theta, t)$ with individual size. The
parameter values we selected (Table 2) yield reasonable intervals for transition from one
stage to the next.

The Gompertz-type function used to express growth rates within a stage was

$$g_i = \alpha_i z \ln \left[ \frac{\beta_i}{z} \right]$$

Eq. 11

Here, $\alpha_i$ controls initial rate of growth and $\beta_i$ controls the asymptotic size. We chose to
ignore density-dependent effects. Stage-specific growth parameters were selected (Table
2) so that mean stage durations were consistent with Butler and Herrnkind (1997). The
resulting growth curve (Fig. 5) is reasonably consistent with results from other studies,
particularly given the variability in reported growth rates among previous studies (Davis
and Dodrill, 1980, 1989; Hunt and Lyons, 1986; Forcucci et al., 1994). As previously
noted, growth-rate parameters for adult males and females are identical (Table 2).

Of the postsettlement stages, only subadults and adults disperse over significant dis­
tances (Herrnkind, 1980, 1983; Herrnkind and Butler, 1986). We described alongshore
flux, $J(z, \theta, t)$, as a one-dimensional diffusion process with a density-dependent diffusion coefficient:

$$J_i(z, \theta, t) = J_i(s_i, \zeta_i) = -\frac{\partial}{\partial z} \left( \kappa_i(\zeta_i) s_i \right)$$  \hspace{1cm} \text{Eq. 12}

where $s_i$ is the stage-classified, size-dependent local density, $\zeta_i(\theta, t)$ is the normalized stage density, and $\kappa_i$ is a stage-specific, density-dependent diffusion coefficient defined as

$$\kappa_i(\zeta_i) = c_i \left[ 1 + c^2 \frac{\zeta_i}{c^2 + \zeta_i} \right]$$  \hspace{1cm} \text{Eq. 13}

In the latter equation, the $c_i$ are stage-specific model parameters. The functional form chosen for $J_i$ in Eq. 12 is appropriate when the direction of movement of individuals is locally unbiased, whereas the rate depends only on conditions at the point of departure (Okubo, 1980). The functional form for the diffusion coefficient $\kappa_i$ allows postsettlement dispersal to be a combination of density-independent and density-dependent effects. We selected parameter values that reflect the generally more sedentary nature of adult spiny lobster than of subadults.

Finally, the benthic model source term, $S_i(z, \theta, t)dzd\theta$, represents the influx of individuals at time $t$ from beyond the model domain into the size increment $[z, z+dz]$ within the coastal region $[\theta, \theta+d\theta]$. For this study, we did not consider immigration from outside Exuma Sound. Thus, the only influx is from settlement of postlarvae (and subsequent metamorphosis into algal phase juveniles), $S_{pl}$. Although postlarvae in Exuma Sound range from 4 to 7 mm CL (Lipcius and Stockhausen, unpublished), we chose, for simplicity, to model all postlarvae as metamorphosing into algal-phase juveniles in the size interval 6–7 mm CL. The source term is therefore

$$S_i(z, \theta, t) = \begin{cases} S_{pl}(\theta, t) & \text{for } i = 1 \\ 0 & \text{otherwise} \end{cases}$$  \hspace{1cm} \text{Eq. 14}

where $i = 1$ refers to the algal-phase juvenile stage.

**Reproduction Model.**—The rate at which larvae are produced locally, $R(\theta, t)$, is expressed as:

$$R(\theta, t) = \sum_i \int dz r_i(z) m_i(z) F_i(z) s_i(z, \theta, t)$$  \hspace{1cm} \text{Eq. 15}

where $r_i$ is the temporal spawning pattern for stage $i$ individuals, $m_i$ is the fraction of stage $i$ individuals that are mature at size $z$, and $F_i$ is individual fecundity. Local production of larvae provides the larval-stage age-0 boundary condition (Eq. 4) for the pelagic model and completes the full life-history model.
In Exuma Sound, peak reproductive activity occurs in spring. The incidence of females occupying offshore reefs that carry fertilized egg masses reaches 80% in June, then declines quickly toward autumn (Herrnkind and Lipcius, 1989). For simplicity, we chose to ignore a possible secondary spawning peak in the fall (Herrnkind and Lipcius, 1989) and expressed the temporal variation in spawning, \( r_p \), as spatially homogeneous using a truncated normal distribution function:

\[
r_p(x, y, t) = r(t) = \begin{cases} 
\int_{0}^{t} \left( \frac{t - \tau}{\tau} \right)^{1/2} & \text{if } \tau_{\text{start}} \leq \tau \leq \tau_{\text{end}}, \ t \leq 5 \\
0 & \text{otherwise}
\end{cases}
\]

Eq. 16

The \( c_j \) in Equation 16 influence the overall level of spawning activity, the time of peak spawning, and the variability about the peak. The parameters \( \tau_{\text{start}} \) and \( \tau_{\text{end}} \) indicate the beginning and ending dates of the spawning season, respectively. The parameter values selected reflect 100% spawning of all mature females during the season and peak spawning in the spring (Fig. 6A, Table 3). For this study, we chose to end the spawning season just before the beginning of the fishing season.

The smallest reported egg-bearing female in Exuma Sound was 85 mm CL (Herrnkind and Lipcius, 1989). Percent female maturity increases to 100% by 100 mm CL. For simplicity, we chose to express the maturity function, \( m_f \), as a knife-edge function of size:

\[
m_f(z) = \begin{cases} 
1 & \text{if } z \geq z_{\text{mm}}, \ t \leq 5 \\
0 & \text{otherwise}
\end{cases}
\]

Eq. 17

where \( z_{\text{mm}} \) reflects the minimum size at maturity (Table 3).

Individual fecundity (i.e., number of eggs in an egg mass) of spiny lobster has been well described by both size-dependent power laws (Mota Alves and Bezerra, 1968; Lipcius et al., 1997) and exponential functions (Lipcius and Stockhausen, unpublished). In Exuma Sound, individual fecundity does not vary spatially (Lipcius et al., 1997). We expressed fecundity, \( F_f \), as an exponential function of size:

\[
F_f(x, y, t) = F_f(z) = \begin{cases} 
\frac{c_f}{1 + \alpha (z - z_{\text{mm}})} & \text{if } \tau_{\text{start}} \leq \tau \leq \tau_{\text{end}}, \ t \leq 5 \\
0 & \text{otherwise}
\end{cases}
\]

Eq. 18

We reanalyzed fecundity data from Exuma Sound (Lipcius et al., 1997) using an exponential model to determine values for the \( c_j \) parameters (Fig. 6B, Table 3).
Chapter 3: A Revised Population Dynamics Model for the Caribbean Spiny Lobster in Exuma Sound, Bahamas

Introduction

The population dynamics model for Caribbean spiny lobster in Exuma Sound, Bahamas described in the previous chapter (see also Stockhausen et al., 2000) was revised prior to the studies reported in subsequent chapters. Although the principal modification was to introduce temporal variation in hydrodynamic current patterns, several other (and relatively minor) modifications were also incorporated. Further, modifying the model processes required changes to some parameter values. In the interest of completeness, then, this chapter provides a detailed description of the revised model.

Population dynamics models can be discussed at two levels: strategic and tactical, if you will. The strategic level consists of properties of the model that may be applicable to a wide range of species and sites, whereas the tactical level consists of model properties which are specific to a given species and site. Here, the strategic portion of the model provides a general description of the dynamics of a benthic marine species with a complex life history along a narrow coastal zone. The tactical portion of the model provides a specific description of Caribbean spiny lobster (Panulirus argus) in Exuma Sound, Bahamas. Consequently, I've divided the following description of the model into two sections that reflect this strategic/tactical division of the model. I then present results
from a model simulation using a set of baseline parameters, and compare them with previous field observations (Lipcius et al., 1997).

**Strategic model description**

In this section, I present a strategic description of the model—a population dynamics model for a coastal benthic species with a complex life history (sensu Thorson, 1950) in which the benthic life-history stages occupy a relatively narrow cross-shelf region along the coast while the pelagic stages may be widely dispersed offshore. The model encompasses demographic processes during each life-history stage and "closes the larval loop," linking post-settlement benthic population dynamics and pelagic larval dispersal (Gaines and Lafferty, 1995; Eckman, 1996). It extends the spatially explicit model of Possingham and Roughgarden (1990), which addressed two life-history stages, to accommodate multiple (>2) life-history stages, age-dependent mortality and behavior in pelagic stages, stage-classified size- and density-dependence in post-settlement demographic rates, post-settlement dispersal and spatially-explicit fishing mortality. Modeled life-history stages include: 1) a planktonic larval stage, which is passively dispersed from spawning grounds via hydrodynamic currents and turbulent diffusion, 2) a postlarval stage that actively reinvades coastal habitats prior to settlement, 3) one or more benthic juvenile stages, and 4) one or more reproductively active adult stages.

The full model is conveniently decomposed into three coupled sub-models (Fig. 1): (1) the pelagic model, (2) the benthic model, and (3) the reproduction model. The pelagic model tracks changes in age-specific pelagic larval/postlarval density within a two-dimensional (horizontal) oceanic region $\Omega$ due to adult spawning along coastal
portions of the one dimensional boundary $\Omega_B$ (Fig. 2), horizontal dispersal via two-dimensional advective currents and turbulent diffusion, transport across open ocean boundaries, age-specific mortality, and settlement along coastal portions of $\Omega_B$. The benthic model tracks changes in size-specific density along the coastline for each benthic life-history stage due to settlement, density- and size-dependent mortality, metamorphosis between successive life-history stages, and alongshore dispersal. Finally, the reproduction model tracks temporal and spatial variation in spawning rates and larval production along the coastal portions of $\Omega_B$.

Pelagic sub-model

Pelagic larvae are spawned along the coastal portion of $\Omega_B$, as determined by the spatial distribution of adults and temporal patterns of spawning (see below). Larvae enter the offshore region $\Omega$, within which they are subject to mortality and transport by hydrodynamic currents as passive particles. Surviving larvae that reach a predefined age, $a_{pl}$, become competent to settle. Individuals competent to settle are referred to hereafter as “postlarvae”. Postlarvae may actively migrate back toward coastal portions of the boundary. The pelagic sub-model represents an extension of that of Possingham and Roughgarden (1990) in that larval age is explicitly incorporated into the model to account for both the duration of the larval phase and changes in behavior and motility after the larvae become competent to settle.

Rather than following individuals, as the preceding description might encourage one to suppose, the pelagic model tracks changes in the spatially-explicit, age-specific density of the pelagic life history stages, $L(x, t, a)$, where $x = [x, y]$ is spatial position, $t$ is time, and $a$ is age (note: italics will be used to represent scalar variables and functions, bold italics will be used to indicates variables and functions which are two dimensional
vector quantities). $L$ is continuous in both space and time. Because the density is age-specific, $L$ has units of $\text{no.} \cdot \text{area}^{-1} \cdot \text{time}^{-1}$. The number of individuals at time $t$ in the age interval $[a, a+da]$ in a small rectangle with area $dx dy$ centered at $x$ is then $L(x,t,a)dx dy da$.

The local time-rate-of-change of $L$ in the interior of $\Omega$ is a function of the rates of aging, mortality, and horizontal transport. Since $L$ is continuous in its component variables, I modelled the local time-rate-of-change using the following partial differential equation:

$$\frac{\partial}{\partial t} L(x,t,a) = -\frac{\partial}{\partial a} L - \mu(x,t,a) L - \nabla \cdot J_L(x,t,a,L)$$  \hspace{1cm} (1)

In the equation, $\mu$ is the instantaneous rate of mortality, $\nabla$ is the horizontal gradient operator $x \partial/\partial x + y \partial/\partial y$, $J_L$ is the horizontal pelagic flux (a two-dimensional vector representing age-specific pelagic transport in the horizontal plane), and $\nabla \cdot J_L$ represents the horizontal divergence of $J_L$.

The first term on the right-hand side of eq. 1 accounts for changes in density at $x$ due solely to aging. The second term is a sink term, representing the loss of individuals through mortality. Depending on the species under consideration, the instantaneous mortality rate $\mu$ may vary both spatially and temporally, as well as with age and population density. The final term in eq. 1 accounts for local net losses or gains in density due to transport by hydrodynamic currents, turbulent diffusion, and active migration.

The flux $J_L$ represents age-specific pelagic transport by a combination of advection and diffusion, and is modeled as:
where $\hat{x}$ and $\hat{y}$ are unit vectors along the $x$- and $y$- axes, respectively, $u$ and $v$ are advective components of velocity along these axes, and $D_x$ and $D_y$ are turbulent diffusivities. The $x$- and $y$-components of $J_L$ represent the net rate at which individuals pass across lines of unit length oriented perpendicular to the $x$- and $y$-axes, respectively, due to advection ($uL$ or $vL$) and diffusion ($-D_x \partial L/\partial x$ or $-D_y \partial L/\partial y$). Both the advective velocity components, $u$ and $v$, as well as the diffusivities, $D_x$ and $D_y$, in eq. 2 may be age-specific to incorporate possible ontogenetic changes related to horizontal movement.

The pelagic sub-model is completed by specifying boundary conditions for eq. 1 at $a = 0$ for all $x$ and along the spatial boundary $x \in \Omega_B$ for all $a$ and $t$. At age 0, larvae are spawned only along the coastal portion of the boundary $\Omega_B$ according to the reproduction sub-model described below. If $R$ is the total rate of larval production (per unit distance along the coastline, see eq. 11 below) the flux of age 0 larvae into the offshore region at position $x_B$ on $\Omega_B$ is then given by

$$J_L(x_B, t, a = 0) = R(\theta(x_B), t) \hat{n}(x_B)$$

where $\theta(x_B)$ is the one-dimensional spatial coordinate along the coastline corresponding to the boundary position $x_B$ and $\hat{n}$ is the unit normal vector (see Fig. 2) into $\Omega$ at $x_B$. For $x \in \Omega$ (i.e., in the interior of the offshore region), then $L(x, t, a = 0) = 0$.

For $a > 0$, the pelagic flux at the boundary is directed outside $\Omega$, either onto the coastline or beyond the deepwater boundaries. Thus, larvae do not enter the model domain from any sources except the spawning population along the coastline. The magnitude, $J_{L,B}$, of the age-specific flux across the boundary at $x_B$ is expressed as
\[ J_{L,B}(x_B, t, a) = \omega(x_B, t, a) \max\{ [-\hat{n}(x_B) \cdot J_L(x_B, t, a)], 0] \]  

(4)

where \( \omega \) is a function in the interval \([0,1]\) which controls the "porosity" of the boundary. When \( \omega(x_B, t, a) = 0 \), the boundary at \( x_B \) is closed (or reflective) and no flux crosses it. When \( \omega(x_B, t, a) = 1 \), the boundary at \( x_B \) is open, and all of the potential flux crosses it. Intermediate cases may also be defined.

The flux across open or partially open boundaries represents a loss to the pelagic sub-model. However, the age-integrated flux of postlarvae crossing a coastal portion of the boundary at \( x_B \) determines the local settlement rate \( S_{pl}(\theta(x_B), t) \) at coastal position \( \theta \):

\[ S_{pl}(\theta(x_B), t) = \int_{\alpha \in x_B} da J_{L,B}(x_B, t, a) \]  

(5)

Consequently, postlarvae that cross the coastal boundary represent a loss to the pelagic sub-model but an input to the benthic sub-model.

The functions \( \mu, u, v, a, D_x, D_y \) and \( \omega \) are species-specific. The specific forms adopted for the spiny lobster model are discussed below.

**Benthic sub-model**

The benthic sub-model tracks changes in the spatially-explicit, stage-classified, size-specific density of benthic individuals along the coastline due to settlement, mortality, growth, transition between benthic life-history stages, and alongshore dispersal using an individual-state distribution model (Metz and Diekmann, 1986; DeAngelis and Rose, 1992) based on a set of coupled partial differential equations and associated boundary conditions. As with the pelagic sub-model, this sub-model is continuous in both space and time. The benthic model represents a further extension of that of Possingham and Roughgarden (1990) in that multiple post-settlement life-history stages
are allowed, size structure is explicitly incorporated, demographic rates may be density dependent, and alongshore dispersal is possible.

As with the pelagic model, the benthic model tracks changes in density, not individuals. Let \( s_i(z, \theta, t) \) denote the stage-classified, size-dependent, spatially explicit density of post-settlement individuals in stage \( i \) with size \( z \) occupying coastal location \( \theta \) (Fig. 2) at time \( t \). The units of \( s_i \) are number-linear distance unit\(^{-1}\)-size unit\(^{-1}\). For small increments \( dz \) in size and distance \( d\theta \) along the coast, \( s_i(z, \theta, t)d\theta dz \) is the number of benthic animals classified as stage \( i \) in the size range \( [z, z+dz] \) occupying the coastline from \([\theta, \theta+d\theta] \) at time \( t \).

In order to introduce density-dependence into the model formulation, I define several auxiliary measures of density and one habitat measure. The stage-classified density for life history stage \( i \) at \( \theta \) and \( t \), \( \sigma_i(\theta, t) \), is defined as the integral of \( s_i(z, \theta, t) \) over all sizes within a life history stage:

\[
\sigma_i(\theta, t) = \int dz \ s_i(z, \theta, t)
\]

Thus, the units of \( \sigma(\theta, t) \) are number-spatial distance unit\(^{-1}\). \( \sigma_i(\theta, t)d\theta \) is the number of individuals in stage \( i \) occupying the coastline from \([\theta, \theta+d\theta] \). Further, I assume life history stages may be defined such that the density dependence of demographic rates in one stage depends on the densities of several other stages. This might be the case when males and females are distinguished as different life history stages because, for example, growth rates are sex-dependent: density dependent rates for either sex may depend on the total density of both sexes rather than that of the individual sex. To incorporate this flexibility, I define an effective stage-classified density, \( \varepsilon_i(\theta, t) \), for life history stage \( i \) at \( \theta \) and \( t \) by
\[ \epsilon_i(\theta, t) = \sum_j c_{ij} \sigma_j(\theta, t) \]  

(7)

where the \( c_{ij} \) are model parameters which account for the influence of the density of animals in stage \( j \) on stage \( i \) demographic rates. Finally, I introduce an index of habitat suitability, \( \Psi_i(\theta, t) \), for stage \( i \)-classified animals at position \( x \) and time \( t \). Essentially, \( \Psi_i(\theta, t) \) represents a measure of the carrying capacity of the local environment for animals in stage \( i \) and is expressed in the same units as \( \sigma_i \). I assumed that density dependent effects on mortality, growth, and other rates within a life history stage are independent of the size distribution within that stage and can be expressed in terms of the normalized life-history stage density \( \zeta_i(\theta, t) = \epsilon_i(\theta, t)/\Psi_i(\theta, t) \). Note that \( \zeta_i \) is non-dimensional.

For \( N \) post-settlement life history stages, I modeled the time-rate-of-change of the stage-classified densities \( s_i \) using the following set of \( N \) coupled partial differential equations:

\[
\frac{\partial}{\partial t} s_i(z, \theta, t) = -\mu_i(z, \theta, t) s_i \\
- \sum_{j=1}^{N} \tau_{ij}(z, \theta, t) s_i + \sum_{j=1}^{N} \tau_{ji}(z, \theta, t) s_j \\
- \frac{\partial}{\partial z} \{ g_i(z, \theta, t) s_i \} \\
- \frac{\partial}{\partial \theta} J_i(z, \theta, t, s_i) \\
+ S_i(z, \theta, t) \quad i = 1 \ldots N
\]  

(8)

Here, \( \mu_i \) is the instantaneous rate of mortality, \( \tau_{ij} \) is the rate at which individuals transition from stage \( i \) to \( j \), \( g_i \) is the instantaneous rate of growth, \( J_i \) is the flux of individuals along the coastline, and \( S_i \) is a source term representing influx from beyond the benthic model. These functions are stage-classified and may be size- and density-dependent, as well as explicitly variable in space and time; the specific forms adopted for the spiny lobster model are discussed below.
The right-hand side of eq. 8 consists of: (1) losses due to natural and fishing mortality (i.e., the first line), (2) losses from individuals transitioning from the \(i\)th to the \(j\)th stage and gains from individuals transitioning from the \(j\)th to the \(i\)th stage (i.e., the second line), (3) losses and gains due to growth of individuals within a stage (i.e., the third line), (4) losses and gains due to movement of individuals along the coast (i.e., the fourth line), and (5) gains from settlement of individuals from the plankton (i.e., the last line).

The benthic sub-model (eq. 8) is completed by specifying boundary conditions at the boundaries of the model domain. The boundary conditions take different forms depending on whether the boundary is in space (along \(\Theta\)) or in size (along \(z\)). Spatial boundary conditions are invoked at the ends of the habitable coastline (e.g., at a termination of the coastline by deep water). These consist of a zero flux condition:

\[
J_i(z,\Theta,t)|_{\Theta_b} = 0
\]  
\(9\)

where \(\Theta_b\) indicates the position of the boundary (in terms of \(\Theta\), the coastal coordinate); individuals cannot move beyond the boundary.

