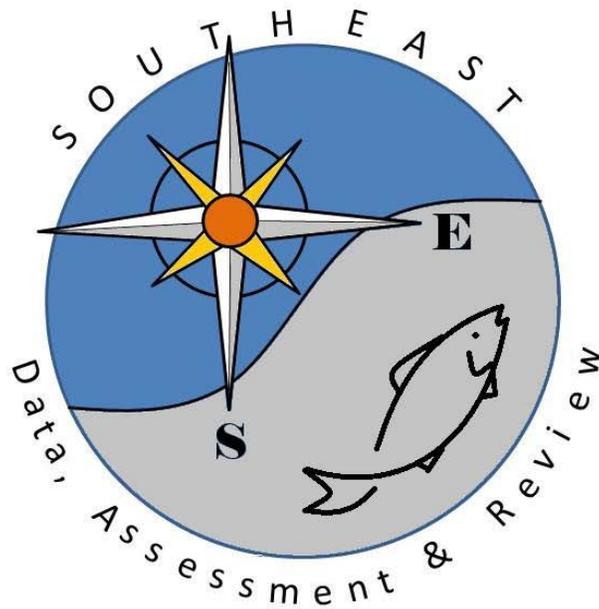


Individual-based modeling of an artificial reef fish community:  
Effects of habitat quantity and degree of refuge

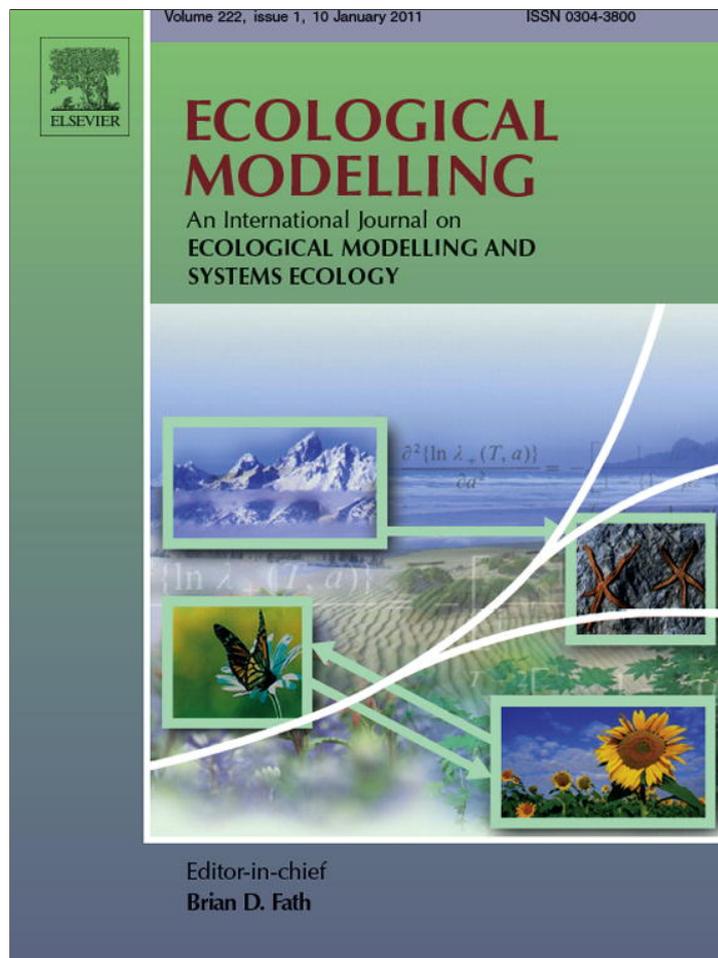
Matthew D. Campbell, Kenneth Rose, Kevin Boswell, James  
Cowan

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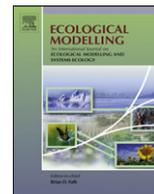
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# Ecological Modelling

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## Individual-based modeling of an artificial reef fish community: Effects of habitat quantity and degree of refuge

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### ABSTRACT

Artificial reefs are often deployed as fishery management tools, and yet there is substantial lack of understanding and agreement on how reefs affect fish population and community dynamics. We developed and applied a multi-species, individual-based model to examine the long-term effects of increasing number of reefs on fish weight, abundance, and biomass. The model simulated the population dynamics of three fish species for 50 years on a 2-dimensional spatial grid. Growth, mortality, and movement were computed each hour for individuals of red snapper (*Lutjanus campechanus*), a croaker-like species (*Micropogonias chromis*), and a pinfish-like species (*Lagodon rhomboides*). We also included individuals of two other species (bluefish – *Pomatomus saltatrix* and a generic jack-like species), but only simulated their hourly movement and their effects on prey and predation of the focal species. The densities of five prey groups were simulated independently in each cell. Our results showed that increasing the number of reefs generally produced higher biomass, but at the cost of slower growth, and smaller individuals. Abundance was higher under fixed-AR recruitment and maximum refuge treatments. In all treatments there were diminishing returns on abundance and biomass with increasing number of artificial reefs. Experiment 2 showed that model results based on regularly spaced reefs were consistent with a real layout of reefs currently being sampled in the northern Gulf of Mexico. Management strategies for determining the habitat-value of reefs in the Gulf of Mexico should consider the number of reefs and the local spatial layout of the reefs to ensure they are optimally arranged. Field experiments performed should assist in resolving how fish recruit to artificial reefs and help determine their roles as fish refuges.

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### 1. Introduction

Artificial reefs (AR) are often deployed as fishery management tools, and yet there is substantial lack of understanding and agreement on how reefs affect fish population and community dynamics. The extent to which artificial reef structures influence exploited fish stocks, either directly via increasing population production rates or indirectly through changes in fishing mortality rates, remains controversial. Many investigations of the effects of reefs ignore potential inter- and intra-specific interactions and focus on static metrics such as diversity indices, while other studies assume simple relationships between reef deployment and fish population responses (Szedlmayer and Shipp, 1994; Ponti et al., 2002; Sherman

et al., 2002; Workman et al., 2002). At a local spatial scale, reefs generally support higher densities of less diverse fish and epibenthic fauna as compared to natural reefs (Fujita et al., 1996; Svane and Petersen, 2001; Badalamenti, 2002; Wilson et al., 2003; Sargent et al., 2006).

There is no clear relationship between reef deployment and sustained regional increases in fish abundance and production. One reason for the lack of definitive empirical evidence is that the relative importance of recruitment versus refuge limitation (which is enhanced by reefs) is often unknown and likely varies by species, location, and from year to year (Tolimieri, 1995; Grossman et al., 1997; Powers et al., 2003). Furthermore, the fish responses to reefs are often affected by site-specific factors related to the design and complexity of the reefs, features of the area (e.g., vertical relief), proximity to other reefs, and biological factors such as competition and density-dependent mortality (Charbonnel et al., 2002; Hanner et al., 2006; Strelcheck et al., 2005). This makes generalizations difficult and the measurements needed to isolate the effects of AR deployment within highly variable population dynamics for any single location impractical (Alevizon and Gorham, 1989; Bohnsack, 1989; Bohnsack et al., 1997; Grossman et al., 1997; Powers et al.,

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2003). In this paper, we explore the interaction among number of reefs and density-dependent competition for resources and predation using an individual-based simulation model of a simple fish community.

Questions that are inherently spatial in nature necessitate an evaluation of how population distributions are affected by the interaction between individual behaviors and spatial resource distributions (Mueller and Fagan, 2008). Modeling behavioral movement becomes especially important so that individuals in the model are responding to the appropriate cues (e.g., temperature, prey fields and predators), and doing so in a manner that results in realistic spatial distributions relative to changing environmental and biological conditions. Many studies on artificial reefs have exhibited a halo effect of low prey abundance near reefs, which is largely attributed to near-reef foraging behavior (Frazer and Lindberg, 1994; Galván et al., 2008). Other studies have shown inconsistent development of prey halo distributions around reefs in favor of non-descript, or patchy, prey distributions that are dependent upon local conditions (Ambrose and Anderson, 1990; Barros et al., 2001; Langlois et al., 2006; Smale, 2008). Finally, reefs are often cited as being beneficial refuge habitat; however, there is evidence that this assumption might be an oversimplification of spatially complex predator–prey interactions (Overholtzer-McLeod, 2004, 2006).

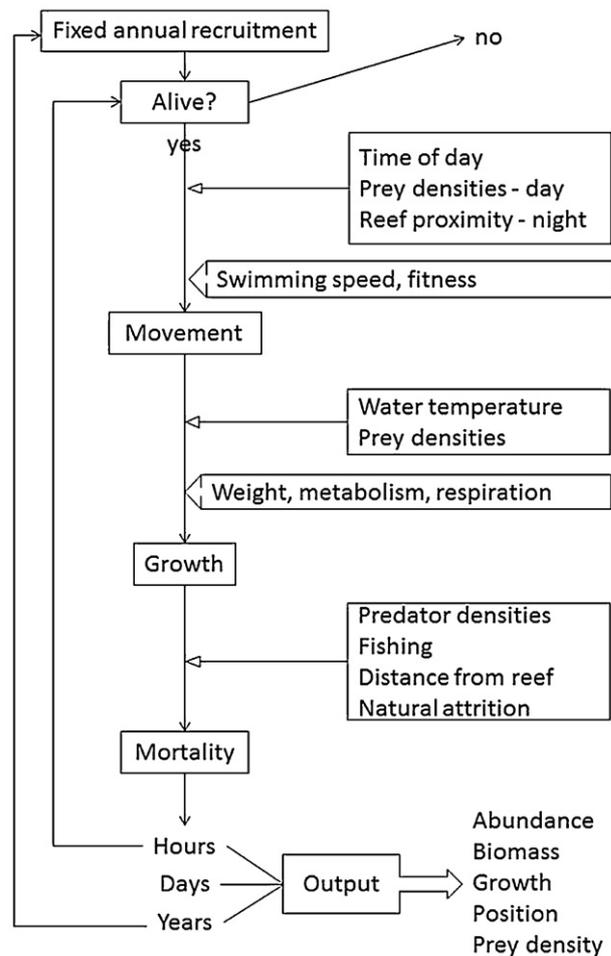
The Gulf of Mexico is an oceanic basin characterized by mud, silt, and sand substrates with sparse natural reef formations (Wilson et al., 2006). Parker et al. (1983) estimated that there was approximately 2800 km<sup>2</sup> of naturally occurring hard-bottom in the region in addition to approximately 4000 oil and gas structures. The paucity of natural reefs in the northern Gulf of Mexico has led to the argument that reef habitat is a limiting factor for populations of red snapper (*Lutjanus campechanus*) stocks. Further, the overfished status of red snapper stocks from the Gulf of Mexico (Schirripa and Legault, 1999), and the economic significance of their landings, has led to increased interest in studies pertaining to red snapper stock enhancement through artificial reef programs.