Boundaries in size occur at the minimum and maximum sizes in each benthic life history stage. Because I explicitly modeled the transition from one stage to the next as occurring over a size range, I set zero flux conditions for the size boundaries:

\[
\{g_i(z,\Theta,t)s_i(z,\Theta,t)\}_{z_{\text{min}}} = \{g_i(z,\Theta,t)s_i(z,\Theta,t)\}_{z_{\text{max}}} = 0
\]  
\(10\)

Individuals that reach the maximum size in each life history stage cease growth until they undergo transition to the next stage.
Reproduction sub-model

The third and final sub-model concerns the spawning of larvae by adults along the coastline. Local production of larvae provides the age 0 boundary condition (eq. 3) for the pelagic sub-model and completes the full life-history model. The rate at which larvae are hatched locally, \( R(\theta,t) \), depends on the time-specific population-level spawning rate, the size and stage at which maturity is achieved, the size-specific and density dependent fecundity, and the stage-classified and size-specific local density. The local rate of larval production is expressed as

\[
R(\theta,t) = \sum_i \int dz \quad m_i(z,\theta,t) \quad r_i(z,\theta,t) \quad F(z,\theta,t) \quad s_i(z,\theta,t)
\]

where \( R \) is the total rate of spawning per unit distance of coastline, \( m_i \) is the fraction of stage \( i \) individuals which are mature at size \( z \), \( r_i \) is the temporal spawning pattern for \( i \)-stage individuals, and \( F \) is individual fecundity. All three functions may be density-dependent, as well as spatiotemporally explicit; the specific forms adopted for the spiny lobster model are discussed below.

Model refinement for Caribbean spiny lobster in Exuma Sound, Bahamas

I selected Exuma Sound, Bahamas for the model site and the Caribbean spiny lobster, *Panulirus argus*, for the model species. As a result of field studies conducted recently in this system, information regarding hydrodynamic currents, spatial patterns of abundance, and demographic parameters for spiny lobster is available (Lipcius et al., 1997). In addition, the Caribbean spiny lobster supports important fisheries throughout the Caribbean and is the target of several existing marine reserves. Finally, a considerable literature concerning additional life history information and demographic characteristics...
already exists for this species. Consequently, as discussed in more detail below, I
developed a baseline model scenario, including demographic parameters, habitat indices

**Site**

Exuma Sound is a deep (> 1000 m), semi-enclosed basin in the central Bahamas,
surrounded by the Exuma Cays and the Great Bahama Bank to the north and west, by
Eleuthera and Cat Island to the east, and by Long Island to the south (Fig. 3).
Approximately 200 km northwest to southeast and 75 km at its widest, the Sound has two
connections to the Atlantic Ocean: a deepwater (2000 m depth) gap 50 km wide between
Long and Cat Islands, and a shallow sill (15-30 m depth) 27 km wide between Eleuthera
and Little San Salvador. Except for these openings, Exuma Sound is bordered by either
low islands or shallow carbonate bank (Colin, 1995). Exuma Sound provides habitat for
spiny lobster on all sides, making the system particularly well suited for analyses of the
relationships between meteorology, oceanography, recruitment and population dynamics.

Circulation in Exuma Sound appears to be dominated by large-scale, vigorous
gyres (Fig. 4, Hickey, in press) extending to depths up to 200 m from the sea surface.
Water exchange with the open ocean occurs on a regular basis, while exchange with the
shallow banks also occurs through dense, high salinity intrusions (Hickey, in press).
Wind-forcing plays an important role in the circulation by influencing the current
structure in the upper 15 m of the water column (Hickey, in press). Mesoscale features
with associated fronts are superimposed on a general northwestward drift and cause
convergence and preferred pathways through the Sound (Colin, 1995; Hickey, in press).
Although the gyres appear to be semi-permanent features in the Sound, they may oscillate
seasonally (Hickey, in press; also, see Fig. 4); substantial variability in near-surface currents exists at 10-30 day time scales (Hickey, in press).

Target species life history

The Caribbean spiny lobster (*Panulirus argus*, Latreille) is a macrobenthic invertebrate which supports commercially important fisheries in Florida and the Caribbean (Bohnsack *et al.*, 1994). Ecologically, spiny lobster have been identified as key predators in benthic habitats (Davis, 1977; Tegner and Levin, 1983; Edgar, 1990). Selective predation by spiny lobster is apparently responsible for major effects on species composition and population structure of prey species (Griffiths and Seiderer, 1980; Tegner and Levin, 1983; Joll and Phillips, 1984; Edgar, 1990).

As with other spiny lobster species, the Caribbean spiny lobster exhibits five distinct life-history stages: egg, phyllosoma larva, puerulus postlarva, benthic juvenile, and adult (Fig. 5; Phillips *et al.*, 1980; Lipcius and Cobb, 1994). Both morphological transformations and habitat shifts characterize transitions between successive stages prior to the juvenile stage (Fig. 6). On the basis of additional ontogenetic habitat shifts during the benthic juvenile stage, there seems to be general agreement in subdividing this stage into three additional sub-stages: algal phase, post-algal phase, and sub-adult (Marx and Herrnkind, 1985; Herrnkind and Butler, 1994).

The larval and postlarval stages constitute the pelagic phase of the spiny lobster life-history. Phyllosome larvae hatch from eggs carried *en masse* on the abdomen of adult females on the seaward fringes of offshore reefs (Phillips and Sastry, 1980; Booth and Phillips, 1994; Lipcius and Cobb, 1994). Subsequently, the larvae are transported offshore and undergo a planktonic existence during which they progress through approximately 11 developmental stages by a series of molting events, with concomitant
growth from less than 1 mm to 12 mm carapace length (CL; Lewis, 1951; Phillips and Sastry, 1980; Booth and Phillips, 1994). After 4-12 months in the plankton (Lewis, 1951; Farmer et al., 1989), surviving larvae undergo radical metamorphosis to the transparent, non-feeding puerulus postlarval stage (Calinski and Lyons, 1983; Booth and Phillips, 1994). Postlarvae are vigorous swimmers, attaining speeds up to 10 cm s⁻¹ over short distances, and actively migrate into coastal waters where they subsequently invade shallow inshore areas during nighttime flood tides associated with the new moon (Little, 1977; Calinski and Lyons, 1983; Herrnkind et al., 1994). The pueruli settle to the benthos in structurally-complex habitats such as clumps of macroalgae (Laurencia, spp.) or among mangrove roots (Marx and Herrnkind, 1985; Butler and Herrnkind, 1992). Within several days of settlement, surviving postlarvae acquire pigmentation and metamorphose into the first juvenile benthic instar (Booth and Phillips, 1994).

The benthic phase of the spiny lobster life-history consists of the algal phase juvenile, post-algal phase juvenile, sub-adult, and adult stages. Algal phase juveniles utilize the structurally-complex settlement habitat for both shelter and foraging (Marx and Herrnkind, 1985; Herrnkind et al., 1994). They undergo a solitary existence, increasing in size through a series of molts from 6 mm CL up to 25 mm CL over a period of several months. Upon reaching 15 mm CL, algal phase lobsters begin to exhibit an ontogenetic habitat shift and begin to utilize crevices, tube sponges and octocorals for shelter (Marx and Herrnkind, 1985, Smith and Herrnkind, 1992, Forcucci et al., 1994; Butler and Herrnkind, 1997). Post-algal phase juveniles (15-45 mm CL) are fairly site-attached, staying within several meters of their daytime shelter (Herrnkind and Butler, 1986). At night they emerge from these daytime shelters to forage for small mollusks and other crustaceans in neighboring habitats (Andree, 1981; Herrnkind et al., 1994). At this
stage, spiny lobsters first exhibit gregarious behavior typical of older juveniles and adults (Berrill, 1975). Sub-adults (> 45 mm CL) are nomadic and forage widely in hard-bottom and seagrass meadow habitats (Hermkind, 1980, 1983; Hermkind et al., 1994). As they approach sexual maturity (~76 mm CL), larger juveniles migrate seaward toward the offshore reefs (Hermkind and Lipcius, 1989). Adults (>75-80 mm CL) are gregarious as well, dwelling in dens of up to 20+ lobsters (Hermkind and Lipcius, 1989). Adult sex ratios are size-dependent; males tend to be larger than females, reflecting greater female reproductive investment and differences in molting patterns (Hermkind and Lipcius, 1989). Patterns of reproductive activity vary over broad geographic distances location. In Exuma Sound, peak reproductive activity occurs in spring, with continued spawning through autumn (Hermkind and Lipcius, 1989).

Hydrodynamic current patterns

I used combinations of two “fundamental” two-dimensional hydrodynamic current patterns to generate the currents used for advective transport in the pelagic sub-model. These patterns are based on near-surface geostrophic currents derived from CTD measurements obtained during cruises in Exuma Sound for November, 1993 and June, 1994 (Fig. 4; Hickey, in press). For each model scenario, a 2-dimensional time-varying hydrodynamic current field, $u_H(x,t)$ was created using

$$u_H(x,t) = \varepsilon_N(t) u_N(x,t) + \varepsilon_J(t) u_J(x,t)$$

(12)

where $u_N(x,t)$ and $u_J(x,t)$ represent the near-surface geostrophic currents obtained for the November and June cruises, respectively, while $\varepsilon_N(t)$ and $\varepsilon_J(t)$ are scenario-specific functions which control the variability in $u_H$ with time (e.g., Fig. 7).
**Pelagic sub-model functions and parameters**

For the Caribbean spiny lobster, the pelagic sub-model encompasses the phyllosome larval and puerulus postlarval life-history stages. To complete a species-specific version of the pelagic sub-model, I specified (Table 1): (1) the age, $a_{pl}$, at which larvae become competent to settle; (2) the functional form and parameters for the rate of mortality, $\mu(x, t, a, L)$; (3) the functional form for the advective transport velocity components, $u(x, t, a)$ and $v(x, t, a)$; (4) the functional form and parameters for the boundary leakiness function, $\alpha(x, t, a)$; and (5) the turbulent diffusivities $D_x$ and $D_y$.

Estimates of larval stage duration for Caribbean spiny lobster range from 4-12 months (Lewis, 1951; Farmer et al., 1989). To reduce computer memory requirements, I set the larval stage duration, $a_{pl}$, at the minimum of this range, 120 days (Table 1). In addition, I set a maximum pelagic duration of 180 days. Postlarvae that reach this age, but have not yet settled, are considered dead.

Mortality rates for Caribbean spiny lobster phyllosomata and postlarvae have not been measured. Consequently, I adopted a very simple form, homogeneous in time and space, for the rate of pelagic mortality:

$$\mu(x, t, a) = \begin{cases} \mu_L & \text{if } a < a_{pl} \\ \mu_{pl} & \text{if } a \geq a_{pl} \end{cases}$$

With the values chosen for $\mu_L$ and $\mu_{pl}$ (Table 1), less than 0.01% of larvae spawned survive to recruit to the benthos (Fig. 8).

Spiny lobster phyllosomes have little intrinsic capacity for horizontal movement (Booth and Phillips, 1994); consequently, larval dispersal is probably primarily passive (however, phyllosomata are capable of vertical movement and may be able to utilize depth-varying current structure to influence dispersal patterns—Phillips, 1981; Yeung and...
McGowan, 1991). Conversely, postlarvae in shallow habitats have been observed actively swimming at rates of several cm s\(^{-1}\) (Calinski and Lyons, 1983), although the duration of such locomotion is unknown. Consequently, postlarval dispersal is likely to have a strong active component to it. I incorporated these age-dependent dispersal modes into the pelagic sub-model by decomposing the advective current field for pelagic transport, \(\mathbf{u}(x,t,a)\), into two separate, additive components:

\[
\mathbf{u}(x,t,a) = \begin{cases} 
\mathbf{u}_H(x,t) & \text{if } a < a_{pl} \\
\mathbf{u}_H(x,t) + \mathbf{u}_A(x) & \text{if } a \geq a_{pl}
\end{cases}
\]

where \(\mathbf{u}_H(x,t)\) represents the hydrodynamic current vector field (e.g., eq. 12) which comprises the passive component of advective transport and \(\mathbf{u}_A(x)\) represents the corresponding vector field for the component of active migration. To model the active component, I made two assumptions: (1) that postlarvae are able to sense and orient towards the nearest coastal habitat, and (2) that postlarvae migrate more efficiently near the coast. Postlarvae in shallow areas may anchor themselves to the bottom temporarily during adverse tides and weather conditions (Calinski and Lyons, 1983). However, anchoring is possible only in the shallow coastal zone, not further offshore. Presumably, then, postlarvae near the coast migrate inshore at a higher effective rate (e.g., over a 24 hour interval) than postlarvae further offshore. Consequently, I set the effective daily swimming speed, \(v_{pl}\), for postlarvae at 0.25 km day\(^{-1}\) (0.22 cm s\(^{-1}\)) in the interior of the Sound and at 1.0 km day\(^{-1}\) (0.88 cm s\(^{-1}\)) for postlarvae within 2.5 km (one grid cell) of the coastal boundary of the sound (Table 1).

I defined a very simple boundary porosity function, \(\alpha(x_B,t,a)\), to account for differences in dispersal modes between larvae and postlarvae, as well as to reflect settlement of postlarvae in coastal habitats, using:
where the $\omega_L$ and $\omega_{PL}$ are parameters, $x_{CB}$ is the set of points associated with coastal boundaries, and $x_{DB}$ is the set of points associated with deepwater boundaries. I selected parameter values for the larval stage such that 50% of the outward-directed flux is lost at open ocean boundaries, while coastal boundaries are closed (Table 1). For the postlarval stage, open ocean boundaries were closed but coastal boundaries were completely "open" (Table 1), reflecting postlarval settlement in the coastal habitats.

Finally, I set the turbulent diffusivities, $D_x$ and $D_y$, to constants (Table 1). I used the same values as Possingham and Roughgarden (1990; see also Okubo, 1971).

**Benthic sub-model functions and parameters**

The benthic sub-model for the Caribbean spiny lobster encompasses five benthic life-history divisions: algal phase juvenile, post-algal phase juvenile, sub-adult juvenile, adult male and adult female. I divided the adult stage into sex-specific components because both adult growth rates (e.g., Hermkind and Lipcius, 1989) and exploitation patterns may be sex-specific.

Because the different post-settlement life-history stages utilize different habitats, I assumed that density dependence within each benthic model stage was independent of the local density within other stages except, of course, for the adult stages. For each adult stage, the effective density was taken as the total density for both sexes. Consequently, I used the following matrix of values for the parameters $c_{ij}$ used in computing the effective stage density (eq. 7):
In the context of the model, size refers to carapace length (CL). Modeled stages range in size from 6 mm to 150 mm CL (Table 2). Although Caribbean spiny lobster occasionally reach sizes larger than 150 mm CL, I restricted the maximum adult size in the model to 150 mm CL in order to reduce computer memory requirements. This is not an unreasonable restriction, since only a small fraction of lobsters achieve greater size in Exuma Sound (Herrnkind and Lipcius, 1989; Lipcius and Stockhausen, unpublished).

To complete the species-specific version of the benthic model, I specified the functional forms and parameters for the following processes: (1) habitat quality, (2) growth, (3) mortality, (4) stage transition, (5) post-settlement dispersal, and (6) settlement. For simplicity, the functional form adopted for each process was identical for all stages; parameter values were stage-specific (Table 2).

**Habitat quality.**—To implement a simple, parametric model for spatiotemporal variation in benthic habitat quality, I ignored temporal fluctuations in habitat abundance/quality (e.g., no time dependence) and incorporated sinusoidal variations along the coast. Thus, I modeled the habitat indices, \( \Psi_i(\theta, t) \), using:

\[
\Psi_i(\theta, t) = \max\{\Psi_{i1} + \Psi_{i2} \cos[2\pi \left( \frac{\theta}{\Psi_{i3}} - \Psi_{i4} \right)], 0\}
\]

(17)

where the \( \Psi_i \) are stage-specific coefficients (Note: to minimize confusion, I will indicate the coefficients of a function by appending the function symbol with indices). For the baseline scenario, I ignored spatial variability in habitat abundance/quality as well, so...
only the \( \mathcal{Y}_{ij} \) are non-zero (Table 2). The values selected for the baseline scenario reflect
an apparent limitation of settlement habitat in Exuma Sound (Lipcius et al., 1997), as
well as an assumed decrease in habitat availability with size.

**Individual growth.**—Because spiny lobster growth occurs in discrete increments through molting, individual growth histories are not well-modeled by a continuous function (Botsford, 1985). However, if molting is not coordinated, such an approach is reasonable to describe changes in size-specific density when the number of individuals is large. While molting patterns are seasonal in temperate zones, they are continuous with minor annual peaks in the tropics (Lipcius, 1985). Consequently, I choose to ignore possible coordination in molting associated with season and modeled the instantaneous individual growth rate, \( g_t(z, \theta, t) \), within each stage as size-dependent but spatially and temporally homogeneous. I adopted a Gompertz-type function (Ricker, 1975; Brown and Rothery, 1993) for individual growth rate:

\[
g_{it}(z, \theta, t) = g_{it} z \ln \left( \frac{g_{t2}}{z} \right)
\]

(18)

where \( g_{it} \) and \( g_{t2} \) are stage-specific model parameters. The stage-specific growth parameters (Table 2) were selected so that mean stage durations would be consistent with those of Butler and Herrnkind (1997). The resulting growth curve (Fig. 9) was reasonably consistent with results from other studies, particularly given the variability in reported growth rates among previous studies (Davis and Dodrill, 1980, 1989; Hunt and Lyons, 1986; Forcucci et al., 1994). Baseline growth rate parameters for adult males and females were identical (Table 2).

**Natural mortality.**—I decomposed the total rate of mortality, \( \mu_t(z, \theta, t) \), into additive components associated with exploitation by fisheries (\( \mu_t'(z, \theta, t) \)—“fishing mortality”) and
other sources ($\mu^n_i(z,\theta,t)$—"natural mortality"). Several studies have determined relative natural mortality of Caribbean spiny lobster among experimental treatments in the field (e.g., Eggleston et al., 1990; Eggleston et al., 1992; Butler and Herrnkind, 1997), but few studies have estimated absolute rates (e.g., Munro, 1974)—and none have done so within Exuma Sound. In the sound, lack of appropriately-scaled shelter may be an important factor influencing density-dependent mortality rates (Lipcius et al., 1997). However, density dependence is likely only at high densities, after most available shelters are occupied. Thus, I modeled the instantaneous rate of natural mortality using the piece-wise linear expression:

$$\mu^n_i(z,\theta,t) = \begin{cases} \mu^n_i & \zeta_i(\theta,t) < \zeta^n_i \\ \mu^n_i (1 + \mu^n_i [\zeta_i(\theta,t) - \zeta^n_i]) & \zeta_i(\theta,t) \geq \zeta^n_i \end{cases} \quad (19)$$

where the $\mu^n_{ij}$ and $\zeta^n_i$ are stage-specific model parameters (Table 2), and $\zeta_i(\theta,t)$ is the local habitat-normalized, stage-specific density (see discussion following eq. 7). Local rates of natural mortality are density-independent when density is low ($\zeta_i(\theta,t) < \zeta^n_i$), but increase linearly with density when density is high. Because the expression is density-dependent, natural mortality rates may vary both spatially and temporally. Because absolute rates have not been measured, I chose parameter values (Table 2) that gave reasonable survival probabilities (Fig. 9, see Butler and Herrnkind, 1997). Modelling of fishing mortality is discussed in a subsequent section.

Transitions between life-history stages.—I selected a simple, but otherwise arbitrary, functional form for the rate of transition between life-history stages, $\tau_{ij}(z,\theta,t)$. The rate at which individuals shift from stage $j$ to stage $i$, as

$$\tau_{ij}(z,\theta,t) = \begin{cases} 0 & z < z^r_i \\ \tau_{ij}[1-e^{-\tau_{ij}(z-z^r_i)}] & z \geq z^r_i \end{cases} \quad (20)$$

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Chapter 3

where the $\tau_{ijk}$ are stage-specific model coefficients and $z_i^*$ is the minimum size at which transitions to later stages occur. In this formulation, the rate of transition is density independent. The coefficients $\tau_{ij}$ represent the asymptotic transition rate from stage $j$ to stage $i$. The coefficient $\tau_{i2}$ governs the rate of increase of $\tau_{ij}(z,\theta,t)$ with individual size. The parameter values I selected (Table 2) yield reasonable intervals for transition from one stage to the next.

Post-settlement dispersal.—Of the post-settlement stages, only sub-adults and adults appear to disperse over significant distances (Herrnkind, 1980, 1983; Herrnkind and Butler, 1986). Spectacular migrations associated with seasonal climatic changes in which individuals “queue up” in single file lines occur in other areas of the Caribbean (Kanciruk and Herrnkind, 1978; Herrnkind, 1980, 1983). Within Exuma Sound, however, alongshore movement of both sub-adults and adults may be nomadic rather than directed (Herrnkind and Lipcius, 1989). Consequently, I modeled alongshore dispersal as a density-dependent diffusion process using:

$$J_i(z,\theta,t) = -\frac{\partial}{\partial \theta} \left[ \kappa_i(\theta,t) s_i(z,\theta,t) \right]$$

(21)

where $s_i$ is the stage-classified, size-dependent local density and $\kappa_i$ is a stage-specific, density-dependent diffusion coefficient defined as

$$\kappa_i(\theta,t) = \kappa_{i1} \left[ 1 + \kappa_{i2} \frac{\zeta_i(\theta,t)}{\kappa_{i3} + \xi_i(\theta,t)} \right]$$

(22)

In the latter equation, the $\kappa_{ij}$ are stage-specific model coefficients and $\zeta_i(\theta,t)$ is the normalized life-history stage density (see discussion after eq. 7).