Individual-based models (IBMs) are important both for theory and management because they allow consideration of aspects usually ignored in analytical models such as individual variability, local interactions in spatially complex habitats, and complex behavior (Grimm et al., 2006). Therefore, our set of questions involving complex spatio-temporal interactions and competition for resources, are best modeled using a spatially explicit IBM. In this paper, we present a 2-dimensional, multi-species, individual-based model to explore how reef abundance affects long-term fish population production. We simulate the hourly growth, mortality, and movement of red snapper, and two major competitor species, across a spectrum of reef configurations under alternative assumptions of high and low recruitment (arrival of new age-1 fish to the reefs) and the level of refuge provided by the reefs. We conclude with a discussion of areas for improvement in the model and in data collection, and the ecological and management implications of our results.

## 2. Model description

### 2.1. Overview

The model simulated the population dynamics of three fish species for 50 years on a 2-dimensional spatial grid and are presented in brief in the conceptual model (Fig. 1), in detail in the sections below, and with detailed equations in an attached section (Appendix A). The model year was from July 1 to June 31. Growth, mortality, and movement were computed each hour for individuals of red snapper, a croaker-like species (*Micropogonias*



**Fig. 1.** Conceptual individual based model. Four sub-models determine annual recruitment, and hourly movement, growth, and mortality. At the beginning of each hour, survival in the previous hour is assessed, and mortalities excluded from processing. External influences on individuals are in the boxes with horizontal arrows. Major processes affecting each sub-model are in the pointed boxes. The model is simulated on an hourly time step however output can occur hourly, daily or annually.

*undulatus*), and a pinfish-like (*Lagodon rhomboides*) species. These three species, which we term the focal species, compete for prey resources. We also included individuals of two other species (bluefish – *Pomatomus saltatrix* and jack-like), but only simulated their hourly movement (not population dynamics) and their consumptive effects on the three focal species. Bluefish individuals acted to remove prey in their spatial cell based on their consumption rates, and both bluefish and jack biomass in each cell were used to adjust the mortality rates of the focal species to mimic spatially dynamic predation.

We used a super-individual approach whereby each model individual is treated like a cohort (Scheffer et al., 1995). Worth was initially assigned when the individuals were created and added to the population as newly recruited age-1 individuals; initial worth was computed as the total number of new recruits in a year divided by the number of model individuals allocated to the first age-class. For the focal species, worth was then reduced each hour by multiplying worth by the fraction surviving. For the two predator species, who did not grow or die, individuals maintained their initially assigned worth throughout the simulation. The worth of an individual was used to adjust consumption rate to compute predation effects on prey, and to compute population abundances and biomass.

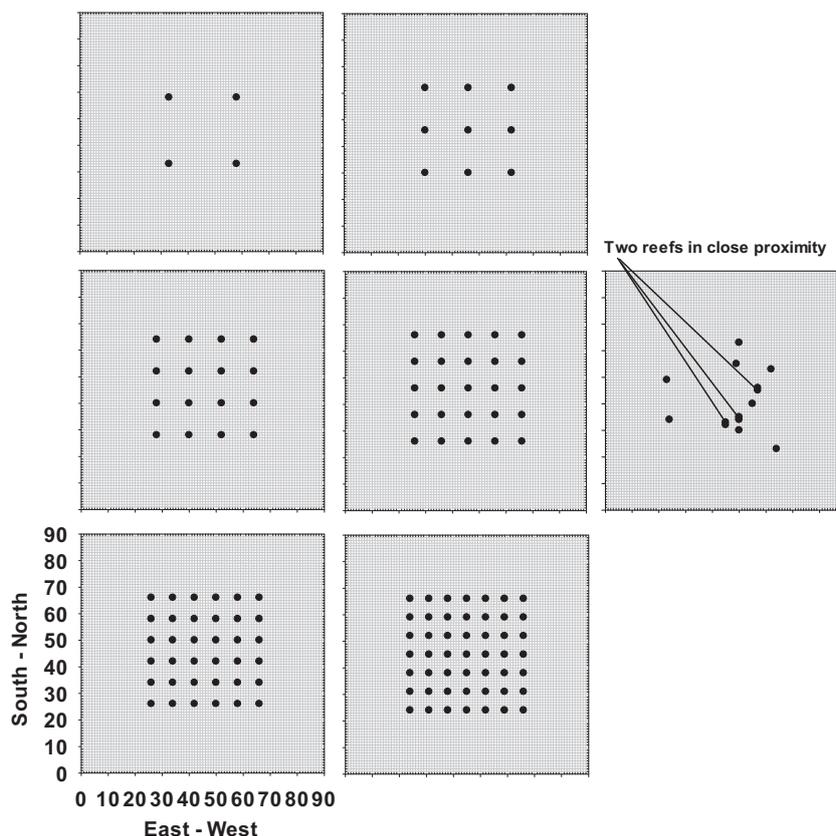


Fig. 2. Spatial layout of the model grid for 4, 9, 16, 25, 36, and 49 regularly spaced reefs, and for an actual layout of 14 reefs.

**Table 1**  
Equilibrium biomass ( $K^*$ ), production rate ( $r$ ) per year and per hour, and energy density ( $E_{prey}$ ) of the five prey groups in the model.