The functional form chosen for $J_i$ in eq. 21 is appropriate when the direction of movement of individuals is locally unbiased while the rate depends only on conditions at
the point of departure (Okubo, 1980). Thus, individuals move away from “poor” habitat in random directions. The functional form for the diffusion coefficient $\kappa$, eq. 22, allows post-settlement dispersal to be a combination of density independent and density-dependent effects. I selected parameter values that reflect the generally more sedentary nature of adult spiny lobster (vs. sub-adults) and generated reasonable dispersal patterns (Table 2).

Settlement.—Finally, the benthic model source term, $S(z, \theta, t)dzd\theta$, represents the influx of individuals at time $t$ from beyond the model domain into the size increment $[z, z+dz]$ within the coastal region $[\theta, \theta+d\theta]$. In the present context, the only influx is the settlement of postlarvae, $S_{pl}(\theta, t)$ from eq. 5, and subsequent metamorphosis into algal phase juveniles. Although postlarvae in Exuma Sound range from 4 to 7 mm CL (Eggleston et al., 1998; Lipcius and Stockhausen, unpublished), I modelled all postlarvae as metamorphosing into algal phase juveniles in the size interval 6-7 mm CL. Consequently, the benthic model source term is

$$S_i(z, \theta, t) = \begin{cases} S_{pl}(\theta, t) & z \in [6,7], \ i = 1 \\ 0 & \text{otherwise} \end{cases} \tag{23}$$

where $i = 1$ refers to the algal phase juvenile stage and $S_{pl}$ is given by eq. 5.

Reproduction sub-model

To complete the reproduction sub-model for the Caribbean spiny lobster, I specified functional forms and parameters describing: (1) the temporal pattern of mating, egg extrusion and hatching, (2) the fraction of individuals mature at size $z$, and (3) individual fecundity. In this model, reproduction is limited to mature females (stage $i = 5$).
In Exuma Sound, peak reproductive activity occurs in spring, with continued extrusion of egg masses and hatching of larvae through autumn (Herrnkind and Lipcius, 1989). The incidence of females occupying offshore reefs which carry fertilized egg masses reaches 80% in June, then declines quickly towards autumn (Herrnkind and Lipcius, 1989). For simplicity, I ignored a possible secondary spawning peak in the fall and assumed that individual rates of larval production did not vary spatially. Thus, I used a single truncated normal distribution function to express temporal variation in the rate of individual spawning, $r_i(z, \theta, t)$:

$$r_i(z, \theta, t) = \begin{cases} 
  r_{i1} \exp \left( \frac{(t - \tau_{2i})^2}{2 \tau_{1i}^2} \right) & t \in [t_{iLP}^{\text{start}}, t_{iLP}^{\text{end}}] \\
  0 & \text{otherwise}
\end{cases}$$

The $r_{ij}$ in eq. 24 influence the overall level of spawning activity, the time of peak spawning, and the variability about the peak. Of the $r_{ij}$ coefficients, only $r_{51}$ is nonzero—since only mature females reproduce. The parameters $t_{iLP}^{\text{start}}, t_{iLP}^{\text{end}}$ indicate the beginning and end of the reproductive season, respectively. The selected parameter values reflect reproductive activity by all mature females during the season, with peak activity during the summer (Table 3, Fig. 10).

Published estimates of minimum and average sizes at which females first spawn vary substantially (reviewed in Lyons et al., 1981). Reported minimum sizes range from 38-83 mm CL, whereas average sizes range from 70-100 mm CL (see Lyons et al., 1981). In Exuma Sound, the smallest reported egg-bearing female was 85 mm CL, whereas the percentage of mature females increased to 100% by 100 mm CL (Herrnkind and Lipcius, 1989). For simplicity, I assumed that the fraction mature, $m_i(z, \theta, t)$, was...
spatially and temporally homogeneous, and I expressed it as a knife-edge function of size:

\[
m_i(z, \theta, t) = \begin{cases} 
1 & z \geq z_i^m, \ i = 5 \\
0 & \text{otherwise}
\end{cases}
\] (25)

where \( z_i^m \) reflects the size at maturity. For the baseline case, \( z_i^m \) was taken as 80 mm CL (Table 3).

Individual fecundity (i.e., number of eggs in an egg mass) of spiny lobster has been well-described by size-dependent power laws (Mota Alves and Bezerra, 1968; Lipcius et al., 1997). In Exuma Sound, individual fecundity does not appear to vary spatially (Lipcius et al., 1997). Consequently, I expressed individual fecundity, \( \text{rf}[z, \theta, t] \), using a spatially and temporally homogeneous power law:

\[
\text{rf}(z, \theta, t) = \text{rf}_1 z^{\alpha_2}
\] (26)

Parameter values for the baseline case (Table 3, Fig. 10) were taken from Lipcius et al. (1997).

Incorporating Fishery Exploitation and Marine Reserves

Harvesting by fishers changes local patterns of abundance (i.e., density) by removing individuals captured in the fishery from the population; from the population perspective, this is equivalent to introducing a new source of mortality, fishing mortality, in addition to natural mortality (eq. 19). When marine reserves (i.e., harvest refugia) are created, fishing effort can no longer be expended within reserve areas (in the presumed absence of poaching). However, it is possible (and perhaps even likely) that the fishing effort expended in the area prior to reserve creation is not simply eliminated (e.g., affected fishers simply stop fishing), but rather is simply displaced to areas outside the reserve (e.g., affected fishers move to continue fishing). Thus, the spatial distribution
(and redistribution) of fishing effort may play a key role in determining reserve effectiveness. Consequently, it was necessary to develop a spatially-explicit model linking fishing mortality and fishing effort on the local scale.

A standard, simplifying assumption in many non-spatial fishery models (e.g., Schaefer, 1954; Beverton and Holt, 1957) is that fishing effort and mortality are proportional, and thus effort is proportional to catch rates, as well (for other possibilities, see Clark, 1985 and Waugh, 1984). In these models, fishing mortality, effort and catch are quantified on a regional spatial scale (e.g., the spatial extent of the stock under consideration) and an annual temporal scale. Clark (1985) observed that catch cannot be proportional to effort on regional/annual scales unless stock density is constant everywhere; however, this relationship may hold at the local scale over short periods of time (Clark, 1985).

To develop a spatially-explicit model for fishing mortality, I assumed that it was possible that several \( j \) different gear types operated simultaneously in the fishery, that the instantaneous, stage-classified, size-specific local rate of mortality due to the fishery, \( \mu_i^j(z,\theta,t) \), could be decomposed into additive components associated with each of the \( j \) gear types, \( \mu_i^j(z,\theta,t) \), and that the latter were proportional to local fishing effort for the \( j \)th gear type, \( E_j(\theta,t) \). I defined the units of effort, \( E \), so that the proportionality constant was 1; thus, the instantaneous rate of local fishing mortality is given by:

\[
\mu_i^j(z,\theta,t) = \sum_j \mu_i^j(z,\theta,t) = \sum_j q_{ij}(z,\theta,t) E_j(\theta,t)
\]

(27)

where \( q_{ij}(z,\theta,t) \) is the local catchability of size \( z \) lobsters in life-history stage \( i \) of at time \( t \) by the \( j \)th gear type.
To reduce model complexity, I assumed that catchability was stage-classified and size-specific, but did not vary spatially or temporally. In addition, I modeled catchability as a knife-edge function in size:

$$q_{ij}(z, \theta, t) = \begin{cases} q_{ij} & z \geq z_{ij}^{\text{fish}} \\ 0 & \text{otherwise} \end{cases}$$ \hspace{1cm} (28)

so that $i$-stage lobsters that were larger than $z_{ij}^{\text{fish}}$ were vulnerable to capture by the $j$th gear type.

In Chapter 2 (and Stockhausen et al., 2000), fishing effort was uniformly distributed over fishable areas during the open season, regardless of the spatial distribution of the lobster population. It seems more likely, however, that fishers concentrate their effort in areas of higher abundance (Clark, 1985). In addition, implementation of marine reserves (i.e., harvest refugia) may simply displace effort from the closed area into remaining open areas, rather than eliminating it, so that regional (total) effort remains constant. To incorporate these possibilities, I modelled spatially explicit effort as

$$E_{j}(\theta,t) = \begin{cases} \left( T_{j}^{-1} E_{j1} \right) \frac{\phi(\theta) \left[ \sum_{i} \int dz q_{ij}(z,\theta,t) s_{i}(z,\theta,t) \right]}{1 - L_{\text{MR}} / L_c} & \text{if } t \in [t_{j}^{\text{start}}, t_{j}^{\text{end}}] \\ 0 & \text{otherwise} \end{cases} \hspace{1cm} (29)$$

where $E_{j1}$ and $E_{j2}$ are model coefficients, $T_{j}$ is the length of the fishing season (as a fraction of the year), $L_{\text{MR}}$ is the length of coastline incorporated within marine reserves, $L_c$ is the total length of coastline, $\phi(\theta)$ is 0 within reserve areas and 1 outside reserve areas, and $[t_{j}^{\text{start}}, t_{j}^{\text{end}}]$ indicates the extent of the fishery season for the $j$th gear type. The
Chapter 3

coefficient $E_{ji}$ represents total (annual) effort for the $j$th gear type. The coefficient $E_{j2}$ controls the degree to which fishers differentially concentrate effort on areas with high local abundance: for $E_{j2} = 0$, effort is uniformly distributed within exploitable areas; for $E_{j2} = 1$, effort is distributed proportional to local abundance; for $E_{j2} > 1$, differences in relative abundance are further emphasized. The first ratio in this expression standardizes annual effort among fisheries with different seasons and different reserve configurations, while the second ratio determines the relative spatial distribution of effort.

The spatially-explicit, instantaneous catch rate, $C(\theta, t)$, is given by

$$C(\theta, t) = \sum_{i} \int dz \mu_i^{fish} (z, \theta, t) s_i (z, \theta, t)$$

(30)

The spatially-explicit pattern of annual catch along the coast, $C(\theta)$, is given by the integral of $C(\theta, t)$ over one year, whereas total annual catch, $C$, is given by the integral of $C(\theta)$ along the coast. Similarly, spatially-explicit, instantaneous yield, $Y(\theta, t)$, is given by the formula:

$$Y(\theta, t) = \sum_{i} \left[ \int dz w_i (z, \theta, t) \mu_i^{fish} (z, \theta, t) s_i (z, \theta, t) \right]$$

(31)

where $w_i (z, \theta, t)$ gives the tail weight for an $i$-stage lobster of carapace length $z$. For this latter function, I ignored potential spatiotemporal variation and used (Munro, 1974):

$$w_i (z, \theta, t) = w_{ii} \left[ 0.00271 z^{2.738} \right]$$

(32)

where $w_{i1} = 0.298$ (males), $w_{i2} = 0.365$ (females), and $w_{i3} = 0.5(0.298+0.365)$ for other life history stages (Pinto Paiva, 1960, cited in Munro, 1974). The spatial pattern along the coast for annual yield, $Y(\theta)$, as well as total yield, $Y$, are computed in a similar manner to the equivalent catch statistics.
Numerical model development

Using appropriate numerical techniques for integrating partial differential equations (e.g., Mitchell, 1969), I developed a computer program which implemented the theoretical model for numerical simulation. The numerical model is programmed in IDL, a high-level programming language oriented towards image analysis and numerical simulation which incorporates vector processing, object oriented programming, and graphics (Research Systems Inc., 1999).

As part of this development, I constructed a grid representation of Exuma Sound, using a digitized map projected into UTM coordinates. The grid consists of 1872 square cells (2.5 km on a side) and 254 boundary sections (Fig. 11). The cells constitute elements of the interior region $\Omega$, while the boundary sections constitute the boundary $\Omega_B$ (see Fig. 1), for which the model is defined. Of the 254 boundary sections, 21 contiguous sections constitute a deepwater boundary (52.5 km), representing the deep-water connection between Exuma Sound and the Atlantic at the southeast corner of the Sound, while the remaining sections constitute coastline available for settlement (582.5 km). Because little evidence for larval transport across the sill has been found (Colin, 1995, but see Hickey, in press), I assumed the shallow sill between Little San Salvador and Eleuthera functions only as coastal habitat—no larval transport occurs across the sill.

Methods

In order to "exercise" the model, I numerically integrated the model over a 30-year time span using the baseline scenario parameters. Initial abundance patterns for each life-history stage were set to zero. Larvae were "injected" into the pelagic sub-model at constant rates along the model boundary during the first three spawning seasons.
After year 3, larval injection was discontinued and the population continued to grow under its own dynamics. During the course of the simulation, regional abundance for the benthic life history stages, as well as regional larval production and settlement rates, were recorded at 5-day intervals. During the final year of simulation, the pelagic and benthic life-history stage density patterns were saved at 15-day intervals. In addition, spatially-explicit instantaneous, and cumulative, rates of larval production and settlement were also saved.

In order to compare the model results with field observations, I defined four equally-sized coastal regions which approximately correspond to the sites used in Lipcius et al. (1997): a) Cat Island ($\theta = [108, 158]$), b) Eleuthera ($\theta = [265, 315]$), c) the Exuma Cays Land and Sea Park (ECLSP; $\theta = [390, 440]$), and d) Lee Stocking Island (LSI; $\theta = [535, 585]$). For each region, I computed mean values for adult abundance and annual settlement at the end of the simulation. Lipcius et al. (1997) found a significant effect of site on adult density and postlarval settlement among their four study sites, but neither year nor the site x year interaction term were significant. Thus, I used the mean adult density and settlement at each site, collapsed over their three year study period. In order to compare the spatial patterns between predictions and observations without confounding overall scale factors, I normalized all sets of results by first log-transforming the means, then computing the standard residuals from the grand mean. To assess how well the model predicted the observed spatial patterns between sites, I regressed the normalized observed means against the normalized predicted means. Regression slopes close to 1 would indicate agreement between the model and field results.
Results

After approximately 25 model years, the simulated population approached a steady state (Fig. 12), with seasonal variations in abundance associated with seasonality in larval production and settlement (but lagged by about 2 years). Over the final year, regional adult abundance changed less than 0.01%—when final regional abundance was compared with that one year earlier. Maximum regional adult abundance during the final year of simulation was 24% of carrying capacity.

Patterns of annual larval production and settlement varied substantially with location along the coast (Fig. 13), reflecting the time-integrated influence of seasonally-variable hydrodynamic current patterns. The pattern for larval production (reflecting the spatial pattern of adult abundance) was a smoothed version of that for settlement (Fig. 13), indicating that post-settlement benthic dispersal and, to a lesser extent, density-dependent mortality acted to reduce variability in abundance at small spatial scales from that imposed by settlement patterns by the time lobsters achieved maturity.

On a finer temporal scale, the relative spatial pattern of settlement varied with season (Fig. 14), primarily due to changes in hydrodynamic current patterns; seasonal variation in regional settlement was primarily due to seasonal changes in spawning and hatching rates (and lagging these by about 120 days). Conversely, the relative spatial pattern of adult abundance changed little with time, although seasonal changes in regional abundance were evident (Fig. 14). Seasonal changes were also apparent in the regional size composition of post-settlement lobsters (Fig. 15), also reflecting the seasonality of settlement. Cohorts from settlement in several different years were evident in the size-frequency compositions (Fig. 15).
Model predictions regarding the spatial population patterns did not agree with previous field observations (Lipcius et al., 1997). Predictions of adult density at four field sites were actually inversely correlated with observed densities (slope = -0.45, Fig. 16a), although the regression was not statistically significant (P = 0.55, adjusted r^2 = 0.0). Predictions for settlement, on the other hand, were positively correlated with observed settlement rates (slope = 0.68, Fig. 16b). However, the regression was not statistically significant (P = 0.33, adjusted r^2 = 0.18)

Discussion

In this chapter, I provided a detailed description of the revised population model for Caribbean spiny lobster in Exuma Sound. The revised model differs from the model used in Chapter 2 (Stockhausen et al., 2000) in several respects. First, the revised model incorporates seasonal variability in the hydrodynamic current patterns which influence pelagic dispersal and settlement. In the original model, the hydrodynamic pattern—although spatially variable—was temporally static. Second, the revised model allows fishing effort to adjust to the spatial pattern of abundance for targeted life-history stages. Fishers can “aggregate”, or concentrate effort, in regions with high lobster abundance. In the original model, fishing effort was uniformly distributed outside areas designated as marine reserves, regardless of the population distribution. Third, the revised model incorporates the power-law expression for size-specific fecundity presented in Lipcius et al. (1997). The original model incorporated an exponential model for size-specific fecundity, based on a preliminary analysis of the data presented in Lipcius et al. (1997). In addition, the numerical model was completely reprogrammed to incorporate object-oriented programming, as well as to take advantage of other new features in the
programming language, IDL. As such, a revised baseline scenario (Tables 1-3) was also developed.

Model results from the baseline scenario are at odds with field observations of the Caribbean spiny lobster population in Exuma Sound (Lipcius et al., 1997; Lipcius, Stockhausen, and Eggleston, unpublished data). In particular, the relative patterns in adult abundance and settlement from four widely-spaced (> 100 km) field sites around the margin of the sound (see Lipcius et al., 1997) were not reproduced by the model (Fig. 16). In addition, results from the baseline model scenario indicate that the spatial patterns of adult density and settlement are well-correlated along the coast (see Fig. 14, with larval production providing a surrogate for adult density), in contrast to the patterns found by Lipcius et al. (1997), which indicated that adult abundance and settlement patterns were spatially decoupled.

There are several important factors which influence population structure in Exuma Sound that are not included in the baseline model scenario, and no concerted attempt has been made to "tune" the baseline model scenario to reproduce patterns observed in the sound. Probably the most important is spatial variation in habitat quality. Habitat quality for each benthic life-history stage is taken as uniform along the coast in the baseline scenario, whereas it actually varies substantially within the sound over large spatial scales (Lipcius et al., 1997). It is likely the joint effect of hydrodynamic transport (of larvae and postlarvae) and spatial variation in benthic habitat quality which decouples adult abundance and settlement over large spatial scales in the sound (Lipcius et al., 1997). The baseline model scenario also ignores fishing, while fishing pressure within the sound may exert a substantial spatial effect on the lobster population, given that one...
of the field sites with the highest lobster abundance was in a marine reserve closed to fishing (Lipcius et al., 1997).

As a consequence, my emphasis in subsequent chapters is to use the model as an heuristic tool to investigate the performance of marine reserves from a theoretical, rather than from an applied, perspective.
Literature Cited


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Chapter 3


Table 1. Baseline parameters for the planktonic sub-model component of the Caribbean spiny lobster model.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Value</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>age at metamorphosis to postlarva, ( a_{pl} )</td>
<td>120</td>
<td>days</td>
</tr>
<tr>
<td>maximum planktonic duration</td>
<td>180</td>
<td>days</td>
</tr>
<tr>
<td>larval mortality rate, ( \mu_{L} )</td>
<td>0.08</td>
<td>day(^{-1})</td>
</tr>
<tr>
<td>postlarval mortality rate, ( \mu_{pl} )</td>
<td>0.05</td>
<td>day(^{-1})</td>
</tr>
<tr>
<td>effective offshore postlarval swimming speed</td>
<td>1.0</td>
<td>km/d</td>
</tr>
<tr>
<td>effective coastal postlarval swimming speed</td>
<td>0.25</td>
<td>km/d</td>
</tr>
<tr>
<td>turbulent diffusivity: ( D_{x}, D_{y} )</td>
<td>0.864, 0.864</td>
<td>km(^{2})/d</td>
</tr>
<tr>
<td>boundary porosities: ( \omega^{CB}<em>{l}, \omega^{DB}</em>{l}, \omega^{CB}<em>{pl}, \omega^{DB}</em>{pl} )</td>
<td>0, 50, 100, 0</td>
<td>%</td>
</tr>
</tbody>
</table>
Table 2. Baseline parameters for the benthic sub-model component of the Caribbean spiny lobster model.

<table>
<thead>
<tr>
<th>Parameters</th>
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<tbody>
<tr>
<td>Life-history stages</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>algal phase</td>
<td>postalgal phase</td>
</tr>
<tr>
<td>Habitat quality ( \Psi_i )</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \Psi_{il} )</td>
<td>20000</td>
<td>10000</td>
</tr>
<tr>
<td>( \Psi_{il} )</td>
<td>0</td>
<td>0</td>
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</tr>
<tr>
<td>( \Psi_{il} )</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Life-history stage size limits ( z_i^{\text{min}} - z_i^{\text{max}} )</td>
<td>6-25</td>
<td>20-45</td>
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<tr>
<td>Growth--( g_i )</td>
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<tr>
<td>( g_{il} )</td>
<td>0.009</td>
<td>0.002</td>
</tr>
<tr>
<td>( g_{il} )</td>
<td>50</td>
<td>150</td>
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<tr>
<td>Natural mortality--( \mu_i )</td>
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<tr>
<td>( \mu_{il} )</td>
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<td>0.005</td>
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<td>( \zeta_i^{\mu} )</td>
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<td>1</td>
</tr>
<tr>
<td>Dispersal--( \kappa_i )</td>
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</tr>
<tr>
<td>( \kappa_{il} )</td>
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<tr>
<td>( \kappa_{il} )</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Life-history stage transition rates--( r_{ij} )</td>
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<td></td>
</tr>
<tr>
<td>( j \rightarrow i )</td>
<td>1 \rightarrow 2</td>
<td>2 \rightarrow 3</td>
</tr>
<tr>
<td>( r_{ij} )</td>
<td>0.05</td>
<td>0.025</td>
</tr>
<tr>
<td>( r_{ij} )</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>( z_j^{r} )</td>
<td>mm CL</td>
<td></td>
</tr>
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</table>

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Table 3. Baseline parameters for the reproductive sub-model component of the Caribbean spiny lobster model.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Values</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Life-history stages</td>
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<td></td>
</tr>
<tr>
<td>maturity -- $m_i$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$z_m^m$</td>
<td></td>
<td>$85$ mm CL</td>
</tr>
<tr>
<td>mean spawning rate -- $r_i$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$[t_{LP}^{start}, t_{LP}^{end}]$</td>
<td></td>
<td>$[90, 270]$ Julian day</td>
</tr>
<tr>
<td>$r_{i1}$</td>
<td>0</td>
<td>$7.94 \times 10^{-3}$ day$^{-1}$</td>
</tr>
<tr>
<td>$r_{i2}$</td>
<td>--</td>
<td>$180$ days</td>
</tr>
<tr>
<td>$r_{i3}$</td>
<td>--</td>
<td>$60$ days</td>
</tr>
<tr>
<td>Fecundity -- $\tilde{\Phi}$</td>
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</tr>
<tr>
<td>$\tilde{\Phi}_i$</td>
<td>0</td>
<td>$10.1$ # eggs</td>
</tr>
<tr>
<td>$\tilde{\Phi}_2$</td>
<td>--</td>
<td>$2.38$ (none)</td>
</tr>
</tbody>
</table>
Figures

Figure 1. Conceptual relationship among sub-models comprising full population model for a benthic invertebrate species with a complex life history.

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Figure 2. Schematic illustrating the conceptual physical geometry and ecological processes for the population dynamics model. The oceanic region, $\Omega$, is a (horizontal) 2-dimensional region with a 1-dimensional boundary, $\Omega_B$, comprising either deep water or shallow coastal regions. The “coastal coordinate”, $\theta$, defines locations along the boundary.
Figure 3. Exuma Sound, Bahamas.
Figure 4. Nearsurface geostrophic currents (Hickey, in press) observed in the sound: a) November, 1993; b) June, 1994.
Figure 5. Conceptualized life-history stages for *Panulirus argus* (Latreille), the Caribbean spiny lobster: egg (not shown), a) phyllosome larva, b) puerulus postlarva, c) algal phase benthic juvenile, d) post-algal phase benthic juvenile, e) sub-adult, and f) adult.

Figure 6. Ontogenetic habitat shifts for the Caribbean spiny lobster (after Lipcius and Cobb, 1994).
Figure 7. Temporal variation in the hydrodynamic pattern multipliers, \( \varepsilon_N \) and \( \varepsilon_J \), for the November, 1993 and June 1994 hydrodynamic current patterns (see Fig. 4) for the baseline model scenario.

Figure 8. Probability of survival vs. age for larvae (age < \( a_{pl} \)) and postlarvae (age > \( a_{pl} \)) for the baseline model scenario (see Table 1).
Figure 9. Survival and growth vs. age during the benthic life-history stages for the baseline model scenario (Table 2). Density dependent effects were ignored.

Figure 10. A) temporal spawning and hatching patterns, and b) size-specific fecundity for the baseline model scenario (see Table 3).
Figure 11. Numerical grid for the Caribbean spiny lobster/Exuma Sound application. Grid cells are 2.5 km x 2.5 km. The value of the "coastal coordinate", θ, is shown at various locations around the grid boundary. The boundary across the mouth of the sound, between Long Island and Cat Island, is classified as a deepwater boundary; the remaining boundary is classified as coastal habitat.
Figure 12. Model results for the baseline scenario: time series of regional adult abundance and larval production during the 30-year simulation period.
Figure 13. Model results for the baseline scenario—the spatial distribution (along the coast) of annual larval production (line) and settlement (shaded bars) for the final model year. The location of the deepwater boundary across the mouth of the sound is indicated by the cross-hatched zone.
Figure 14. Model results for the baseline scenario—the spatial distribution (along the coast) of adult abundance (line) and settlement (shaded bars) during the final model year: a) Spring (Julian day 90), b) Summer (Julian day 180), c) Fall (Julian day 270), and d) Winter (Julian day 364). Settlement patterns were time-integrated over the previous quarter-year (thus, the settlement pattern for Winter integrates instantaneous rates over Julian days 271-364), whereas patterns of adult abundance are for the day in question (thus, the pattern for Winter is that on Julian day 364). The location of the deepwater boundary across the mouth of the sound is indicated by the cross-hatched zone.
Figure 15. Model results for the baseline scenario—regional benthic size distributions at four different times during the final model year: a) Spring (Julian day 90), b) Summer (Julian day 180), c) Fall (Julian day 270), and d) Winter (Julian day 364).
Chapter 3

Figure 16. Comparison of baseline model predictions and observed patterns at four field sites (Lipcius et al., 1997) for a) mean adult density and b) mean settlement. Model predictions were computed by averaging over a 50 km region approximating the extent of each field site. Observed values were averaged over 3 field seasons. Predicted and observed values were log-transformed and standardized prior to comparison. Agreement between model predictions and observed values would yield a slope close to 1.
Chapter 4: Model Sensitivity Analyses

Introduction

Specific results from any model depend on the values chosen for its parameters, as well as its structure. Changes to model parameters, like changes to model structure, may result in substantially different results. Conclusions drawn from a model with a particular set of parameter values may not be the same as those that would be drawn if the model had been considered with a different set of parameters. Thus, an important component of model design involves testing the completed model for sensitivity.

A model is "sensitive" to those parameters which, when varied, result in substantially different model output. Conversely, a model is insensitive, or "robust", to changes in parameters which, when varied, result in similar model output. The process of quantifying model sensitivity is referred to as performing a sensitivity analysis (Caswell, 2001).

The purpose of model sensitivity analysis changes with the goal of the model (Turchin, 1998; Caswell, 2001). For example, the purpose of a sensitivity analysis for a model designed to predict future trends in population growth might be to identify which model parameters need to be the most accurately determined from field data (Turchin, 1998). Since I used the spiny lobster model to test various hypotheses on how reserve function may be affected by environmental and behavioral factors, the purpose of performing a model sensitivity analysis for the spiny lobster model was to assess the
likely robustness of conclusions drawn in the various marine reserve studies (Chapters 2, 5, and 6) to changes in the parameterization of the basic spiny lobster model. Also, although I did not use the present model to predict actual lobster population trajectories within the sound, it was still of considerable interest to determine the robustness of the baseline model predictions for spatial patterns and regional abundance.

In the study reported here, consequently, I tested the sensitivity of the baseline spiny lobster model (Chapter 3) to changes in parameter values affecting: 1) hydrodynamic current patterns, 2) porosity of the deepwater boundary to larval flux, 3) larval duration, 4) postlarval dispersal, 5) post-settlement dispersal, and 6) habitat quality. I assessed model sensitivity in terms of changes to spatial population patterns, as well as regional abundance, relative to the baseline model scenario (Chapter 3).

Methods

I tested the sensitivity of the baseline spiny lobster model (Chapter 3) to changes in various parameters by creating a variety of alternative model "scenarios" (Table 1). For each scenario, I numerically integrated the model over a 30-year time span. Initial abundance patterns for each life-history stage were set to zero. Larvae were "injected" into the pelagic sub-model at constant rates along the model boundary during the first three spawning seasons. After year 3, larval injection was discontinued and the population continued to grow under its own dynamics; typically, a steady state was reached after 25 model years. I then evaluated changes, relative to the baseline scenario, in spatial patterns for larval production and settlement along the coast (Fig. 1), as well as in spatially-integrated abundance for the regional population, for the final year of simulation. Changes in spatial patterns were quantified by computing cross-correlations with the corresponding patterns from the baseline scenario. Changes in regional abundance...
(spatially-integrated) abundances were quantified by computing the fractional difference with the corresponding value from the baseline scenario.

Variations in the pelagic sub-model

Hydrodynamic transport patterns.—A numerical model for hydrodynamic currents in Exuma Sound is not currently available. Hence, I used a very simple strategy to introduce temporal variation into the model current fields that advect larvae and postlarvae within the sound. Basically, I simulated a current field, $u(x,t)$, which varied in time ($t$) and space ($x$) by using a time-varying superposition of two “snapshots,” $u_N(x)$ and $u_J(x)$, of current flow in Exuma Sound (Fig. 2; Hickey, in press). [Note: I use the bold notation to distinguish variables which represent vector quantities in the horizontal plane; thus, $u(x,t) = u(x,t)x + v(x,t)y$, with $u$ and $v$ as the components of the current velocity along the $x$- and $y$-axes, respectively.] Thus,

$$u_H(x,t) = \varepsilon_N(t)u_N(x) + \varepsilon_J(t)u_J(x)$$

(1)

where $\varepsilon_N(t)$ and $\varepsilon_J(t)$ can change with time. The “snapshots” represent nearsurface geostrophic current flows in the sound, and were derived from CTD data collected by B. Hickey during physical oceanographic cruises in November, 1993 and June, 1994 (Hickey, in press). Assuming that interannual variability in the current patterns is small, then $u_N(x)$ characterizes the flow field during peak settlement, while $u_J(x)$ characterizes the flow field during peak larval production.

To test the model’s sensitivity to different hydrodynamic conditions, I defined six hydrodynamic scenarios using different intra-annual temporal patterns for $\varepsilon_N$ and $\varepsilon_J$: D1, AD1, AD2, AD12a, AD12b, and AD12c (Fig. 3). For D1, $\varepsilon_N$ and $\varepsilon_J$ were identically zero; D1 thus represents a scenario where pelagic dispersal occurs through turbulent diffusion alone. The next two scenarios represent the two basic hydrodynamic patterns.
(u_N and u_J, respectively) with no temporal variation; for AD1, \( \varepsilon_N = 1 \) and \( \varepsilon_J = 0 \) while for AD2, \( \varepsilon_N = 0 \) and \( \varepsilon_J = 1 \). The latter three scenarios incorporated different levels of intra-annual variability; AD12a had the slowest variation while AD12c had the fastest (Fig. 3). The intermediate case, AD12b, was adopted for the baseline hydrodynamic scenario.

**Boundary porosity.**—Transport of larvae and postlarvae across the deepwater boundary at the mouth of the sound represents an additional source of loss for the lobster population within the sound. Thus, total abundance within the sound may depend on the extent to which the sound is a closed or open system—i.e., the “porosity” of the boundary. In order to test what effect the exchange at the mouth might have, I varied the baseline deepwater boundary porosity to larval transport (\( \omega_{LB} = 50\% \)) to create two additional scenarios: one with the boundary completely closed to transport (\( \omega_{LB} = 0 \)) and one with the boundary completely open to transport (\( \omega_{LB} = 100\% \)).

**Larval duration.**—Although the duration of the larval phase imposes a fundamental timescale on pelagic processes, one might expect that population processes should be insensitive to changes in larval duration—if larval mortality also changes, but in an inverse manner. However, transport rates also impose timescales on pelagic processes; consequently, the interaction between larval duration and transport rates may affect both local abundance patterns and regional population levels. To determine whether such an interaction was would be biologically significant for the model, I created two additional larval duration scenarios: a short duration (\( a_{pl} = 60 \) d) case and a long duration case (\( a_{pl} = 180 \) d). These correspond to 50% and 150%, respectively, of the baseline larval duration (\( a_{pl} = 120 \) d). For both cases, I simultaneously varied larval mortality so that the product of larval duration and mortality was constant. Thus, the fraction of larvae which survive to settlement should be similar, if losses due to advection beyond the mouth of
the sound are similar. However, the spatial patterns of settlement may be considerably different.

_Puerulus dispersal._—In contrast to the larval stage, in which dispersal is assumed to be passive, the postlarval, or puerulus, stage is assumed to undertake an active migration toward coastal habitats prior to settlement. To test whether patterns of local abundance or regional population levels were sensitive to the assumed swimming speed of postlarvae prior to settlement, I created two puerulus dispersal scenarios, Passive Dispersal and Fast Swimming, by multiplying the effective swimming speeds for the baseline scenario (Chapter 3) by 0 and 2, respectively.

_Variations in the benthic sub-model_

_Post-settlement dispersal._—Post-settlement dispersal may have important population-level effects. High dispersal rates may reduce the potential for local density-dependent regulation by allowing emigration from high density areas to nearby low density areas. Conversely, low dispersal rates may exacerbate local density dependence. To determine the sensitivity of the baseline model to post-settlement dispersal, I created four additional dispersal scenarios—Very Low, Low, High, and Very High—by varying the stage-specific baseline dispersal coefficients (Chapter 3) by factors of 0.1, 0.3, 3.0 and 10.0, respectively.

_Spatial variation in habitat quality._—In the baseline scenario, stage-specific habitat quality is spatially uniform around the sound. To test whether spatial variation in habitat quality would have an appreciable effect on population levels, I created four additional habitat quality scenarios (Fig. 4): Large Scale Variation with Match (LSVwM), Large Scale Variation with Mismatch (LSVwMM), Small Scale Variation with Match (SSVwM), and Small Scale Variation with Mismatch (SSVwMM). For each case, stage-
specific local habitat quality (i.e., carrying capacity) varied sinusoidally with distance around the sound. Mean habitat quality was identical to that for the baseline case. For the Large Scale cases, the length scale of variation was 1/3 of the length of the coastline (~200 km); for the Small Scale cases, the length scale was 1/12 (~50 km). For the Match cases, variations in stage-specific habitat quality were in-phase for all life history stages. For the Mismatch cases, algal phase and postalgal phase habitat quality varied in phase, as did sub-adult and adult habitat quality; however, variation in the youngest two stages was directly out-of-phase with that of the older stages.

**Stage-specific variation in habitat quality.**—The stage-specific carrying capacities adopted for the baseline case create the potential for stage-specific population bottlenecks in the model. To test whether such bottlenecks existed, I created eight additional scenarios by increasing or decreasing the baseline carrying capacity for each benthic stage (Chapter 3) by 10% (carrying capacities for both adult stages were varied simultaneously, rather than individually).

**Results**

*Variations in the pelagic sub-model*

**Hydrodynamic transport patterns.**—Different intra-annual patterns of hydrodynamic currents resulted in substantially different spatial patterns of postlarval settlement, as well as adult abundance and larval production, along the coast (Fig. 5, Tables 2, 3). For each scenario, the spatial pattern of larval production was similar to a smoothed version of the spatial pattern for settlement; thus, hydrodynamic transport did not decouple adult abundance and recruitment.

When larval dispersal occurred through diffusion alone (D1), settlement (and larval production) was highest where the coastal geometry was highly concave (i.e., at the
northwestern end of the sound between Eleuthera and the Exuma Cays, as well as at the southernmost part of the sound west of Long Island, see Fig. 1) and smallest where the coastal geometry was linear or convex (e.g., between Cat Island and Eleuthera). Zones of high or low settlement had spatial scales of 150-200 km (ignoring variation at scales the order of a grid cell). For the other Hydrodynamic Scenarios, the spatial patterns of settlement and larval production were more complex, with one (AD2) to several peaks (AD1, AD12a, AD12b, AD12c) in abundance (Fig. 5). The spatial scale for these cases was smaller than for the diffusion-only case, approximately 50-75 km.

Hydrodynamic transport patterns also affected the level of regional settlement and larval production, not just local patterns. Among the scenarios considered here, regional settlement and larval production varied up to a factor of 5 (Fig. 6). Larval production was highest for AD12c and lowest for AD2, whereas settlement was highest for AD1 (which had the 3rd largest larval production) and lowest for AD2.

**Boundary porosity.**—Spatial patterns for settlement and larval production were only slightly affected by changes in whether the system was open or closed (Fig. 7, Tables 4, 5). Settlement and larval production were somewhat enhanced near the mouth of the sound when the system was closed (boundary porosity = 0), relative to the baseline (boundary porosity = 50%) and open systems (boundary porosity = 100%). Spatial patterns for the baseline and open systems were nearly identical.

Regional larval production was marginally enhanced (25%) over the baseline case when the system was closed; it was nearly identical for the open scenario and baseline (Fig. 8).

**Larval duration.**—Spatial patterns of settlement and larval production were substantially altered from the baseline case when larval duration was decreased by half, but not when it
was increased by two (Fig. 9, Tables 6, 7). When larval duration was short, peaks in settlement near the mouth of the sound were enhanced and broadened, relative to the baseline case. Spatial patterns for the baseline and long duration cases were much more similar.

Both regional larval production and settlement were enhanced (2-3x) over the baseline case when larval duration was short; whereas both were only marginally smaller then the baseline when larval duration was long (Fig. 10).

*Puerulus dispersal.*—Spatial patterns for settlement and larval production were marginally affected by changes in the manner in which pueruli re-invaded the coastal zone (Fig. 11, Tables 8, 9). Settlement and larval production were somewhat reduced, relative to the baseline case, everywhere when dispersal by pueruli was passive. When pueruli swimming speeds were doubled, relative to the baseline, settlement was somewhat enhanced everywhere. In contrast, larval production for this scenario remained approximately the same as the baseline over a 25-50 km window on either side of the highest peak in production (near coastal coordinate value 525, Fig. Jc). It was, however, somewhat larger everywhere else along the coast.

In all, regional settlement decreased marginally (~37%) over the baseline case when dispersal was passive, while it increased marginally (~42%) when pueruli swimming speeds were doubled (Fig. 12). Similarly, regional larval production decreased marginally (~33%) over the baseline case when dispersal was passive, while it increased marginally (~34%) when pueruli swam quickly (Fig. 12).

*Variations in the benthic sub-model*

*Post-settlement dispersal.*—Spatial patterns of larval production were more affected than those for settlement by changes in benthic dispersal rates (Fig. 13, Tables 10, 11). While
the minimum cross-correlation between the baseline and each of the alternative scenarios was extremely high (0.997) for settlement, it was somewhat reduced (0.886) for larval production. The principal effect of changes in the rates of benthic dispersal was either to increase the coherence between settlement patterns and subsequent larval production (when dispersal rates were decreased), or to reduce the coherence by “smoothing” out variations in settlement patterns at small spatial scales (when dispersal rates were increased).

Regional larval production and settlement changed somewhat (<±10%; Fig. 14) from the baseline case when dispersal rates were varied. Both decreased when rates decreased and both increased when rates increased. In contrast, increases in larval production and settlement over the baseline were smaller when dispersal rates increased by 10% than when rates increased by only 3%, indicating that further increases in dispersal might further reduce enhanced larval production and settlement.

Spatial variation in habitat quality.—Spatial patterns of larval production were more affected than settlement by spatial variation in local habitat quality (Fig. 15, Tables 12, 13). While the minimum cross-correlation between the baseline and each of the alternative scenarios was extremely high for settlement (0.997), it was somewhat reduced for larval production (0.852).

Introducing spatial variation into local habitat quality reduced regional larval production and settlement by 50-60% (Fig. 16). Reductions were approximately 10% larger when the spatial scale of variation was large rather than small. The relative phasing of variation in habitat quality between early benthic stages and later benthic stages had less impact than did the spatial scale of the variations.
Stage-specific variation in habitat quality.—Regional larval production and settlement were positively related to ±10% changes in assumed habitat quality for algal phase and adult lobsters, but not for post-algal phase and sub-adult lobsters (Fig. 17). For sub-adults, larval production and settlement were inversely related to ±10% changes in habitat quality, although the differences were extremely small. Similar changes in post-algal phase habitat quality had no impact at all on regional larval production or settlement.

Discussion

Results of the sensitivity analysis indicate that model results were most sensitive to factors which altered spatial patterns of abundance along the coast. Here, these factors included hydrodynamic current patterns, larval duration, and spatial variation in habitat quality. When parameters affecting these factors were varied, spatial patterns for abundance indices (annual larval production and settlement) varied dramatically (Tables 2, 3, 6, 7, 12; Figs 5, 6, 9, 10, 15, 16). For these factors, total (i.e., regionally-integrated) abundance indices changed by over 50% from the baseline case for some parameter variations. Conversely, model results were robust to changes in factors which did not substantially affect spatial patterns. These included boundary porosity, puerulus swimming abilities, benthic dispersal, and overall carrying capacity. Spatial patterns of abundance indices remained essentially unchanged by variations in parameters affecting these factors (Tables 4, 5, 8, 9, 10, 11; Figs 7, 8, 11, 12, 13, 14, 17). For these factors, regional abundance indices changed by less than 50% from the baseline case.