Prey type	$K^*$ (g ww/m <sup>2</sup> )	$r$ (1/year)	$r$ (1/h)	$E_{prey}$ (J/gww)
Zooplankton	6.7	17.3	0.00197	2939.9
Crabs	4.0	4.0	0.00046	2627.6
Shrimp	4.0	4.0	0.00046	3260.6
Pelagic fish	17.0	4.0	0.00046	4142.4
Benthic fish	17.0	4.0	0.00046	4142.4

### 2.2. Environmental variables and spatial grid

The spatial grid consisted of 8100 cells, each measuring 200 m side<sup>-1</sup>, making the domain 324 km<sup>2</sup> (Fig. 2). Spatial cells were denoted as benthic (natural) or artificial reef. We tracked each individual's continuous location as distance in meters from the origin along the  $x$  and  $y$  axes. A 20-cell buffer from the edge was created by confining reef cells to the 50 × 50 cell area (100 km<sup>2</sup>) in the center of the grid. Water temperature was assumed to vary daily, and was assumed to be uniform over all spatial cells on any given day. Five prey groups were simulated on each benthic (non-reef) cell (Table 1): zooplankton, crabs, shrimp, pelagic fish, and benthic fish. Each hour, on every cell, the density of each prey type was updated using a logistic growth equation (Appendix A, Eq. (1)).

### 2.3. Growth

Growth in weight of focal species individuals ( $W$ , gww) was calculated each hour based on a slightly modified Wisconsin bioenergetics model (Appendix A, Eq. (2)). Total hourly consumption for an individual ( $C_j$ ) was calculated as the sum of the

consumption rates over the five prey groups (Appendix A, Eq. (5)). Consumption and weight were updated for each of the 12 nighttime hours each day when individuals were assumed to be foraging. Consumption stopped when either all 12 nighttime hours ended, or the daily maximum consumption rate ( $C_{max}$ ) was exceeded.

Maximum daily consumption rate (Appendix A, Eq. (3)) is calculated using cell specific densities of each of the five prey groups, current temperature (celsius), individual weight (gww), and species specific bioenergetics parameters (Table 2). Hourly consumption of each prey type by an individual was calculated using a type 2 functional response (Appendix A, Eq. (4)) which requires individual  $C_{max}$ , cell specific prey densities, vulnerability of a prey type to the species ( $\nu$ ), and a half saturation parameter ( $K$ ) (Table 3). Vulnerabilities of each prey type, to each focal species, were set *a priori* based on diet information. Half saturation values ( $K$ ) were then calibrated so that weights-at-age for each of the three focal species in the baseline model simulation were similar to published values (Shipley, 2008).

Excretion ( $Ex$ ) and egestion ( $F$ ) were represented differently for red snapper than for pinfish and croaker (Table 1). For red snapper, excretion and egestion were related to water temperature ( $T$ , °C), consumption rate, and proportion of  $C_{max}$  realized (Appendix A, Eq. (6)). Excretion was represented using a similar formulation as egestion but applied to the assimilated food, which is consumption minus egestion (Appendix A, Eq. (7)). Egestion and excretion for pinfish and Atlantic croaker were simply defined as constant proportions (Appendix A, Eqs. (8) and (9)). When  $C_{max}$  is exceeded fish do not forage, and because egestion and excretion depend on consumption occurring, those values were set to zero when  $C_{max}$  was exceeded and during daylight hours when fish are not foraging.

**Table 2**  
Species-specific coefficients and parameter values for length, weight, bioenergetics, movement, and recruitment.

Species	Red snapper	Pinfish	Croaker	Bluefish	Jack spp.
<i>Maximum consumption</i>					
$a_G$	0.182	0.7	0.17	0.5197	n/a
$b_G$	-0.274	-0.274	-0.25	-0.288	n/a
$T_{max}$	35	40	38	38	n/a
$T_{opt}$	27	27.5	28	28	n/a
$\Theta$	2.3	1.8	2	3	n/a
<i>Respiration</i>					
$a_R$	0.0045	0.0633	0.013	0.054	n/a
$b_R$	-0.2	-0.35	-0.202	-0.2	n/a
$T_{max}$	35	40	38	38	n/a
$T_{opt}$	32	27.5	28	28	n/a
$\Theta$	2.1	1.8	2	3	n/a
Act	2	1.45	1.25	1.25	n/a
<i>Egestion</i>					
$a_F$	0.212	n/a	n/a	n/a	n/a
$b_F$	-0.222	n/a	n/a	n/a	n/a
$g_F$	0.631	n/a	n/a	n/a	n/a
$p_F$	n/a	0.2	0.2	0.15	n/a
<i>Excretion</i>					
$a_U$	0.031	n/a	n/a	n/a	n/a
$b_U$	0.58	n/a	n/a	n/a	n/a
$f_U$	-0.299	n/a	n/a	n/a	n/a
$p_U$	n/a	0.1	0.07	0.1	n/a
<i>Daytime movement</i>					
Distance	200 m/h	180 m/h	240 m/h	300 m/h	300 m/h
<i>Nighttime movement</i>					
Distance	200 m/h	200 m/h	240 m/h	300 m/h	300 m/h
<i>Age-1 recruits (numbers)</i>					
Fixed-grid					
Low	8000	20,000	12,000	2000	2000
Medium	32,000	80,000	48,000	8000	8000
High	72,000	180,000	108,000	18,000	18,000
Per AR	2000	5000	3000	500	500

Red snapper parameters: Patterson et al. (2001) and Shipley (2008); pinfish parameters: Hoss (1974), Thompson (2000), and Nelson (2002); Atlantic croaker parameters: Barger (1985) and Murphy (2006); bluefish parameters: Hartman and Brandt (1995), Scharf et al. (2006) and Robillard et al. (2009).

Respiration caused weight loss every hour of all 24 h and was dependent on body weight and water temperature (Appendix A, Eq. (10)). Hourly respiration was increased by 30% ( $R \times 1.3$ ) for every hour an individual was not on a reef cell during daylight hours. Spawning ( $S$ ) was computed as a weight loss on a single day (day 201) by subtracting an additional 8% of each individual's body weight (0% for age-1 and 4% for age-2), spread evenly over the 12 hourly nighttime time steps. The same percentage of weight lost from spawning and the day spawning occurred were the same for all focal species. Respiration losses were imposed for all 24 h, and spawning losses were imposed evenly spread out over the 12 h on day 201 (July 21st).

**Table 3**  
Vulnerabilities ( $V$  in Eq. (4)) and feeding efficiency parameter values ( $K$  in Eq. (4)) by prey type, and energy densities ( $E_{fish}$ , J/g ww) for the focal species (red snapper, pinfish, and croaker).

Parameter	Prey type	Red snapper	Pinfish	Atlantic croaker	Bluefish
$V$	Zooplankton	0.3	0.9	0.12	0.0
	Crab	0.3	0.9	0.12	0.0
	Shrimp	0.2	0.9	0.12	0.0
	Pelagic fish	0.0	0.0	0.06	0.2
	Benthic fish	0.2	0.0	0.06	0.2
$K$	Zooplankton	153.0	855.0	185.0	0.0
	Crab	150.0	855.0	185.0	0.0
	Shrimp	150.0	855.0	185.0	0.0
	Pelagic fish	0.0	0.0	185.0	30.0
	Benthic fish	100.0	0.0	185.0	30.0
$E_{fish}$	n/a	4186	3516	4594	6279

2.4. Movement

Each individual was tracked in  $x$ - $y$  continuous space as their distance in meters from the lower left corner of the grid. Each hour, the  $x$  and  $y$  positions of each individual were incremented, and their cell location updated. The individual then experienced the environmental conditions in their current cell for the next hour until movement was invoked again. Nighttime movement began at hour 1 (sunset) and continued for each of the next 12 hourly time steps; daytime movement was for hours 13 through 24 of each day.

All individuals moved towards cells deemed the best (i.e., fitness movement). For focal species during nighttime (feeding), best cells were determined as the cell offering the greatest growth within a 25-cell neighborhood (2 cells in eight directions from the current cell); during daylight, the best cell was the nearest reef cell. Cells within the neighborhood were evaluated in random order, and the projected growth rate in a candidate cell had to be 5% larger than the current best cell's growth rate in order for that cell to be selected. For daytime hours, focal species individuals moved towards the closest reef cell from their current location. Selection of this primary community movement rule is based on the resource mosaic hypotheses that reef habitat is used as a refuge from which feeding excursions take place, thereby depleting resources in a 'halo' pattern about the reef (Lindberg et al., 1990). For bluefish and jack, the best cell was the cell with highest summed biomass of the focal species within a 25-cell neighborhood, and this was used for all 24 h. Both of these movement patterns relate to optimally foraging and maximizing net energetic gain.

To move individuals towards the best cell we calculated a trajectory in radians ( $\theta$ ), randomly adjusted the trajectory  $\pm 0.5$  rad, and adjusted the angle for any negative signs that were lost with the absolute values in Eq. (12) (Appendix A, Eqs. (12) and (13)). The  $x$ -axis and  $y$ -axis positions were then updated for the individual based on  $\theta$  and an assumed movement distance in meters per hour (Appendix A, Eqs. (14) and (15)). Distance also included a random component ( $ranv$ ) which added between  $\pm 0.3$  of the average movement distance. Different values for distance were used for daytime and nighttime movement (Table 1). If the individual's calculated movement resulted in an off-grid position, then the individual was reflected by moving the individual the exact distance that was intended but in the opposite direction (i.e., reversed the sign of distance).

2.5. Mortality

Four separate sources of instantaneous mortality were imposed hourly on focal species: constant basal rate, distance-from-reef, predation by bluefish or jack, and fishing. All sources of mortality were calculated separately for an individual, summed (to obtain total mortality  $Z$ ), and then used to reduce the worth of the

individual (i.e.,  $worth_{t+1} = worth_t \times e^{-Z}$ ). Hourly basal mortality rates were  $0.02 \text{ year}^{-1}$  for red snapper and  $0.12 \text{ year}^{-1}$  for pinfish and croaker (Table 4).

Two alternative regimes of distance, predator, and fishing mortality rates were applied to represent the reef acting as maximum or minimum refuge (Table 4). The logic was that under maximum refuge, mortality of individuals from distance, predation, and fishing while in reef cells was zero. Under the minimum refuge assumption, mortality of individuals in reef cells was either the same or higher than for individuals not in reef cells.

Distance-from-reef mortality was applied for nighttime and daylight hours and decreased as a function of increasing distance between an individual and the nearest AR (Table 4). Distance mortality was intended to simulate predation from reef based predators such as groupers. When reefs provided minimum refuge the highest mortality rate occurred on the reef cell, whereas under maximum refuge the highest mortality rate occurred in the eight cells surrounding the reef.

Predation mortality was applied during daylight and nighttime hours, and increased linearly as a function of cell-specific bluefish and jack normalized biomasses (Table 4). Under maximum refuge conditions predation mortality was only applied while subjects were located in non-reef cells. Under minimum refuge conditions predation mortality was applied in both reef and benthic cells. Predation is expected to be more difficult in darkness and so all predation mortality rates were multiplied by 0.5 during evening hours.

Fishing mortality occurred at fixed rates during daylight hours and at half that rate during nighttime hours. The hourly rate during daylight is equivalent to annual rate of  $0.1 \text{ year}^{-1}$ . Fishing was set to zero for individuals in reef cells under the maximum refuge condition.

## 2.6. Recruitment

Annual recruitment of new age-1 individuals of each focal species to the model grid was simulated under two alternative assumptions (fixed-grid and fixed-AR). New recruits are assigned an initial weight equal to the mean weight of newly arriving age-1 fish (111.5 g ww for red snapper, 36.9 g ww for pinfish, and 88.7 g ww for croaker). All individuals are randomly placed on the grid at the beginning of each year (day 1, which is July 1).