These results indicate the importance of local density-dependent mortality during at least one benthic life-history stage in structuring the population for the model system.
In the model, the stage-specific mortality rate for the benthic stages is a function of the local stage-specific density; once a local threshold density has been exceeded, the rate increases linearly with density (Chapter 3). Thus, regional abundance is limited by the spatial extent of the population, although the details may depend on the spatial structure of assumed habitat distributions (see below). For the baseline scenario, settlement and population abundance was concentrated along the southwestern flank of the sound, roughly in the coastal region corresponding to $0 = [500, 600]$ (Fig. 5e). Alternative scenarios which yielded more diffuse settlement patterns (e.g., hydrodynamic scenarios D1 and AD12c; Fig. 5a and f) resulted in higher regional abundance (Fig. 6), because a larger section of coastal habitat supported the population.

Clearly, then, factors which directly impact settlement patterns, such as hydrodynamic transport patterns, may significantly alter model results, in terms of both spatial patterns and regional abundance. Similarly, factors which influence the effects of hydrodynamic currents, such as larval duration, will also have an impact.

In the model, however, density-dependent, benthic stage mortality rates are also affected by habitat quality. The impact of settlement patterns on subsequent benthic mortality rates may thus be alleviated, or exacerbated, by the spatial patterns of habitat quality (Fig.s 15 and 16). For scenarios where patterns of settlement and habitat quality vary spatially in a similar fashion, regional abundance will be enhanced vis-à-vis scenarios where the spatial patterns are dissimilar.

One might also expect changes in factors affecting benthic dispersal ability, influencing the ability for individuals to disperse from sections of coast with high abundance, to also have an influence on spatial pattern and regional abundance.

Although this does seem to be the case, the effects appear to be relatively small (i.e., less
than 10% change in abundance for a 1000% change in dispersal ability; Fig. 14).

However, these effects may be small because only sub-adults and adults disperse. Algal phase and post-algal phase juveniles do not disperse (Chapter 3). Perturbing the stage-specific carrying capacities indicated that local habitat abundance may be a limiting factor for algal phase juveniles in the baseline scenario (Fig. 17). Thus, the algal phase may constitute a local bottleneck for the population, in sections of the coast where settlement is high, which subsequent dispersal by later benthic stages does not alleviate.

In conducting the sensitivity analysis presented here, I focused on factors in the model which seemed most likely to have an impact on the spatial patterns of abundance for Caribbean spiny lobster in Exuma Sound. From this analysis, hydrodynamic current patterns and spatial patterns of benthic habitat quality appear to have the greatest impact on model results. Within the larger context of this dissertation, I have focused on the potential effects of the former, rather than the latter, on marine reserve function.
Literature Cited


Table 1. Scenarios for model sensitivity studies.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>sub-model</th>
<th>parameters varied</th>
<th>values</th>
</tr>
</thead>
<tbody>
<tr>
<td>hydrodynamic patterns</td>
<td>pelagic</td>
<td>$c_n(t), c_p(t)$</td>
<td>see Fig. 3</td>
</tr>
<tr>
<td>boundary porosity</td>
<td>pelagic</td>
<td>$a_{DB}$</td>
<td>50% x 0.2</td>
</tr>
<tr>
<td>larval duration</td>
<td>pelagic</td>
<td>$a_{PL}$</td>
<td>120 d ± 50%</td>
</tr>
<tr>
<td>puerulus dispersal</td>
<td>pelagic</td>
<td>[offshore, nearshore] swimming speeds</td>
<td>[0.25, 1.0] km d$^{-1} \times 0.2$</td>
</tr>
<tr>
<td>benthic dispersal ability</td>
<td>benthic</td>
<td>$K_t$</td>
<td>0.1, 0.3, 3.0, 10</td>
</tr>
<tr>
<td>spatial variation in habitat quality</td>
<td>benthic</td>
<td>$\Psi_{il}, \Psi_{ol}, \Psi_{ul}, \Psi_{pl}$</td>
<td>see Fig. 4</td>
</tr>
<tr>
<td>stage-specific habitat quality</td>
<td>benthic</td>
<td>$\Psi_{il}$</td>
<td>±10%</td>
</tr>
</tbody>
</table>
Table 2. Cross-correlations for spatial patterns of larval production among the Hydrodynamic Scenarios (row x column).

<table>
<thead>
<tr>
<th></th>
<th>D1</th>
<th>AD1</th>
<th>AD2</th>
<th>AD12a</th>
<th>AD12b</th>
</tr>
</thead>
<tbody>
<tr>
<td>AD1</td>
<td>0.63</td>
<td>-x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>AD2</td>
<td>-0.27</td>
<td>-0.28</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>AD12a</td>
<td>-0.024</td>
<td>0.42</td>
<td>0.034</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>AD12b</td>
<td>-0.19</td>
<td>0.38</td>
<td>0.22</td>
<td>0.76</td>
<td>x</td>
</tr>
<tr>
<td>AD12c</td>
<td>0.57</td>
<td>0.82</td>
<td>-0.19</td>
<td>0.22</td>
<td>0.39</td>
</tr>
</tbody>
</table>

Table 3. Cross-correlations for spatial patterns of settlement among the Hydrodynamic Scenarios (row x column).

<table>
<thead>
<tr>
<th></th>
<th>D1</th>
<th>AD1</th>
<th>AD2</th>
<th>AD12a</th>
<th>AD12b</th>
</tr>
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<tr>
<td>AD1</td>
<td>0.17</td>
<td>-x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>AD2</td>
<td>-0.11</td>
<td>-0.08</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>AD12a</td>
<td>-0.11</td>
<td>0.78</td>
<td>-0.03</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>AD12b</td>
<td>-0.17</td>
<td>0.63</td>
<td>0.10</td>
<td>0.79</td>
<td>x</td>
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<tr>
<td>AD12c</td>
<td>0.35</td>
<td>0.62</td>
<td>-0.09</td>
<td>0.50</td>
<td>0.51</td>
</tr>
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</table>
Table 4. Cross-correlations for spatial patterns of larval production among the Larval Duration scenarios (row x column). For the baseline, $a_{PL} = 120$ d.

<table>
<thead>
<tr>
<th></th>
<th>baseline</th>
<th>short duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>short duration ($a_{PL} = 60$ d)</td>
<td>0.60</td>
<td>x</td>
</tr>
<tr>
<td>long duration ($a_{PL} = 180$ d)</td>
<td>0.96</td>
<td>0.46</td>
</tr>
</tbody>
</table>

Table 5. Cross-correlations for spatial patterns of settlement among the Larval Duration scenarios (row x column). For the baseline, $a_{PL} = 120$ d.

<table>
<thead>
<tr>
<th></th>
<th>baseline</th>
<th>short duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>short duration ($a_{PL} = 60$ d)</td>
<td>0.53</td>
<td>x</td>
</tr>
<tr>
<td>long duration ($a_{PL} = 180$ d)</td>
<td>0.95</td>
<td>0.36</td>
</tr>
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</table>

Table 6. Cross-correlations for spatial patterns of larval production among the Boundary Porosity scenarios (row x column). For the baseline, the porosity of deepwater boundaries to larval transport ($\omega^D_{DB}$) was 50%.

<table>
<thead>
<tr>
<th></th>
<th>baseline</th>
<th>closed system</th>
</tr>
</thead>
<tbody>
<tr>
<td>closed system ($\omega^D_{DB} = 0%$)</td>
<td>0.95</td>
<td>x</td>
</tr>
<tr>
<td>open system ($\omega^D_{DB} = 100%$)</td>
<td>1</td>
<td>0.95</td>
</tr>
</tbody>
</table>

Table 7. Cross-correlations for spatial patterns of settlement among the Boundary Porosity scenarios (row x column). For the baseline, the porosity of deepwater boundaries to larval transport ($\omega^D_{DB}$) was 50%.

<table>
<thead>
<tr>
<th></th>
<th>baseline</th>
<th>closed system</th>
</tr>
</thead>
<tbody>
<tr>
<td>closed system ($\omega^D_{DB} = 0%$)</td>
<td>0.97</td>
<td>x</td>
</tr>
<tr>
<td>open system ($\omega^D_{DB} = 100%$)</td>
<td>1</td>
<td>0.97</td>
</tr>
</tbody>
</table>
Table 8. Cross-correlations for spatial patterns of larval production among the Puerulus Dispersal scenarios (row x column). For the baseline scenario, daily swimming speeds were 0.25 km d\(^{-1}\) offshore, and 1.0 km d\(^{-1}\) nearshore.

<table>
<thead>
<tr>
<th></th>
<th>baseline</th>
<th>passive dispersal</th>
</tr>
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<tbody>
<tr>
<td>passive dispersal (0 x baseline)</td>
<td>0.99</td>
<td>x</td>
</tr>
<tr>
<td>fast swimming (2 x baseline)</td>
<td>0.98</td>
<td>0.94</td>
</tr>
</tbody>
</table>

Table 9. Cross-correlations for spatial patterns of settlement among the Puerulus Dispersal scenarios (row x column). For the baseline scenario, daily swimming speeds were 0.25 km d\(^{-1}\) offshore, and 1.0 km d\(^{-1}\) nearshore.

<table>
<thead>
<tr>
<th></th>
<th>baseline</th>
<th>passive dispersal</th>
</tr>
</thead>
<tbody>
<tr>
<td>passive dispersal (0 x baseline)</td>
<td>0.99</td>
<td>x</td>
</tr>
<tr>
<td>fast swimming (2 x baseline)</td>
<td>0.99</td>
<td>0.97</td>
</tr>
</tbody>
</table>

Table 10. Cross-correlations for spatial patterns of larval production among the Benthic Dispersal scenarios (row x column).

<table>
<thead>
<tr>
<th></th>
<th>baseline</th>
<th>very slow</th>
<th>slow</th>
<th>fast</th>
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</thead>
<tbody>
<tr>
<td>very slow (0.1 x baseline)</td>
<td>0.97</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>slow (0.3 x baseline)</td>
<td>0.99</td>
<td>1.00</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>fast (3 x baseline)</td>
<td>0.98</td>
<td>0.92</td>
<td>0.94</td>
<td>x</td>
</tr>
<tr>
<td>very fast (10 x baseline)</td>
<td>0.89</td>
<td>0.80</td>
<td>0.83</td>
<td>0.95</td>
</tr>
</tbody>
</table>

Table 11. Cross-correlations for spatial patterns of settlement among the Benthic Dispersal scenarios (row x column).

<table>
<thead>
<tr>
<th></th>
<th>baseline</th>
<th>very slow</th>
<th>slow</th>
<th>fast</th>
</tr>
</thead>
<tbody>
<tr>
<td>very slow (0.1 x baseline)</td>
<td>1.00</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>slow (0.3 x baseline)</td>
<td>1.00</td>
<td>1.00</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>fast (3 x baseline)</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>x</td>
</tr>
<tr>
<td>very fast (10 x baseline)</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
</tbody>
</table>
Table 12. Cross-correlations for spatial patterns of larval production among the Benthic Habitat Variability scenarios (row x column).

<table>
<thead>
<tr>
<th></th>
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<th>LSVwM</th>
<th>LSVwMM</th>
<th>SSVwM</th>
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<tbody>
<tr>
<td>LSVwM</td>
<td>0.85</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>LSVwMM</td>
<td>0.95</td>
<td>0.94</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>SSVwM</td>
<td>0.90</td>
<td>0.66</td>
<td>0.77</td>
<td>x</td>
</tr>
<tr>
<td>SSVwMM</td>
<td>0.93</td>
<td>0.84</td>
<td>0.93</td>
<td>0.72</td>
</tr>
</tbody>
</table>

Table 13. Cross-correlations for spatial patterns of settlement among the Benthic Habitat Variability scenarios (row x column).

<table>
<thead>
<tr>
<th></th>
<th>baseline</th>
<th>LSVwM</th>
<th>LSVwMM</th>
<th>SSVwM</th>
</tr>
</thead>
<tbody>
<tr>
<td>LSVwM</td>
<td>1.00</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>LSVwMM</td>
<td>1.00</td>
<td>1.00</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>SSVwM</td>
<td>1.00</td>
<td>0.99</td>
<td>0.99</td>
<td>x</td>
</tr>
<tr>
<td>SSVwMM</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
</tbody>
</table>

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Figure Captions

Figure 1. Exuma Sound, Bahamas. The righthand figure also shows the computational grid for the pelagic sub-model, as well as values of the coastal coordinate (in km) at various locations along the coastal boundary of the sound. Spatial patterns relative to the coastline (i.e., settlement, abundance in different benthic life-history stages, and larval production) are graphed as functions of the coastal coordinate (see Results).

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Figure 4. Variation in stage-specific habitat quality (i.e., carrying capacity) for each Habitat Variation scenario. The cross-hatched area indicates the deepwater boundary across the mouth of the sound. The wavelength for large scale variation (LSVwM, LSVwMM) is ~200 km; for small scale variation (SSVwM, SSVwMM) it is ~50 km. Regional habitat quality (i.e., spatially-averaged carrying capacity) is identical for all cases. For the “matched” cases (LSVwM, SSVwM), habitat quality for later benthic stages (sub-adult, dashed line; adult, dash-dotted line) is in-phase with that for early stages (algal phase, solid line; postalgal phase, dotted line); for “mismatched” cases (LSVwM, SSVwMM), habitat quality for later benthic stages is 180° out-of-phase with that for early stages.

Figure 5. Spatial distributions of larval production (solid line) and settlement (shading) in model year 30 under different Hydrodynamic Scenarios: a) D1, b) AD1, c) AD2, d) AD12a, e) AD12b, f) AD12c. The cross-hatched area indicates the deepwater boundary across the mouth of the sound. See text for description of individual scenarios.

Figure 6. Comparison of regional larval production (a, c) and settlement (b, d) during the final model year for the Hydrodynamic Scenario cases (see text for description of individual scenarios). In graphs a) and b), results are plotted using absolute scales; in graphs c) and d), results are plotted relative to the baseline scenario (AD12b).

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Figure 8. Regional larval production (a) and settlement (b), relative to the baseline scenario (porosity = 50%), during the final model year for the Boundary Porosity scenarios: 1) Closed (porosity = 0) and 2) Open (porosity = 100%).

Figure 9. Spatial distributions of larval production (solid line) and settlement (shaded bars) in model year 30 under different Larval Duration Scenarios: a) Short Duration
(60 d), b) baseline (120 d), and c) Long Duration (180 d). The cross-hatched area indicates the deepwater boundary across the mouth of the sound.

Figure 10. Regional larval production (a) and settlement (b), relative to the baseline scenario (120 d larval period), during the final model year for the Larval Duration scenarios: Short (0.5 x baseline) and 2) Long (1.5 x baseline).

Figure 11. Spatial distributions of larval production (solid line) and settlement (shaded bars) in model year 30 for the Puerulus Dispersal scenarios: a) passive settlement (i.e., no swimming), b) baseline, and c) fast swimming (2 x baseline). The cross-hatched area indicates the deepwater boundary across the mouth of the sound.

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Figure 14. Regional larval production (a) and settlement (b), relative to the baseline scenario, during the final model year for the Benthic Dispersal Ability scenarios: 1) Very Slow (0.1 x baseline), 2) Slow (0.3 x baseline), 3) Fast (3 x baseline), and 4) Very Fast (10 x baseline).

Figure 15 Spatial distributions of larval production (solid line) and settlement (shaded bars) during the final model year for the Benthic Habitat Variability scenarios: a) baseline, b) in-phase (matched) large scale variations (LSVwM), c) out-of-phase, mismatched large scale variations (LSVwMM), d) in-phase, matched small scale variations (SSVwM), and e) out-of-phase, mismatched small scale variation (SSVwMM). Average habitat quality is identical for all scenarios. The spatial pattern of sub-adult and adult habitat quality is shown in the upper third of each graph; the dotted line indicates completely unfit habitat. The spatial pattern of algal and post-algal phase habitat quality is either in phase (b and d) or out of phase (c and e) with the pattern shown. The cross-hatched area indicates the deepwater boundary across the mouth of the sound.

Figure 16. Regional larval production (a) and settlement (b), relative to the baseline scenario, during the final model year for the Benthic Habitat Variability scenarios: 1) in-phase (matched) large scale variations (LSVwM), 2) out-of-phase, mismatched large scale variations (LSVwMM), 3) in-phase, matched small scale variations (SSVwM), and 4) out-of-phase, mismatched small scale variation (SSVwMM).
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Figure 10. Regional larval production (a) and settlement (b), relative to the baseline scenario (120 d larval period), during the final model year for the Larval Duration scenarios: Short (0.5 x baseline) and 2) Long (1.5 x baseline).
Figure 11. Spatial distributions of larval production (solid line) and settlement (shaded bars) in model year 30 for the Puerulus Dispersal scenarios: a) passive settlement (i.e., no swimming), b) baseline, and c) fast swimming (2 x baseline). The cross-hatched area indicates the deepwater boundary across the mouth of the sound.
Figure 12. Regional larval production (a) and settlement (b), relative to the baseline scenario, during the final model year for the Puerulus Dispersal scenarios: 1) passive (0 x baseline) and 2) fast swimming (2 x baseline).
Figure 13. Spatial distributions of larval production (solid line) and settlement (shading) in model year 30 under different Benthic Dispersal Scenarios: a) baseline, b) Very Slow (0.1 x baseline), c) Slow (0.3 x baseline), d) Fast (3 x baseline), and e) Very Fast (10 x baseline). The cross-hatched area indicates the deepwater boundary across the mouth of the sound.
Figure 14. Regional larval production (a) and settlement (b), relative to the baseline scenario, during the final model year for the Benthic Dispersal Ability scenarios: 1) Very Slow (0.1 x baseline), 2) Slow (0.3 x baseline), 3) Fast (3 x baseline), and 4) Very Fast (10 x baseline).
Figure 15 Spatial distributions of larval production (solid line) and settlement (shaded bars) during the final model year for the Benthic Habitat Variability scenarios: a) baseline, b) in-phase (matched) large scale variations (LSVwM), c) out-of-phase, mismatched large scale variations (LSVwMM), d) in-phase, matched small scale variations (SSVwM), and e) out-of-phase, mismatched small scale variation (SSVwMM). Average habitat quality is identical for all scenarios. The spatial pattern of sub-adult and adult habitat quality is shown in the upper third of each graph; the dotted line indicates completely unfit habitat. The spatial pattern of algal and post-algal phase habitat quality is either in phase (b and d) or out of phase (c and e) with the pattern shown. The cross-hatched area indicates the deepwater boundary across the mouth of the sound.
Figure 16. Regional larval production (a) and settlement (b), relative to the baseline scenario, during the final model year for the Benthic Habitat Variability scenarios: 1) in-phase (matched) large scale variations (LSVwM), 2) out-of-phase, mismatched large scale variations (LSVwMM), 3) in-phase, matched small scale variations (SSVwM), and 4) out-of-phase, mismatched small scale variation (SSVwMM).
Figure 17. Regional larval production (a) and settlement (b), relative to the baseline scenario, during the final model year for 10% variation in stage-specific carrying capacity (positive variation, dark bars; negative variation, light bars).
Chapter 5: The Influence of Fishery Aggregation and Benthic Dispersal on the Performance of Marine Reserves

Introduction

By altering the spatial pattern of fishing mortality of exploited species, no-take marine reserves alter important spatially-explicit processes affecting the regional population dynamics of targeted (and other) species. When additional factors which influence the population also vary substantially across space, the interaction between these factors and reserve design may have complex and unanticipated consequences for reserve function (Chapter 2; Stockhausen et al., 2000). For example, spatial variation in hydrodynamic transport patterns resulted in complex and unanticipated behaviors for population responses to reserve design (Chapter 2; Stockhausen et al., 2000).

In this chapter, I considered two other factors which may influence reserve performance through their impact on spatially-driven population processes: fishing effort and benthic dispersal. First, I used the spiny lobster model to address whether changes in the behavior of a fishery, in terms of its ability to focus effort on regions with high abundance, would substantially impact reserve function. To my knowledge, this issue has not been addressed in the marine reserve literature. In addition, I also considered what impact changes in dispersal rates for older juveniles and adults might have for reserve function.
Methods

*Modelling fishing effort, fishing mortality, and marine reserves*

In my previous study of reserve function (Chapter 2; Stockhausen *et al.*, 2000), fishing effort was uniformly distributed over fishable areas during the open season, regardless of the spatial distribution of the lobster population. It seems more likely that fishers concentrate their effort in areas of higher lobster abundance; thus, I modelled the spatial distribution of fishing effort as a function of the spatial distribution of lobster abundance using

\[
E(\theta, t) = \left( \frac{E'}{1 - \frac{L_{MR}}{L}} \right) \left( \frac{\phi_F(\theta) D^e(\theta, t)}{\int \phi_F(y) D^e(y, t) dy} \right)
\]

(1)

where \(E(\theta, t)\) is the spatial distribution of effort as a function of the spatial position along the coast \((\theta)\) and time \((t)\), \(E'\) is the instantaneous rate of effort (adjusted for the closed season), \(L\) is the length of lobster-habitable coastline, \(L_{MR}\) is the total length of coastline designated as marine reserves, \(\phi_F(\theta)\) indicates whether fishing is allowed locally (i.e. \(\phi_F = 1\) outside reserve areas, \(\phi_F = 0\) inside reserve areas), \(D(\theta, t)\) represents the local density of legal-size lobsters, and \(e\) controls the degree to which fishers concentrate effort in areas of higher lobster abundance. The first term in parentheses on the righthand side of eq. 1 represents the displacement of effort due to reserve implementation, while the second term represents the spatial concentration of displaced effort in areas of higher lobster abundance. As a simplification, I assumed that catchability was fixed; thus, the local rate of fishing mortality was proportional to local fishing effort.
**Effects of spatial aggregation in fishing effort**

I used the baseline model parameters (Chapter 3) to create a baseline scenario with no exploitation. Initial abundance patterns for each life-history stage were set to zero. Larvae were "injected" into the pelagic sub-model at constant rates along the model boundary during the first three spawning seasons. After year 3, larval injection was discontinued and the population continued to grow under its own dynamics, reaching a steady state after 25 model years. The complete model state was saved at the beginning of model year 30 to initialize subsequent model runs that incorporated exploitation but no reserves.