Fixed-grid recruitment used the same number of recruits each year for all simulations regardless of the number of reefs. Fixed-grid recruitment therefore assumes that recruitment operates on a larger scale than we defined. Under this assumption, we simulated low, medium, and high levels to roughly bracket field estimates (Table 1). The medium recruitment level was treated as the baseline value.

Fixed-AR recruitment used a fixed number of recruits per reef, and then the total number of recruits added each year differed based on the number of reef cells in each simulation. Fixed-AR recruitment assumes that recruitment processes operate on the scale we defined. We used the medium number of recruits from the

fixed-grid assumption, and divided by 16 reefs to obtain the value for recruits per reef. Then the total number of recruits added per year was the recruits per reef times the number of reefs on the grid. Therefore, six levels of recruitment were simulated because there were six different reef layouts used in the fixed-AR simulations.

## 2.7. Numerics and initial conditions

Initial weights of individuals are assigned using mean length-at-age and length-weight relationships from the literature (Patterson et al., 2001; Nelson, 2002; Barger, 1985; Robillard et al., 2009). Initial abundances by age were computed by first specifying the age-1 abundance from the recruitment level, and then estimating the abundance for ages 2–10 by decrementing numbers by age using the sum of basal and fishing mortality rates. All individuals of all age classes were randomly placed on the grid at the beginning of a run. Prey densities are started at species specific equilibrium densities ( $K$ , Table 2).

All simulations used 1000 super-individuals per each of the 10 age classes of the five species. Thus, a total of 50,000 super-individuals were followed. Upon reaching age-11, the 1000 super-individuals of red snapper, croaker, and pinfish were removed and replaced with 1000 super-individuals of age-1 individuals for each species. The initial worths of the newly introduced 1000 super-individuals were set at the assumed recruitment abundance divided by 1000.

## 3. Design of simulations

### 3.1. Calibration

We calibrated the model using 16 reefs, maximum refuge conditions, and with the fixed-grid recruitment at the medium level. First, we used daily temperatures and simulated the growth of individual fish of each focal species from age-1 to age-10 (i.e., off-grid). We adjusted values of the bioenergetics parameters for the three focal species, assuming that consumption ( $C$ ) was 0.7 of maximum consumption (i.e., no prey dynamics) until daily growth was approximately 0.8% of body weight per day at optimum temperature and weights-at-age were similar to field estimates (Shiple, 2008). Second, we used these bioenergetics parameters in the full model, and adjusted the  $K$  values (half-saturation parameter) with dynamic prey until we obtained similar growth rates, weights-at-age, and diets as reported from the literature (Hartman and Brandt, 1995; Thompson, 2000; Murphy, 2006; Shiple, 2008). Third, given realistic growth of the three focal species with dynamic prey on the grid, bluefish and jack were added, and the basal mortality rates of the focal species were adjusted until we obtained realistic densities of the focal species and steady state (persistent) population biomasses. Finally, we confirmed that the model was showing the desired movement patterns of the focal species (nighttime off-reef movement to forage, daytime movement back to the reefs) and the predator species (tracking their prey biomasses).

**Table 4**

Differences in basal, distance-from-reef, predation by bluefish or jack, and fishing mortalities between the minimum and maximum refuge conditions.

Mortality	Timing	Explanatory variable	Refuge	
			Minimum	Maximum
Basal	Daylight and nighttime	Constant	Allowed to occur on reef cell	Allowed to occur on reef cell
Distance from reef	Daylight and nighttime	Decreases with distance from nearest reef cell	Highest on reef cell	Zero on reef cell
Predation by bluefish and jack	Daylight and small amount at nighttime	Increases with bluefish or jack biomass in the cell relative to the grid-wide average biomass	Allowed to occur on reef cell	Zero on reef cell
Fishing	Daylight and nighttime	Constant rate that is halved during nighttime	Allowed to occur on reef cell	Zero on reef cell

Movement of individuals was sensitive to the size of the neighborhood search allowed. Reducing the search neighborhood from 25 to 9 cells decreases the number of best cells' to select from and therefore trajectories taken by an individual in each hour (fish move towards the center of the best cell). The result of reducing the neighborhood search was some directional bias and destabilization about where biomass moved as well as resource use in those cells. Increasing the search neighborhood from 25 cells to 49 cells made the model prohibitively slow to run (i.e., run time was excessive), with no improvement in the spatial properties of the model, and so the 25 cell neighborhood search was used.

### 3.2. Simulation experiments

We performed two simulation experiments: one to test the effect of the number of reefs on red snapper population dynamics (e.g., changes in abundance and biomass), and the second using an actual arrangement of reefs from the Gulf of Mexico to confirm that our simulations with regularly spaced reefs were representative. We do not present the results for the other species, rather we focus on red snapper because it is of commercial importance, the center of controversy about habitat, overfishing, and the role of artificial reefs in fisheries production in the Gulf of Mexico (Powers et al., 2003; Shipp and Bortone, 2009; Cowan et al., 2010).

In experiment 1, we simulated 4, 9, 16, 25, 36, and 49 reefs placed uniformly on the grid (Fig. 2). We did this for all combinations of the two levels of refuge quality (maximum and minimum) and the 3 levels (low, medium, high) of fixed-grid recruitment ( $6 \times 2 \times 3 = 36$  combinations), and for maximum and minimum refuge with the 6 levels of fixed-AR recruitment ( $2 \times 6 = 12$  combinations). There were no low, medium, and high levels of recruitment for the fixed-AR because recruitment was specified based on the number of reef cells. This resulted in a grand total of 48 simulations for experiment 1.

In experiment 2, we simulated four combinations with the actual reef (14-reefs) configuration from an ongoing field study in the Gulf of Mexico (Fig. 2): medium recruitment with fixed-grid and fixed-AR, each with maximum and minimum refuge. We compared model predictions of the 14-reef actual layout with the corresponding 9-reef and 16-reef regularly spaced results from experiment 1.

Model results for both simulation experiments were summarized by the average weight at age-5, total grid-wide biomass, and total grid-wide abundance of red snapper, averaged for years 10–50 (Table 5). We used daily values (age-2 and older for abundance and biomass) on the last hour of each day, and then averaged these for all 40 years. For experiment 1, we plotted the averaged weight at age-5, biomass, and abundance against number of reefs for the fixed-grid recruitment simulations, and then for the fixed-AR recruitment simulations. For experiment 2, we compared mean weight at age-5, abundance, and biomass for the four combinations using the actual 14-reef layout with the values from same four combinations with the 9-reef and 16-reef results with the regularly spaced reefs.

To further understand and describe the red snapper model results for experiment 1, we also report additional variables (Table 5). Shrimp was a major prey item of the focal species, and the other prey types showed similar patterns as shrimp. To interpret how the number of reefs affected prey distributions, we used the shrimp values by grid cell for hour 12 (after feeding for the night) of day 56 of year 20. We only included the cells with shrimp biomass less than 0.98 of the shrimp carrying capacity (i.e.,  $<3.92$  g ww). This represents a crude way to identify prey halos.

To illustrate the movement dynamics of red snapper and to understand how increasing the number of reefs affected mortality (abundance), we computed four additional variables related to

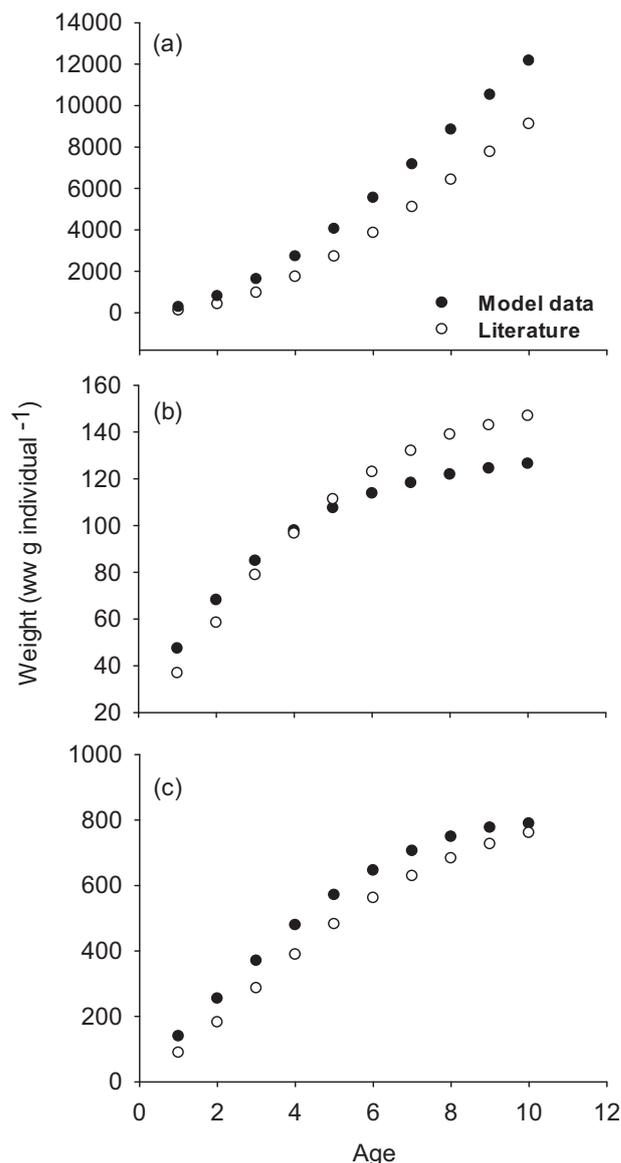


Fig. 3. Average weight-at-age (ages 1–10) for the calibration simulation and reported by Patterson et al. (2001) for (a) red snapper, (b) pinfish, and (c) croaker.

distances moved by individuals and time spent vulnerable to predation (Table 5). These variables were computed as the overall average values over all individuals and all hours during years 10–50 of each simulation. The first variable was the average distance (meters) moved by an individual during nighttime (feeding) hours. The second variable was the average displacement distance moved away from their starting reef cell each day while feeding. The third variable was the average number of hours of daylight spent off of reef cells, computed as the number of hours starting at sunrise each day when they end feeding and begin to move to the nearest reef cells until they returned the reef cell. The fourth variable was the average number of unique reef cells visited per week.

## 4. Results

### 4.1. Calibration

Predicted mean weights-at-age were similar to published values (Fig. 3). Predicted mean weights-at-age for older red snapper were higher than observed and for pinfish were smaller than observed,

**Table 5**

Summary of model output used to describe the results for calibration, simulation experiment 1, and simulation experiment 2. RS, red snapper; CR, croaker; PF, pinfish.