To test whether different degrees of spatial aggregation in fishing effort had substantially different consequences for the lobster population, I varied the value of the exponent, $e$, in eq. 1, to create three Fishery Aggregation Scenarios corresponding to different levels of spatial aggregation by the fishery: 1) No Aggregation ($e = 0$), 2) Proportional Aggregation ($e = 1$), and 3) High Aggregation ($e = 20$). The No Aggregation scenario represents a situation where fishing effort is uniformly distributed along the coast, independent of spatial patterns of lobster abundance; this might arise, for example, where fishers are assigned individual and equal-sized territories (Fig. 1). The Proportional Aggregation scenario represents a situation where fishers direct effort in proportion to local lobster abundance; this might arise, for example, where fishers do not have assigned territories and have no constraints on movement (Fig. 1). The High Aggregation scenario represents a situation similar to the previous scenario, but where effort concentrates on almost exclusively in areas with high lobster abundance (Fig. 1). This last scenario is intended to represent the limits of aggregation, but it is probably too extreme to represent actual behavior by fishers.
For each Fishery Aggregation Scenario, I mapped out the population response to different levels of effort, ranging from 0 to 0.5 yr$^{-1}$. The modeled fishing season ran from Julian day 181 to Julian day 365; total effort was scaled to reflect this. Only adults larger than 75 mm CL were vulnerable to the fishery. For each combination of effort (13 levels) and Fishery Aggregation Scenario, I created an Exploitation-Only model case by integrating the model for a 20 year period, initializing the model with the baseline model state at the beginning of year 30. For each case, the model state from the corresponding unexploited case at the beginning of model year 30 was used to initialize the simulation run. The model was subsequently integrated numerically for 20 years. The complete model state was saved at the beginning of model year 50 to initialize subsequent model runs with marine reserve scenarios. Total annual catch, $C$, and total annual larval production, $LP$, were computed as described in Chapter 3. The mean population growth rate in year $i$, $r_i$, was computed using the formula

$$ r_i = \ln(A_{i+1} / A_i) $$  

where $A_i$ was the total adult abundance at the beginning of model year $i$. Finally, effective annual fishing mortality in year $i$, $F^m_i$, was approximated using the formula

$$ F^m_i = \int_{year \ i} dt \left( \frac{\int dy C(y,t)}{\int dy D(y,t)} \right) $$  

where $D(y,t)$ is the density of legal-sized lobsters at coastal coordinate $y$ and time $t$ and $C(y,t)$ is the corresponding spatially-explicit, instantaneous catch rate (in lobsters year$^{-1}$). The averaging in eq. 3 is both spatial (over the coast) and temporal (over one year).

To compare the response of the lobster population to different degrees of fishing effort aggregation, I plotted the values for catch, larval production and population growth.
rate for the final model year (i.e., year 49) for each Fishery Aggregation Scenario as functions of total annual effort, and again as functions of effective annual fishing mortality.

*Reserve response to spatial aggregation in fishing effort*

To test whether different degrees of spatial aggregation in fishing effort had substantially different consequences for marine reserve function, I created three Equal Effort (EE) Fishery Scenarios, each corresponding to one of the fishery aggregation scenarios defined in the previous section, for a single level of fishing effort (0.4 yr⁻¹) at which the lobster population was overexploited. For each EE Fishery Scenario, I used the model to simulate the lobster population response to 16 marine reserve configurations (four locations x four sizes, Fig. 2), plus one configuration with no reserve area. The latter configuration was used as a control for each EE Fishery Scenario to assess reserve performance (i.e., to provide the results for no management action). The four reserve locations were roughly evenly distributed around the Sound (in the SE, NE, NW, and SW quadrants of the Sound; Fig. 2). The four reserve sizes ranged from 5-20% of available coastal habitat (30-120 km); for larger sizes, reserves at different locations would overlap. Fishing effort displaced by the reserve was redistributed within the exploited coastal region in accordance with the particular EE Fishery Scenario.

For each EE Fishery Scenario x Marine Reserve combination, I used the model state at the end of the appropriate exploitation-only model run (at the beginning of year 50) to initialize the model run. I subsequently integrated the model for an additional 20 years. I computed total catch and larval production for the final model year, as well as the average population growth rate during the reserve period. I normalized these values
by taking the ratio (total catch, larval production) or difference (average population growth rate) with respect to the appropriate control case.

To determine whether reserve function was sensitive to different degrees of aggregation in fishing effort, I plotted the normalized total catch and larval production for the final model year, as well as the average population growth rate for each EE Fishery Scenario as functions of reserve size for each reserve location. To quantify this sensitivity, I compared the variation in average population growth rate due to fishery aggregation for the No Aggregation and Proportional Aggregation scenarios against that associated with reserve location for the largest reserve size (20%). I used a main effects ANOVA model for two random factors (EE Fishery Scenario, Reserve Location) to compute the variation in population growth associated with each factor. Because the High Aggregation scenario represented the extreme, and highly unlikely, limit of fishery aggregation, it was excluded from this calculation. Additionally, because it would be inappropriate to interpret the ANOVA results in terms of hypothesis testing (e.g., quoting significance levels), I simply report the estimated variance associated with each factor.

Although total effort was identical for the three Equal Effort Fishery Scenarios in this experiment, effective annual fishing mortality in the no-reserve scenario was not. Thus, I created three additional Fishery Scenarios: the Equal Fishing Mortality (EFM) Fishery Scenarios, one corresponding to each level of fishery aggregation (i.e., None, Proportional, and High). For each EFM Fishery Scenario, I selected a level of effort which yielded $F^m = 0.4 \text{ yr}^{-1}$ in model year 49 (no reserve present). Finally, I repeated the experimental procedure previously described, substituting the EFM Fishery Scenarios for the EE Fishery Scenarios.
Chapter 5

Reserve response to benthic dispersal

Prior theoretical studies of reserve function indicate that transfer rates between reserve and exploited areas can be a critical factor in optimal reserve size (e.g., Polacheck, 1990; DeMartini, 1993). However, these results were obtained using extremely simple models for emigration from reserve areas. To test whether reserve function predicted by the spiny lobster model would be similarly affected, I used three Benthic Dispersal scenarios developed in Chapter 4: 1) Very Low Dispersal, 2) Nominal Dispersal (i.e., the baseline scenario), and 3) Very High Dispersal.

For each Benthic Dispersal scenario, I used the model state at the beginning of year 30 from the corresponding simulation run with no exploitation (Chapter 4) to initialize a model run with exploitation (the Proportional Aggregation Fishery Scenario, with total effort fixed at 0.4 yr⁻¹), but no reserves. The model was subsequently integrated for 20 years. I used the 16 marine reserve and no-reserve control configurations described in the previous section (see Fig. 2) to evaluate reserve function. As in the previous section, the configuration with no reserve was used to provide a control case (i.e., to provide results for no management action) for each Benthic Dispersal scenario. Analysis of the model results paralleled that for the Fishery Scenarios.

Results

Spatial aggregation in fishing effort—no reserves

Spatial effects—The principal spatial effect of aggregated fishing effort on the simulated lobster population was to homogenize local adult densities (Fig. 3). As the degree to which fishing effort concentrated on areas of high abundance (i.e., as the parameter e in eq. 1 increased), spatial variability of adults after the fishing season decreased (Fig. 3),

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even though settlement patterns (and thus patterns of abundance for juvenile benthic stages) were similar (Fig. 4).

**Effective annual fishing mortality vs. effort**—Effective annual fishing mortality was proportional to total effort when effort was uniformly distributed along the coast (Fig. 5; the No Aggregation Fishery Scenario). However, the relationship between effective fishing mortality and total effort was curvilinear when fishers concentrated effort in areas with high lobster density (Fig. 5, the Proportional Aggregation and High Aggregation Fishery Scenarios). For a given level of effort, effective fishing mortality was larger when effort was spatially aggregated than when it was uniformly distributed. When total effort was low (i.e., < 0.05 yr\(^{-1}\)), the marginal increase in fishing mortality with effort was largest when fishers concentrated effort exclusively on areas of high abundance (i.e., in the High Aggregation scenario), whereas the marginal increase was smallest when effort was uniformly distributed. For a given total effort, effective fishing mortality was largest under the High Aggregation Fishery Scenario and intermediate under the Proportional Aggregation scenario. When total effort was greater than > 0.05, the marginal rate of increase in fishing mortality with effort was largest for the Proportional Aggregation Fishery Scenario, with the result that effective fishing mortality was largest under this scenario when total effort was greater than \(\sim 0.125\) yr\(^{-1}\).

**Catch**—As total effort and effective fishing mortality increased, catch increased to a maximum, then declined in all three Fishery Scenarios (Fig. 6). The maximum catch was similar in all three scenarios (roughly 15,000 individuals); however, the level of effort at which catch was maximized, \(E_{C_{\text{max}}}\), differed (Fig 6a). \(E_{C_{\text{max}}}\) was inversely related to the level of aggregation. It was largest when effort was uniformly distributed (\(e = 0\), No Aggregation) and smallest when effort was most aggregated (\(e = 20\), High Aggregation),
although the difference between values for the two scenarios with aggregation was fairly small (Fig. 6a). However, the maximum catch occurred at the same effective fishing mortality for all three scenarios (Fig. 6b).

*Larval production*—Larval production was inversely related to total effort and effective fishing mortality for all three Fishery Scenarios (Fig. 7). Larval production was highest, for a given level of effort, when effort was uniformly distributed (Fig. 7a, b). Trends in larval production with effort were mirror images of those for effective fishing mortality. When effort was small, larval production was lowest when the fishery was highly aggregated (Fig. 7b). In contrast, when effort was large, larval production was lowest when the fishery distributed effort in proportion to local abundance (Fig. 7a). However, trends in larval production with effective fishing mortality were nearly identical, and declined exponentially as fishing mortality increased (Fig. 7c, d).

*Population growth*—As with larval production, population growth rates were also inversely related to total effort and effective fishing mortality (Fig. 8). Growth rates were highest, for a given level of effort, when effort was uniformly distributed (Fig. 8a, b). As with larval production, trends in population growth rates with effort were mirror images of those for effective fishing mortality. When effort was small, population growth rates were lowest when the fishery was highly aggregated (Fig. 8b). In contrast, when effort was large, population growth rates were lowest when the fishery distributed effort in proportion to local abundance (Fig. 8a). Trends in population growth with effective fishing mortality were similar, but not identical, and declined as fishing mortality increased (Fig. 8c, d). When fishing mortality was large (i.e., > 0.3 yr-1), population growth rates were smallest (most negative) under the Proportional Aggregation scenario,
intermediate for the High Aggregation scenario, and largest (least negative) for the No Aggregation scenario (Fig. 8c).

*Reserve response to spatial aggregation of fishing effort*

*Equal Effort Fishery Scenarios*—Relative to the appropriate “no reserve” control cases, reserve function varied with the level of spatial aggregation in the modeled fishery, as well as with reserve size and location, when total effort was fixed among scenarios (Fig.s 9-11). At the largest reserve size, the variation in population growth rate associated with the level of fishery aggregation was approximately one-third that associated with reserve location (Table 2). The pattern of response was remarkably similar among the three variables considered to quantify reserve function: catch, larval production, and average population growth rate (compare, for example, Fig.s 9b, 10b, and 11b).

Overall, reserves performed best when aggregation of fishing effort was proportional to abundance, and worst when effort was uniformly distributed, with intermediate results when aggregation was high. However, this was not true for all reserve configurations: reserve function was lowest when aggregation was high and the reserve was small- to medium-sized (5-15%) in the NW corner of the sound (Fig.s 9c, 10c, 11c). Alternatively, reserve function was (marginally) higher when aggregation was high, rather than proportional, when the reserve was small- to medium-sized (5-15%) but located in the southwest corner of the sound (Fig.s 9d, 10d, 11d).

Reserves had no demonstrable effects over the control cases, even for the largest reserve size, when effort was uniformly distributed and the reserves were located in the southeast and northeast quadrants of the sound (Fig.s 9a-b, 10a-b, 11a-b). In contrast, reserves functioned quite well in these configurations when effort was aggregated.
Differences in reserve function among levels of fishing aggregation increased with reserve size. When reserves were large (20%), catch (relative to the no reserve case) was 2-5 times larger, while larval production was 2-7 times larger, when effort was aggregated proportional to abundance than when it was uniformly distributed. Similarly, relative mean population growth rates were 4-10% higher when effort was aggregated proportional to abundance than when it was uniformly distributed.

*Equal Fishing Mortality Fishery Scenarios*— Relative to the appropriate "no reserve" control cases, reserve function varied substantially with reserve size and location. In contrast to the Equal Effort Fishery Scenarios, the effect of spatial aggregation of fishing effort on reserve function was small (Fig.s 12-14). At the largest reserve size, the variation in population growth rate associated with the level of fishery aggregation was only ~2.5% that associated with reserve location (Table 3). As with the Equal Effort Fishery Scenarios, the pattern of response was remarkably similar among the three variables considered to quantify reserve function: catch, larval production, and average population growth rate (compare, for example, Fig.s 12b, 13b, and 14b).

*Reserve response to benthic dispersal*

Relative to the appropriate "no reserve" control cases, reserve function varied substantially with reserve size and location. However, the effect of benthic dispersal was small (Fig.s 15-17), despite a 100-fold change in the rates over the factor levels. At the largest reserve size, the variation in population growth rate associated with differences in benthic dispersal rates was less than 5% that associated with reserve location (Table 3). As with the fishery aggregation results, the pattern of response was remarkably similar among the three variables considered to quantify reserve function: catch, larval production, and average population growth rate (compare, for example, Fig.s 15b, 16b,
and 17b). For all three response variables, reserve function was largest for the Very Low Dispersal Scenario and smallest for the Very High Dispersal Scenario for all combinations of reserve size and location (Fig.s 15-17).

**Discussion**

Results from this study fall into two categories: 1) the impact of fishery aggregation (i.e., spatially-targeted effort) on exploited populations and 2) the impact of fishery characteristics and benthic-stage dispersal on reserve performance. Simulations using the spiny lobster model (Chapter 3) indicated that the manner in which fishing effort is spatially distributed over an exploited population can have a substantial effect on catch rates and population parameters (e.g., larval production, population growth rate), even when total effort is fixed and when fishing mortality is proportional to effort over small spatial and temporal scales. When the effect of a marine reserve was considered, results from model simulations indicated that, compared with the variation associated with reserve location, relative reserve performance varied substantially with the level of aggregation of effort in the fishery when total effort was fixed. However, relative performance did not vary substantially with fishery aggregation when fishing mortality (prior to reserve establishment) was fixed. Finally, results from another set of model simulations indicated that relative reserve performance was insensitive to the rate of dispersal of benthic (i.e., juvenile and adult) life-history stages.

In the model, instantaneous fishing mortality was proportional to fishing effort at small spatial and temporal scales (i.e., 2.5 km and 5 d). However, the spatial distribution of effort was allowed to vary over larger scales in response to the spatial distribution of the simulated lobster population; local effort was distributed relative to the local
population density raised to some power \((e \text{ in eq. 1)}\), while total (i.e., spatially-integrated) effort was fixed. The effect of aggregation level on catch, larval production, and population growth rate under the same level of total effort could be quite large (e.g., up to an order of magnitude difference for catch and larval production; Figs 6a, 7a and b, 8a and b).

These differences disappeared, however, when results were compared at equal levels of effective annual fishing mortality (i.e., averaged spatially over the coast and temporally over one year, eq. 3; Figs 6b, 7c and d, 8c and d). Thus, population and fishery response to different levels of effort aggregation could be understood simply in terms of changes in effective annual fishing mortality. However, effective annual fishing mortality was not a simple (or even not so simple) function of total effort and aggregation level alone; rather, it was an emergent quality of the fishery-population interaction because it also depended intrinsically on the spatial distribution of the exploited population. This observation has important consequences for spatially-explicit models which attempt to be prognostic, rather than heuristic: accurately capturing the spatial behavior of both the exploited population and the fishery will be a key requirement to obtain reliable results.

Given this observation, the results obtained here for the impact of fishery aggregation on marine reserve performance come as no surprise. The performance of a particular reserve configuration (i.e., size and location) varied substantially with fishery aggregation level when total effort was fixed (table 2) primarily because pre-reserve fishing mortalities differed (see Fig. 5: compare values for fishing mortality where total effort \(= 0.4 \text{ yr}^{-1}\)). However, when differences in pre-reserve fishing mortality were accounted for, reserve performance under different levels of fishery aggregation was
quite similar (table 3). Thus, reserve location and size, as well as the level of pre-reserve fishing mortality, will likely have a large impact on reserve function for an exploited population and its associated fishery, whereas specific details of the fishery itself will not.

In contrast to previous model-based reserve studies (i.e., Polacheck, 1990; DeMartini, 1993), changes in rates of benthic dispersal for post-settlement life-history stages (i.e., sub-adults and adults) also had relatively little impact on reserve function (table 4, Fig.s 15-17). However, this disagreement may be more apparent than real, since different performance measures were used here. For example, DeMartini (1993) found that changing the transfer rate by a factor of 10 for one species (a species of jack, Caranx ignobilis) resulted in a corresponding change in SSB/R of 30% when reserve size was 20% and fishing mortality was 0.4 yr\(^{-1}\) (his Fig. 3c). For a similar range in dispersal rates, larval production here varied by up to a factor of 3 at a reserve size of 20%; however, it varied by a factor of almost 100 at different locations (Fig. 16). Thus, the conclusion drawn here that benthic dispersal rates do not substantially affect reserve performance is made in relation to the much larger effect that location has—a factor which was not included in the other studies.

Finally, for the population model considered here, spatial variation in the abundance of benthic juveniles and adults was driven primarily by the pattern of pelagic larval dispersal via hydrodynamic currents. The interaction between the pattern of hydrodynamic dispersal and that imposed by reserve configuration was the key factor affecting reserve function. Details concerning the other spatial aspects of the fishery (i.e., effort aggregation), as well as rates of benthic dispersal by post-settlement animals, were much less important in determining optimal reserve configuration. Thus, I conclude that, while it is critical to consider processes which determine the spatial structure of exploited
populations in attempting to design optimal no-take marine reserves, incorporating other aspects of the population and fishery into the design will be less important on resulting performance.
Literature Cited


Tables

Table 1. Nominal level of effort, resulting in $F_m = 0.40$ in year 49 with no reserve, for the three Equal Fishing Mortality Fishery Scenarios.

<table>
<thead>
<tr>
<th>Fishery Aggregation Level</th>
<th>Nominal Effort (yr(^{-1}))</th>
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<tbody>
<tr>
<td>No Aggregation</td>
<td>0.4</td>
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<tr>
<td>Proportional Aggregation</td>
<td>0.225</td>
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<tr>
<td>High Aggregation</td>
<td>0.259</td>
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</table>

Table 2. Estimated variance in (relative) average population growth rate associated with Reserve Location and Equal Effort Fishery Scenario, for the largest reserve size considered (20%). Reserve Location and EE Fishery Scenario were treated as random factors in a main effects analysis of variance to obtain expected mean square estimates. Standard formulas (Underwood, 1981) were used to compute the variance ($\sigma^2$) associated with each factor. The High Aggregation Fishery Scenario was excluded from the analysis (see text).

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Adjusted SS</th>
<th>MS</th>
<th>$\sigma^2$</th>
</tr>
</thead>
<tbody>
<tr>
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<td>0.00108</td>
<td>0.000359</td>
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</table>

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Table 3. Estimated variance in (relative) average population growth rate associated with Reserve Location and Equal Fishing Mortality (EFM) Fishery Scenario, for the largest reserve size considered (20%). Reserve Location and EFM Fishery Scenario were treated as random factors in a main effects analysis of variance to obtain expected mean square estimates. Standard formulas (Underwood, 1981) were used to compute the variance ($\sigma^2$) associated with each factor. The High Aggregation Fishery Scenario was excluded from the analysis (see text).

<table>
<thead>
<tr>
<th>Source</th>
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<th>Adjusted SS</th>
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<th>$\sigma^2$</th>
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Table 4. Estimated variance in (relative) average population growth rate associated with Reserve Location and Benthic Dispersal Scenario, for the largest reserve size considered (20%). Reserve Location and Benthic Dispersal Scenario were treated as random factors in a main effects analysis of variance to obtain expected mean square estimates. Standard formulas (Underwood, 1981) were used to compute the variance ($\sigma^2$) associated with each factor.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Adjusted SS</th>
<th>MS</th>
<th>$\sigma^2$</th>
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<td>0.00115</td>
<td>0.00019</td>
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Figure Captions

Figure 1. Example of spatial allocation of fishing effort under the three Fishery Scenarios: No Aggregation (e = 0; dashed line), Proportional Aggregation (e = 1; dotted line), and High Aggregation (e = 20; solid line). The dotted line also corresponds to the spatial pattern of lobster abundance used to create this example.

Figure 2. Spatial configuration for the marine reserve scenarios (the 15% reserve size is not illustrated). Smaller reserves are shown offset from the coast for clarity.

Figure 3. Final spatial patterns of adult lobster abundance (line), and annual catch (shaded area) under Exploitation (No Reserves) for the different Fishery Scenarios: a) No Aggregation, b) Proportional Aggregation, and c) High Aggregation. Fishing effort was 0.4 yr⁻¹ in each case. The cross-hatched area indicates the deepwater boundary across the mouth of Exuma Sound. The coefficient of spatial variation for adult abundance in these cases was: a) 1.96, b) 0.78, and c) 0.41.

Figure 4. Final spatial patterns of settlement under Exploitation (No Reserves) for the different Fishery Scenarios: a) No Aggregation, b) Proportional Aggregation, and c) High Aggregation. Fishing effort was 0.4 yr⁻¹ in each case. The cross-hatched area indicates the deepwater boundary across the mouth of Exuma Sound where settlement does not occur. The patterns were highly correlated; correlation coefficients were: a-b) 0.95, b-c) 0.99, and c-a) 0.90.

Figure 5. Effective fishing mortality in model year 49, as a function of total fishing effort, for the three Fishery Aggregation Scenarios.

Figure 6. Model results for total catch during the final year of the Exploitation-Only cases, plotted as functions of total effort (a) and effective fishing mortality (b) for the three Fishery Aggregation Scenarios: No Aggregation (e = 0, circles), Proportional Aggregation (e = 1, squares), and High Aggregation (e = 20, triangles). The righthand graphs provide a “blow-up” for the area denoted by dotted rectangle in the corresponding lefthand graph.

Figure 7. Model results for larval production during the final year of the Exploitation-Only cases, plotted as functions of total effort (a, b) and effective fishing mortality (c, d) for the three Fishery Scenarios: No Aggregation (e = 0, circles), Proportional Aggregation (e = 1, squares), and High Aggregation (e = 20, triangles). The righthand graphs (b, d) provide a “blow-up” for the area denoted by dotted rectangle in the corresponding graph to the left.

Figure 8. Model results for population growth rate during the final year of the Exploitation-Only cases, plotted as functions of total effort (a, b) and effective fishing mortality (c, d) for the three Fishery Scenarios: No Aggregation (e = 0, circles), Proportional Aggregation (e = 1, squares), and High Aggregation (e = 20, triangles). The righthand graphs (b, d) provide a “blow-up” for the area denoted by dotted rectangle in the corresponding graph to the left.
Figure 9. Model results for the effect of reserves on total catch during the final year of the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Equal Effort Fishing Scenarios [No Aggregation \((e = 0, \text{circles})\), Proportional Aggregation \((e = 1, \text{squares})\), and High Aggregation \((e = 20, \text{triangles})\)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

Figure 10. Model results for the effect of reserves on total larval production during the final year of the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Equal Effort Fishing Scenarios [No Aggregation \((e = 0, \text{circles})\), Proportional Aggregation \((e = 1, \text{squares})\), and High Aggregation \((e = 20, \text{triangles})\)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

Figure 11. Model results for the effect of reserves on mean population growth during reserve implementation for the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Equal Effort Fishing Scenarios [No Aggregation \((e = 0, \text{circles})\), Proportional Aggregation \((e = 1, \text{squares})\), and High Aggregation \((e = 20, \text{triangles})\)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

Figure 12. Model results for the effect of reserves on total catch during the final year of the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Equal Fishing Mortality Fishing Scenarios [No Aggregation \((e = 0, \text{circles})\), Proportional Aggregation \((e = 1, \text{squares})\), and High Aggregation \((e = 20, \text{triangles})\)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

Figure 13. Model results for the effect of reserves on total larval production during the final year of the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Equal Fishing Mortality Fishing Scenarios [No Aggregation \((e = 0, \text{circles})\), Proportional Aggregation \((e = 1, \text{squares})\), and High Aggregation \((e = 20, \text{triangles})\)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

Figure 14. Model results for the effect of reserves on mean population growth during reserve implementation for the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Equal Fishing Mortality Fishing Scenarios [No Aggregation \((e = 0, \text{circles})\), Proportional Aggregation \((e = 1, \text{squares})\), and High Aggregation \((e = 20, \text{triangles})\)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

Figure 15. Model results for the effect of reserves on total catch during the final year of the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Dispersal Scenarios [Very Low Dispersal \((\text{circles})\), Baseline Dispersal \((\text{squares})\), and Very High Dispersal \((\text{triangles})\)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

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Figure 16. Model results for the effect of reserves on larval production during the final year of the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Dispersal Scenarios [Very Low Dispersal (circles), Baseline Dispersal (squares), and Very High Dispersal (triangles)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.

Figure 17. Model results for the effect of reserves on mean population growth during reserve implementation for the Exploitation with Reserves cases, relative to the case where no reserve was implemented, for the three Dispersal Scenarios [Very Low Dispersal (circles), Baseline Dispersal (squares), and Very High Dispersal (triangles)], plotted as functions of reserve size for the four reserve locations considered: a) Cat Island, b) Eleuthera, c) ECLSP, and d) LSI.
Figure 1. Example of spatial allocation of fishing effort under the three Fishery Scenarios: No Aggregation (e = 0; dashed line), Proportional Aggregation (e = 1; dotted line), and High Aggregation (e = 20; solid line). The dotted line also corresponds to the spatial pattern of lobster abundance used to create this example.
Figure 2. Spatial configuration for the marine reserve scenarios (the 15% reserve size is not illustrated). Smaller reserves are shown offset from the coast for clarity.
Figure 3. Final spatial patterns of adult lobster abundance (line), and annual catch (shaded area) under Exploitation (No Reserves) for the different Fishery Scenarios: a) No Aggregation, b) Proportional Aggregation, and c) High Aggregation. Fishing effort was 0.4 yr\(^{-1}\) in each case. The cross-hatched area indicates the deepwater boundary across the mouth of Exuma Sound. The coefficient of spatial variation for adult abundance in these cases was: a) 1.96, b) 0.78, and c) 0.41.
Figure 4. Final spatial patterns of settlement under Exploitation (No Reserves) for the different Fishery Scenarios: a) No Aggregation, b) Proportional Aggregation, and c) High Aggregation. Fishing effort was 0.4 yr⁻¹ in each case. The cross-hatched area indicates the deepwater boundary across the mouth of Exuma Sound where settlement does not occur. The patterns were highly correlated; correlation coefficients were: a-b) 0.95, b-c) 0.99, and c-a) 0.90.
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Chapter 6: Single large or several small marine reserves for the Caribbean spiny lobster?

In press as:

Single large or several small marine reserves for the Caribbean spiny lobster?

William T. Stockhausen and Romuald N. Lipcius

Virginia Institute of Marine Science, The College of William and Mary, Gloucester Point, Virginia 23062-1346, USA. email: buck@vims.edu, rom@vims.edu

Abstract. The 'SLOSS' debate—Single Large Or Several Small protected areas—remains unresolved. We used a heuristic model based on population dynamics of Caribbean spiny lobster in Exuma Sound, Bahamas, to compare impacts of regional reserve designs that configured 20% of available coastal habitat as either a randomly located single large reserve or a network of six small, randomly located reserves on three performance indicators (fishery yield, larval production, population growth rate) for a hypothetical overexploited lobster population. Two additional management strategies were considered: one reduced effort by 20% (without protected areas), and one did nothing. Effects were evaluated for two levels of hydrodynamic variability. In general, performance indicators ranked the management strategies, independent of hydrodynamic variability, from best to worst in the order (1) single large reserve (2) several small reserves (3) reduced effort (4) no management action, but differences were not always significant. Therefore, for the model regional system investigated here, a single large reserve is preferable to several small ones. We propose that this conservation strategy is most suitable at the regional scale (~100s of kilometres) and that such single, large regional reserves would function most effectively within a broad-scale (~1000s of kilometres) reserve network, barring local catastrophes.

Extra keywords: no-take zones, fisheries management, spatially explicit population models, hydrodynamic transport, larval dispersal, SLOSS, Panulirus argus

Introduction

Marine reserves (i.e., no-take areas) represent an increasingly attractive alternative to conventional strategies of fisheries management for simultaneously enhancing catch rates and population viability of fully or over-exploited populations (Dugan and Davis 1993; Allison et al. 1998; Guenet et al. 1998). Recently, concerned scientists have called for the creation of reserve areas covering 20% of the area of the oceans by the year 2020 for protection and management of world fishery resources (McManus 1998). On a slightly smaller scale, Roberts (1997) has championed the creation of a network of small reserve areas within the Caribbean to rebuild and protect over-exploited reef-fish and invertebrate populations.

Theoretically, population biomass will increase within protected areas because total mortality is reduced when fishing mortality is eliminated (Roberts and Polunin 1991; Dugan and Davis 1993; Polunin and Roberts 1993). Greater spawning biomass increases larval production within the reserve, which may subsequently increase regional recruitment as larvae are dispersed from the reserve (Carr and Reed 1993; Polunin and Roberts 1993; Bohnsack 1996). Higher regional recruitment may increase regional fishery yields (Carr and Reed 1993; Dugan and Davis 1993; Bohnsack 1996). In addition, as biomass builds up within reserve areas, motile juveniles and adults may emigrate into adjacent exploited areas, thereby enhancing the fishery adjacent to the reserve (Davis and Dodrill 1980; Alcala and Russ 1990; Russ and Alcala 1996).

A practical issue in reserve design concerns the spatial configuration of the reserve area; i.e., whether a given reserve area should be configured as a single contiguous large reserve or as a network of smaller reserves (Allison et al. 1998; Lauck et al. 1998). For example, would a network of small reserves within the Caribbean rebuild and protect over-exploited reef-fish and invertebrate populations, as Roberts (1997) suggested? In terrestrial ecosystems, a similar issue regarding the optimal spatial configuration of terrestrial parks for conserving biodiversity has been termed SLOSS (Single Large or Several Small) and has generated a vigorous debate (see, e.g., Diamond 1975; Simberloff and Abele 1982; Soulé and Simberloff 1986) and continuing interest (see, e.g., Shafer 1995; Etienne and Heesterbeek 2000; Pelletier 2000). Although SLOSS remains controversial, the original recommendation (Diamond 1975), based on considerations from the theory of island biogeography and which spawned the debate itself, remains one of the guiding principles in terrestrial reserve design:

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large reserves should generally be preferred over networks of small reserves (Meffe and Carroll 1997; Schwartz 1999).

Principles drawn from the SLOSS debate for terrestrial reserves may, however, not hold for marine reserve design (Allison et al. 1998). Marine and terrestrial systems differ fundamentally in the scale and variability of processes affecting population dynamics (Steele 1985). Furthermore, the extractive nature of fisheries adds an additional dimension to reserve design for fisheries management. For example, terrestrial reserves are principally concerned with protecting biodiversity, whereas reserves for fisheries management are concerned with ensuring population sustainability while maximizing extracted economic value from the same population. Hence, the SLOSS issue needs to be considered anew, and perhaps separately, for fisheries management and marine conservation.

The simplest SLOSS tradeoffs for marine reserves arise from two considerations of spatial scale. First, because perimeter-to-area ratios decrease with increasing size, the transfer of individuals from reserve areas to adjacent exploited areas by random (as opposed to directed) movement is lower for a contiguous large reserve than for a network of small reserves (Polacheck 1990; DeMartini 1993). Lower transfer rates maintain higher population densities within reserve areas, increasing spawning biomass and potentially preventing local Allee effects (e.g., lowered fertilization success; Levitan and Sewell 1998), but may also reduce catch rates in exploited areas adjacent to reserves. Note, however, that increasing reserve size may not lower transfer rates if movement is directed, such as in seasonal or spawning migrations.

The second consideration of spatial scale depends on the scale of population replenishment (Carr and Reed 1993; Allison et al. 1998). For marine species with long-lived, pelagic larvae such as the Caribbean spiny lobster, Panulirus argus, dispersal by regional hydrodynamic currents may decouple local adult populations and subsequent recruitment (Lipcius et al. 1997), such that the scale of population replenishment is regional, not local. For such species, networks of widely spaced small reserves may be self-replenishing, whereas a contiguous reserve of similar total size may not. Wider spatial extent may also reduce risks associated with local catastrophes (e.g., pollution, disease, hurricanes; Allison et al. 1998).

Conducting field investigations that address the optimal design of marine reserves using sound experimental designs (e.g., replication, random allocation of treatments) is logistically difficult because of the social, political, cultural, and economic issues associated with creating reserve areas. As an alternative, numerical models have been used to examine factors such as reserve size, fishing mortality, and life-history characteristics that influence reserve characteristics (see references cited by Guénette et al. 1998; Stockhausen et al. 2000).

Here, we use a previously developed, integrated hydrodynamic and population model for Caribbean spiny lobster in Exuma Sound, Bahamas (Stockhausen et al. 2000), to compare the performance (i.e., catch rates, larval production, and population growth rates) of marine reserves of equal total size configured as either a single large reserve or a network of several small ones. We focus on reserve function for regional-scale population dynamics (i.e., over spatial scales of 100s of kilometres), in contrast to broad-scale dynamics (i.e., over spatial scales of 1000s of kilometres). Specifically, we determined (1) which configuration was optimal for a given level of hydrodynamic variability and (2) whether the optimal configuration depended on the level of hydrodynamic variability. In addition, we addressed the efficacy of reserve implementation in the more general context of fisheries management by including two alternative management strategies (i.e., reduced effort and no action) as factor levels in our experimental design.

Methods

In the present study, we emphasized patterns of larval dispersal, subsequent juvenile recruitment, and reserve configuration. As part of recent (Lipcius et al. 1997) and continuing work with the Caribbean spiny lobster, Panulirus argus, in Exuma Sound, Bahamas, we have developed a population-dynamics model for this system (Stockhausen et al. 2000) that encompasses demographic processes during all life-history stages and "closes the larval loop", thereby coupling postsettlement benthic population dynamics, adult spawning, and planktonic larval dispersal (Gaines and Lafferty 1995; Eckman 1996). The model is heuristic; we use it to explore the impact of reserve features on a hypothetical population described by the model, although many of the model's attributes use empirical data for the Caribbean spiny-lobster population and hydrodynamics in Exuma Sound. Our model extends the two-dimensional spatially structured, coupled pelagic/benthic population model of Possingham and Roughgarden (1990) to include multiple pelagic and benthic life-history stages, curvilinear coastal geometry, complex current patterns, and postsettlement dispersal. For the present study, we modified the original model (Stockhausen et al. 2000) to incorporate temporal variability in hydrodynamic current patterns, as well as spatial variation in fishing effort. We used the model to simulate population trajectories, with concurrent fishery yields, for an over-exploited spiny-lobster population in Exuma Sound. For two levels of hydrodynamic variability, we compared performance of four different management strategies: (1) a reserve area configured as a single large reserve (2) a reserve area configured as several small reserves (3) a reduction in effort with no reserve area, and (4) no management action (i.e., no reserve, no effort reduction).

Model description

Details of the spiny-lobster population-dynamics model are given by Stockhausen et al. (2000). Here, we briefly summarize the model's features. The full model is composed of three coupled submodels: the pelagic model, the benthic model, and the reproduction model. The spatial domain for the full model consists of a two-dimensional (horizontal), oceanic region and its one-dimensional boundary, which encompasses both shallow coastal regions where settlement occurs and deep-water regions (Fig. 1).
Chapter 6

coastal boundary. Pelagic-stage densities are modelled as continuous dimensional advective currents and turbulent diffusion (e) currents and dispersed through turbulent diffusion. In Exuma Sound, dynamics of the pelagic stages. Seasonal spawning and subsequent associated boundary conditions describe the temporal and spatial functions of space (x, y) metamorphosis from larva to postlarva, and (f) settlement along the coast for algal-phase (x), postalgal phase and postlarvae. within the oceanic region due to (a) hatching of larvae after adult reproduction along the coast (b) ageing (c) mortality (d) horizontal dispersal via two-dimensional advective currents and turbulent diffusion (e) metamorphosis from larva to postlarva, and (f) settlement along the coastal boundary. Pelagic-stage densities are modelled as continuous functions of space (x, y), time (t), and age within stage (a); coupled reaction-advection-diffusion partial differential equations with associated boundary conditions describe the temporal and spatial dynamics of the pelagic stages. Seasonal spawning and subsequent larval production along the coastal boundary determine the local influx of age-0 pelagic larvae into the oceanic region; larvae are subsequently transported from their hatching grounds by spatially variable advective currents and dispersed through turbulent diffusion. In Exuma Sound, the larval phase probably lasts from 4 to 6 months (on the basis of the interval between peak spring reproduction and fall settlement; Herrnkind and Lipcius 1989; Eggleston et al. 1998). To reduce computational resources for the model, we used the shortest duration, so after four months, surviving larvae become postlarvae, which actively migrate toward the coast. At the coastal boundary, the local flux of postlarvae across the boundary determines local settlement rates and provides the population ‘source’ term for the benthic model.

The benthic model tracks changes in the size-specific, spatially structured density along the coast for algal-phase (x), postalgal phase (y), subadult (z), and adult (male, z, female, z) life-history stages due to (a) settlement (b) mortality (c) growth within a life-history stage (d) transition between successive life-history stages, and (e) alongshore dispersal. The stage-specific benthic densities are continuous functions of size (z) (rather than age), space (x, y, the position along the coastal boundary), and time (t). As with the pelagic stages, a set of coupled partial differential equations with associated boundary conditions describes the population dynamics within the benthic life-history stages.

Finally, the reproduction model tracks temporal and spatial variation in spawning and subsequent larval production along the coast, incorporating spawning seasons, size-specific fecundity, and size-specific adult female density. Coming full circle and ‘closing the larval loop’ (Ekman 1996), the local rate of larval production in coastal regions along the spatial boundary determines the flux of age-0 pelagic larvae into the oceanic region in the pelagic model.

Modifications to the model

For the present study, we modified our original model (Stockhausen et al. 2000) to incorporate temporal (in addition to spatial) variation in hydrodynamic current patterns. We also allowed the spatial distribution of fishing effort to change in response to the spatial pattern of spiny-lobster abundance. These two modifications are described below. In addition, we used the size-specific fecundity relationship from Lipcius et al. (1997), rather than the one described by Stockhausen et al. (2000), because the former provided a better description of field data.

Site modelling

Exuma Sound is a deep (>1000 m), semi-enclosed basin in the central Bahamas, surrounded by the Exuma Cays and the Great Bahama Bank to the north and west, by Eleuthera and Cat Island to the east, and by Long Island to the south (Fig. 2). Approximately 200 km north-west to south-east, and 75 km at its widest, the sound has two connections to the Atlantic Ocean: a deep (2000-m depth) gap 50 km wide between Long and Cat islands and a shallow sill (15–30-m depth) 27 km wide between Eleuthera and Cat Island. Except for these openings, Exuma Sound is bordered by either low islands or shallow carbonate banks. Exuma Sound provides habitats for spiny lobster on all sides, so the system is particularly well suited for analyses of the relationships between oceanography, recruitment, and population dynamics (Lipcius et al. 1997).

The two-dimensional (horizontal) spatial grid for the pelagic submodel consists of 1872 cells; each cell is 2.5 km x 2.5 km (Fig. 2). The one-dimensional spatial grid for the benthic model consists of 254 linear segments (632.5 km total length) forming the coast and deep-water boundary to the pelagic model grid. In the benthic model grid, the 21 segments (52.5 km) crossing the mouth of the sound are classified as a deep-water boundary, which benthic-phase lobsters cannot inhabit. The remaining 580 km of coastline is classified as shallow coastal habitat, available to settling postlarvae and benthic-phase lobsters.

Hydrodynamic current modelling

Circulation in Exuma Sound appears to be dominated by large-scale, vigorous gyres extending to depths as great as 200 m (Fig. 3a; Hickey in press). Water exchange with the Atlantic Ocean occurs regularly, and exchange with the shallow banks also occurs through dense, high-salinity intrusions. Wind forcing plays an important role in circulation by influencing the current structure in the upper 15 m of the water column. Mesoscale features with associated fronts are superimposed on a general north-westward drift and cause convergence and preferred pathways through the sound (Colin 1995; Hickey in press). Although the gyres appear to be semipermanent features in the sound, they may oscillate seasonally; substantial variability in near-surface currents exists at 10- to 30-day time scales (Hickey in press).

Because spatial patterns of larval dispersal and settlement may vary with hydrodynamic current patterns (see, e.g., Flierl and Wroblewski 1985; Roughgarden et al. 1988; McConnaughey et al. 1992; Tremblay et al. 1994; Shanks 1995; Eckman 1996; Garvine et al. 1997), the relative performance of different reserve-implementation strategies may depend on the level of spatiotemporal variability associated with these currents. To incorporate this variability in larval advection, we used a stochastic feature-based approach to generate temporally and spatially variable current patterns based on a characteristic ‘twin gyre’ hydrodynamic feature in Exuma Sound (Fig. 3a; Hickey in press). The two-dimensional hydrodynamic current field consisted of a number of ‘twin gyre features’ (TGFs; Fig. 3b). Each TGF was defined by its
Fig. 2. Exuma Sound, Bahamas with overlay showing model spatial computational grid. Numbers indicate geographic locations corresponding to values (in kilometres) of the coastal coordinate (θ in Fig. 1), a coordinate used to describe the spatial distribution, along the coastal margins of the sound, of the benthic life-history stages.

Fig. 3. (a) Spatial pattern of near-surface geostrophic currents, computed from CTD observations, observed during November, 1993 (Hickey in press). The small rectangle highlights the 'twin gyre' feature (TGF). (b) Snapshot of stochastic current pattern, based on TGFs, used to model advective transport of pelagic life history stages. Two TGFs are evident in the current field.

Parameter values for individual TGFs were randomly drawn from a set of probability distributions that determined the level of hydrodynamic variability. Individual TGFs were added to the south-east corner of the hydrodynamic current field outside the mouth of Exuma Sound at intervals consistent with the mean speed of TGF propagation and the distribution of distances between successive TGFs (see Fig. 3b). After propagating across the sound, individual TGFs were removed from the hydrodynamic current field, as they no longer affected transport within the sound.
Chapter 6

Large or small marine reserves?

Fishing effort and mortality

In Stockhausen et al. (2000), fishing effort was uniformly distributed over fishable areas during the open season, regardless of the spatial distribution of the lobster population. It is more likely that fisheries concentrate their effort in areas of higher lobster abundance, so for the present study we modelled the spatial distribution of fishing effort as a function of the spatial distribution of lobster abundance using

$$E(t, r) = \frac{E^*}{1 - \frac{t}{2}} \left[ \ln \left( \frac{\theta^*}{\theta(t)} \right) D^*(t, r) \right]$$

where $E(t, r)$ is the spatial distribution of effort along the coast at time $t$, $E^*$ is the instantaneous rate of effort (adjusted for the closed season), $L$ is the length of lobster-habitable coastline, $\theta^*$ is the total length of coastline designated as marine reserves, $\theta(t)$ indicates whether fishing is allowed (i.e., $N_p = 1$ outside reserve areas; $N_p = 0$ inside reserve areas), $D^*(t, r)$ represents the local density of lobster stock, and $e$ controls the degree to which fishers concentrate effort in areas of higher lobster abundance. The first term in parentheses on the right-hand side of Eq. 1 represents the displacement of effort due to reserve implementation, whereas the second term represents the spatial concentration of displaced effort in areas of higher lobster abundance. For this study, we used $e = 1$, so that displaced effort varied linearly with local lobster abundance (i.e., fishing effort outside reserve areas was distributed according to an ideal free distribution). In order to simplify the model, we assumed that catchability was fixed; thus, the local rate of fishing mortality was proportional to local fishing effort.

Experimental design for model studies

We simulated population trajectories, with concomitant fishery yields, to compare reserve performance in a crossed experimental design with management strategy (four levels) and hydrodynamic scenario (two levels) as fixed factors. We used the same model parameters describing spiny-lobster population processes for all model runs.

We examined four management strategies: (1) single large reserve (2) several small reserves (3) reduced effort, and (4) no management action. We created single large (SL) reserve cases by designating a randomly-located no-take zone covering 120 km (20%) of the coastal boundary. We created several small (SS) reserves by designating six randomly located no-take zones; each zone covered 20 km (3.2%) each, for a total of 20% of the coastal boundary and was separated by at least 5 km of fishable habitat from other no-take zones. Fishing effort was displaced from protected areas, not eliminated. Because reserves protected 20% of available coastal habitat, we felt that a management strategy that reduced total effort by 20%, but did not protect any habitat, would provide a fair alternative to the marine reserve scenarios. We termed this the reduced effort strategy. Finally, the no management action (NMA) strategy represented no reduction in effort and no reserves.

Hydrodynamic variability was incorporated by two hydrodynamic scenarios, fast and slow, which differed in the speed of propagation of TGFs through the sound. Outside Exuma Sound, mesoscale eddies have been observed propagating at speeds up to 5-6 km d$^{-1}$ (e.g., Florida: Lee et al. 1994; Georges Bank: Flierl and Wroblewski 1985), but the gyres in the sound may be semipermanent features (Hickey in press). Consequently, in the fast case, TGFs propagated relatively quickly (1 km d$^{-1}$) across the sound; in the slow case, TGFs propagated more slowly (0.1 km d$^{-1}$). Otherwise, the parameters used to create TGFs were identical for the two scenarios.

For each hydrodynamic scenario, we created a baseline, 'unfished' population by running the model for 30 years with no fishing. This procedure eliminated transients in the population structure caused by initial conditions and allowed the simulated populations to reach equilibrium with the hydrodynamic conditions.

Next, we continued each baseline population simulation (under the appropriate hydrodynamic conditions) for 20 additional years with a fishery in which total fishing effort was fixed ($E = 0.4$ km$^2$ d$^{-1}$); fishing occurred during an 'open season' in the second half of the year (Julian days 181 to 365). This procedure gave us two 'over-fished' populations, one for each hydrodynamic sea-state, which we subsequently used as initial conditions to compare reserve performance. When exploited, the population declined under both hydrodynamic scenarios. The mean rate of population growth for years 40-50 was $-0.166$ y$^{-1}$, and the two hydrodynamic scenarios did not differ significantly in this feature (ANOVA: $df = 1,0; p = 0.43$).

Finally, for each hydrodynamic scenario, we used the over-fished population to create eight regional management scenarios for each management strategy. For each replicate run, hydrodynamic current patterns evolved independent of other model runs. In addition, for management scenarios involving reserves, reserve location(s) were randomly selected before the simulation was begun. We recorded spatial patterns of lobster abundance, larval production, settlement, and catch at quarterly intervals during each model run.

Response variables and statistical analysis

We compared performance of the different management strategies by quantifying annual catch, larval production, and population growth rate for the final year of the model simulations. Larval production represents the local rate at which larvae are released by female lobsters along the coast (for details, see Stockhausen et al. 2000); it provides a single measure that combines adult abundance and spawner biomass. We integrated the spatially explicit, instantaneous rates of catch and larval production over time and space (both reserve and no-reserve areas) to obtain total annual catch and larval production. To estimate average population growth rates over the 20-year period in which the management scheme was applied, we compared the total abundance of adult lobsters on day 364 in the final model year (year 49) with that on the same day in model year 49, just prior to the application of the management scheme. We computed average population growth rate as

$$\frac{P_{b0} - P_{b1}}{t}$$

where $P_b$ is the length of lobster-habitable coastline,

$$\frac{P_{b0}}{P_{b1}} > 0.43$$.  

We used a two-factor (hydrodynamic scenario, management strategy) ANOVA to test for significant differences among treatment levels for each performance indicator (catch, larval production, and population growth rate). Both factors were regarded as fixed, and the design was both orthogonal and balanced. We conducted analysis of variance prior to analysis. The data exhibited significant heterogeneity of variance among factor combinations ($P < 0.001$, Levene's test; $P < 0.001$, Cochran's test) for all three variables; other transformations (e.g., square root) did not reduce the heteroscedasticity of the data, but heteroscedasticity does not invalidate the interpretation of non-significant outcomes in ANOVA (Underwood 1981). Moreover, the analysis of variance is particularly robust with respect to heterogeneous variances when sample sizes are equal (Box 1953; Scheffe 1959), as was the case here. We further minimized potential problems with inflated Type I errors by adopting a conservative approach to interpreting the significance of reported $P$-values for ANOVA effects: we chose to interpret an effect as significant only when the $P$-value for the test was less than 0.001; otherwise, the effect was regarded as non-significant.

When effects were found to be significant, we performed multiple comparisons using the Student Neumann Kuels test (SNK; Zar 1996) to determine which factor levels differed significantly. As with factor effects, we interpreted differences as significant only when the standard $P$-value for the test was less than 0.001 to reduce the likelihood of Type I error due to heteroscedasticity.
Chapter 6

William T. Stockhausen and Romuald N. Lipcius

Fig. 4. Spatial distributions of total larval production (dark grey bars), which reflects local adult abundance and size structure, and catch (solid line) over the final year of simulation for model runs incorporating the (a) single large reserve and (b) several small reserves management scenarios under the fast hydrodynamic scenario. Reserve locations are indicated by coastal regions that are shaded light grey background; lobsters are vulnerable to the fishery in unshaded coastal areas. The coastal coordinate defines the spatial location of points along the edge of the sound as the distance, following the outside edge of the model grid in a counter-clockwise fashion, from the southernmost point in the sound to the location of the point in question (see Fig. 2).

Results

Spatial distributions

Marine reserves substantially affected the spatial distribution and magnitude of catch and larval production (Fig. 4). Larval production was up to five times higher within reserves than in exploited areas, reflecting higher adult abundances within the reserves. The spatial patterns of catch peaked just outside each reserve, as a consequence of high exploitation of lobsters emigrating from the reserve.

Catch

Catch rates varied significantly with management strategy (df = 3.56; $F = 13.61; P < 0.001$) and hydrodynamic scenario (df = 1.56; $F = 104.68; P < 0.001$), but the interaction between these factors was not significant (df = 3.56; $F = 0.47; P = 0.705$; Fig. 5a). Catch rates with single large and several small reserves were significantly higher than with no management action (SNK Test: SL > NMA, $P < 0.001$; SS > NMA, $P = 0.001$; Fig. 5a) but did not differ significantly from one another (SNK Test, $P = 0.576$; Fig. 5a). Catch under the reduced effort scenario was not significantly different from that under the other three management schemes (SNK Test, $P > 0.01$ for all comparisons; Fig. 5a).
Larval production

As with catch, rates of larval production varied significantly with management strategy (df = 3.56; F = 61.37; P < 0.001) and hydrodynamic scenario (df = 1.56; F = 62.97; P < 0.001), and the interaction effect was not significant (df = 3.56; F = 0.28; P = 0.837; Fig. 5b). Larval production was significantly greater under a single large reserve than under any other management strategy (SNK Tests: P < 0.001 for each comparison; Fig. 5b). Larval production was also significantly smaller under no management action than under the three other management strategies (SNK Tests: P < 0.001 for each comparison; Fig. 5b). Larval production under the several small reserve and reduced effort schemes did not differ significantly (SNK Test, P > 0.001; Fig. 5b).

Population growth

Like the other two performance indicators, population growth rates over the 20-year management period varied significantly with management strategy (df = 3.56; F = 58.50; P < 0.001) and hydrodynamic scenario (df = 1.56; F = 23.15; P < 0.001); the interaction effect was not significant (df = 3.56; F = 0.32; P = 0.814; Fig. 5c). Similar to larval production, population growth rate was significantly higher under a single large reserve than under all other management strategies (SNK Tests; P < 0.001 for each comparison; Fig. 5c). Population growth rate was also significantly lower under no management action than under any other management strategy (SNK Tests; P < 0.001 for each comparison; Fig. 5c). Growth rates under the several small-reserve and reduced-effort schemes did not differ significantly (SNK Test, P > 0.001; Fig. 5c).

Discussion

Our simulations based on the Caribbean spiny lobster in Exuma Sound, Bahamas, indicate that regional marine reserves perform better, on average, when configured as single, large no-take areas than as multiple, smaller no-take areas of equal total size. A single large reserve for an over-exploited population yielded significantly higher increases in larval production and population growth rate than a set of small reserves; the two reserve designs did not differ significantly in catch rates (Fig. 5). In addition, the results were insensitive to changes in hydrodynamic current patterns. Furthermore, marine reserves were either more effective than, or equivalent to, alternative management strategies (reduced effort and no management action) in maximizing catch, larval production, and population growth rate (Fig. 5). Although performance differences between management strategies were not always significant, the strategies ranked similarly for all three performance indicators (mean catch, larval production, and population growth rates) under the two hydrodynamic scenarios. From best to worst, management strategies ranked in the order (1) single large reserve (2) several small reserves (3) reduced effort, and (4) no management action (Fig. 5). Therefore, the simple answer to the SLOSS question for the model regional system considered here is that a single large reserve is to be preferred over a network of several small reserves.

Our modelling results also indicate that marine reserves can be an alternative to management strategies that reduce fishing effort, at least when the population is severely overfished and substantial areas can be protected. In this study, reserves protected 20% of available coastal area but displaced, rather than eliminated, fishing effort. We felt that a management strategy that reduced total effort by 20%, but did not protect specific areas, would provide an alternative to the marine reserve scenarios. Even so, both types of reserve design performed as well, or better than, this reduced effort strategy in terms of all three performance indicators, despite the lack of reduced effort with reserves.

Two other features of our model results should be noted. First, for a given hydrodynamic scenario, the ranking of the variance among management strategies for each performance indicator followed a pattern similar to the mean: the single large reserve scheme exhibited the largest variance, followed by the single small reserve network, whereas reduced effort and no management action exhibited the smallest variances (Fig. 5). In particular, then, the uncertainty associated with the effect of a set of small reserves appears to be smaller than that with a single large reserve. Reduced uncertainty may make small reserves preferable to a single large reserve as a fisheries-management strategy.

The second feature is that, even after 20 years of reserve protection in which 20% of the coastal zone was closed to exploitation, many model populations had not returned to the total abundance levels they showed before reserve creation (as evidenced by the mean 20-year population growth rate's being less than zero). Because exploitation levels were quite high, long-term population growth rates with reserves were nonetheless significantly larger than those in the no management action strategy (Fig. 5). This result suggests that population recovery rates, even when reserves cover as much as 20% of the available area, may be quite slow—particularly for long-lived species such as spiny lobster. In the absence of comparable control populations, reserves (and other management strategies) may consequently appear to have failed to increase population trajectories because a population continues to decline, even though no action would have resulted in a faster decline.

Two major factors influenced our simulations. The first was physical geometry. The shape and size of Exuma Sound limit the spatial scale of larval and postlarval dispersal relative to that for an open coastal zone—e.g., a linear or convex coastal zone like the western coasts of Australia and North America. Within the sound, then, single large reserves are partially self-recruiting, regardless of hydrodynamic...
pattern, because the scale of dispersal is limited. This need not be the case for similarly sized reserves in open systems, which impose fewer geographic constraints on dispersal; for these systems, the scale of larval dispersal may depend more closely on hydrodynamic current patterns. Thus, in an open system with long-distance dispersal, a network of widely dispersed small reserves may be self-recruiting (the network, that is, not the individual reserves), whereas a single large reserve may not. Under these circumstances, a network of small reserves might perform more effectively than a single large one (Carr and Reed 1993; Allison et al. 1998). Moreover, at a broad scale such as the Caribbean basin, a network of large regional reserves may be more effective than either a single 'mega'-sized reserve or numerous small reserves. In Exuma Sound, however, the expected advantages of a network of small reserves were nullified by the system’s physical geometry.

The second factor influencing our simulations was dispersal! along the coast by benthic individuals. We assumed that dispersal by older juveniles and adults occurred at relatively low rates (only a few km year$^{-1}$) and incorporated it into the model as a diffusive process—i.e., lobsters underwent a random walk over time. This choice resulted in a net flow of older juveniles and adults from regions of high abundance (i.e., reserves) to areas of low abundance (adjacent exploited areas). Consequently, when equivalent gradients in abundance existed across reserve–exploited area interfaces, per capita emigration rates were greater from the network of small reserves than from the single large reserve, simply because networks have more reserve–exploited interfaces. Hence, the network of small reserves exacerbated edge effects, whereas the contiguous large reserve reduced edge effects (e.g., Fig. 4). We expect that systems in which benthic-phase dispersal mechanisms are greatly different (e.g. the directed migrations of $P$. argus in Florida or $P$. cygnus in Western Australia) or nonexistent (e.g., oysters, mussels, abalone) will exhibit results qualitatively different from those presented here, because the relative importance of edge effects will be different.

Another important factor influencing SLOSS considerations is the spatial scale of habitat heterogeneity. Evidence from field studies suggests that large-scale ($\sim 100$-km) spatial variation in habitat abundance and quality has important consequences for spiny-lobster demography in Exuma Sound (Lipcius et al. 1997), which may result in the formation of population source and sink areas (sensu Pulliam 1988). In the interest of simplicity, we ignored habitat variation in this study; habitat quality in model runs was similar at all locations in the coastal zone. However, the spatial scales and patterns of source and sink habitats may affect the performance of different reserve designs (Crowder et al. 2000). Where the spatial scale of habitat variation is small relative to the minimum size of individual reserves, our results should apply, because 'average' habitat quality will be similar for individual reserves, regardless of location. Where the spatial scale of habitat variation is larger, our results may not apply because potential reserve locations would differ in 'average' habitat quality. In this case, the preferred reserve design might be the set of small reserves. It might be possible to achieve higher 'average' habitat quality by placing small reserves individually within areas with high habitat quality, whereas a single large reserve would necessarily contain both low- and high-quality areas. However, the converse might also be true—much lower average habitat quality would be achieved if several small reserves were placed within areas of poor habitat quality, suggesting that, in this situation, the uncertainty associated with reserve effects is greater for several small reserves than for a single large one, in contrast to our results with no habitat variation.

In our simulations, we also ignored the role that catastrophes may play in reserve design. One frequently postulated advantage for several small reserves is that this configuration has a lower risk than a single large reserve that an environmental catastrophe (e.g., oil spill, hurricane damage, global warming) could destroy the entire reserve area (Shafer 1995; Roberts 2000). However, whether small reserves spread the risk sufficiently to offset their disadvantages (i.e., higher transfer rates) may depend on the likelihood and scale of the catastrophes considered.

Although we have used the Caribbean spiny lobster in Exuma Sound as the basis for our model, we urge caution in any attempt to apply the results presented here directly to fisheries-management strategies within the sound. We used our population dynamics model in an heuristic, not predictive, fashion to examine the SLOSS issue in the context of an exploited marine species. In particular, although the twin gyre features used to create the hydrodynamic scenarios were based on feature of the hydrodynamics of Exuma Sound, the hydrodynamic scenarios used here are simple artificial constructs of mathematical convenience. Although useful for this investigation, these scenarios may not be representative of actual conditions within the sound. Nonetheless, pending an examination of the reserve effects of habitat quality and catastrophes, we conclude that a single large reserve is the optimal regional management option.

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Large or small marine reserves?

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References


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Corrections to text

(1) on p. 180, in the 2nd paragraph, the symbol “θ” should be the symbol “Θ”

(2) on p. 182, in the text following eq. 1, the three terms “N_F” should be “ϕ_F”
Chapter 7: Summary

Results from the numerical modeling studies presented here for the Caribbean spiny lobster in Exuma Sound, Bahamas indicate that optimally-designed marine reserves can be effective tools for fisheries management (Chapters 2, 5, 6). Management strategies which implemented optimal reserves—in terms of size and location—simultaneously enhanced both larval production and fishery catch rates, compared to a management strategy which simply continued the status quo fishery and did nothing, even though effort was spatially displaced, not eliminated, by reserve creation (Chapters 2, 5). Conversely, sub-optimally placed reserves sometimes led to simultaneously decreased larval production and fishery catch rates relative to the status quo (Chapters 2, 5). On average, though, marine reserve implementation led to higher larval production and catch rates than a “do-nothing” strategy. In addition, reserves led to larval production and catch rates which were on average greater than, or at worst similar to, a management strategy which reduced overall effort but did not create no-take areas (Chapter 6).

The studies presented in Chapters 2 and 5 suggest that hydrodynamic current patterns can play a pivotal role in determining the optimal size and location for a reserve, while benthic dispersal rates and the distribution of fishing effort have much smaller, though significant, impacts. Optimal reserve configuration (i.e., size and location) was different for each of the hydrodynamic scenarios considered, and the optimal
configuration for one hydrodynamic scenario often led to decreased larval production and catch rates under the other two scenarios. These results suggest that configuration of a marine reserve should incorporate knowledge of regional hydrodynamic patterns that drive larval dispersal for the targeted species to maximize the probability of simultaneously enhancing larval production and catch rates.

However, faced with inadequate funding and lead-time for the required oceanographic studies, this will not be feasible for most fishery managers. Given this lack of knowledge, then, reserves will be located according to other criteria, but in a random fashion regarding hydrodynamic transport patterns. Although selected sites will not be in optimal locations under these conditions (except by chance), the model study presented in Chapter 6 suggests that, at least on the regional scale (100’s of km) in Exuma Sound, marine reserves provide a better avenue for rebuilding spawning stock abundance and enhancing catch of an over-exploited spiny lobster population than do management strategies that either continue the status quo fishery or reduce overall fishing effort but don’t create no-take areas.

In this study, randomly-placed reserves configured as either a single large contiguous reserve or as a network of six small reserves performed, on average, as well as, or better than, management strategies which either reduced effort or maintained the status quo (Chapter 6). In addition, reserves were more effective, on average, when configured as a single contiguous reserve than as a network of small reserves with equivalent total size. However, variances were greater with the single large reserve than with the network of small reserves, such that a large reserve in a particularly poor location could perform much worse than a network of smaller reserves. Thus, the choice...
of a single large or several small reserves under circumstances of uncertainty will likely be dictated by other regional conditions (e.g., the likelihood of a catastrophe).
VITA

William Thomas Stockhausen, Jr.