Simulations	Output variable	Species	Computation
Calibration	Averaged weight at age for ages 1–10	RS, CR, PF	Average age-at-weight was computed over all individuals on hour 24 of December 31 of each year and then averaged over years
	Abundance	RS, CR, PF	Abundance of age-2 and older on hour 24 of each day from years 10 to 20
	Biomass	RS, CR, PF	Biomass of age-2 and older on hour 24 of each day from years 10 to 20
	Diets by prey type for each species	RS, CR, PF	Proportion by biomass of each prey type eaten by each individual each hour during nighttime (feeding), and then averaged over all individuals and all feeding hours between years 10 and 20
	Hourly position of a red snapper	RS	Position on the grid each hour for four days of a red snapper individual during year 20
	Biomass snapshots on the grid	All five species	Biomass snapshots of each species for hours 3, 9, 15, and 21 during day 56 of year 20
Experiments 1 and 2	Prey biomass snapshots on the grid	All five prey species	Biomass snapshots of each of the five prey groups on hour 12 (end of foraging by fish) during day 56 of year 20
	Averaged weight at age-5	RS	Average age-5 weights are computed over all individuals on hour 24 of December 31 of each year and then averaged over years 10–50
	Averaged abundance	RS	Daily abundance of age-2 and older from hour 24 are averaged over all individuals and hours from years 10 to 50
Additional variables for experiment 1	Averaged biomass	RS	Daily biomass of age-2 and older from hour 24 are averaged over all individuals and hours from years 10 to 50
	Contour plots of relative biomass in shrimp halo cells	Shrimp	Relative shrimp biomass (cell biomass divided by carrying capacity), based on hour 12 during day 56 of year 20
	Average distance moved during nighttime	RS	Summed the distance moved each hour by each individual between years 10 and 50, and then averaged these values
	Average displacement	RS	Summed the distance from the new location each hour to the originating reef cell for that day over individuals and hours from years 10 and 50; averaged the values
	Average hours of daylight off reef cell	RS	Summed the number of hours between sunrise and when returned to a reef cell over individuals and days between years 10 and 50; averaged the values
	Average number of unique reef cells visited per week	RS	Summed the number of unique reef cells by each individuals each week during years 10 and 50, and then averaged these values

but considered reasonable given the generality of the model. Red snapper consumed mostly pelagic fish (51% by weight) and zooplankton (33%), while benthic fish, shrimp and crabs were about 16% of their diet. Pinfish diet consisted of zooplankton (48%), crabs (23%), and shrimp (28%), and croaker consumed benthic fish (38%), crabs (28%), shrimp (23%), and pelagic fish (9%).

Biomass of red snapper increased while pinfish and croaker biomass decreased within each year (Fig. 4a). Daily abundances of all three species decreased within each year as expected (Fig. 4b). Red snapper growth outpaced mortality, whereas mortality overrode growth for pinfish and croaker within each year. Red snapper dominated the community in biomass (37% red snapper, 26% pinfish, 16% croaker, 10% pinfish, and 10% croaker) and abundance (78% red snapper, 1.6% pinfish, 3.6% croaker, 8.5% bluefish, and 8.5% jack).

The hourly position of an individual red snapper and biomass contour plots illustrated diurnal movement of red snapper (Fig. 5 and leftmost column of Fig. 6). Beginning at hour 1 (evening) red snapper moved away from reefs to forage, continuing that pattern until hour 12 (sunrise), at which point individuals began moving back towards a reef (Fig. 5). Red snapper biomass was dispersed away from reefs at hour 9 (near end of nighttime foraging), concentrating back on the reefs by hour 15 (after 3 h of daylight), and completely back on reef cells by hour 21 (Fig. 6). Pinfish and croaker exhibited the same pattern of movement as red snapper. Bluefish and jack movement tended to loosely concentrate around reef cells (Fig. 6) because their movement was based on locating focal community biomass.

The concentration of focal species near reef cells resulted in a halo effect on prey distributions (Fig. 7). Relative biomass of each prey type was lowest on reef cells and below their carrying capacity for approximately 5 cells surrounding each reef cell (2 km in diameter). These prey halos were persistent for all days within the year and occurred in all years.

#### 4.2. Simulation experiment 1: increasing reefs under fixed-grid recruitment

Increasing the number of reefs with fixed-grid recruitment caused density-dependent growth (Fig. 8a), which with almost constant (minimum refuge) or increasing abundances (maximum refuge, Fig. 8b), resulted in increasing biomasses (Fig. 8c). Low, medium, and high recruitment had consistent effects (parallel lines). With the number of recruits constant to the grid, increasing the number of reefs resulted in faster growth because the same abundances of red snapper were distributed over a larger portion of the grid. For example, under medium recruitment, average biomass of red snapper per reef cell was 49.2, 19.9, and 7.7 MT reef<sup>-1</sup> for the 4, 16, and 49 reef layouts respectively. The rate of increase in growth leveled off beyond 20 reefs (Fig. 8a). The combined effect of faster growth that leveled off with constant abundances was a rising but leveling off of biomass with increasing number of reefs (Fig. 8c).

Halo cells held higher shrimp biomass as the number of reefs increased from 4 to 49 (Fig. 9a). The spatial proximity among reefs decreased on the grid with increasing number of reefs (Fig. 2) and consequently, prey halos increasingly overlapped and grid-wide prey biomass decreased resulting in a cap of mean weight at age-5 despite increasing reef availability. The amount of shrimp missing from the grid (i.e., biomass below carrying capacity) due to consumption by focal species and bluefish was computed from the prey biomass plots as 2.6%, 2.7%, and 3.2% for 4, 16 and 49 reefs respectively. With about the same number of red snapper and other species spread out over many more reefs, the net effect of more reefs was faster but decelerating growth of red snapper and more efficient use of resources.

For each fixed-grid recruitment level, distance moved (Fig. 10a) and displacement both decreased by about 0.6 m/h with each incremental increase in AR number (Fig. 10a and b). Increasing the

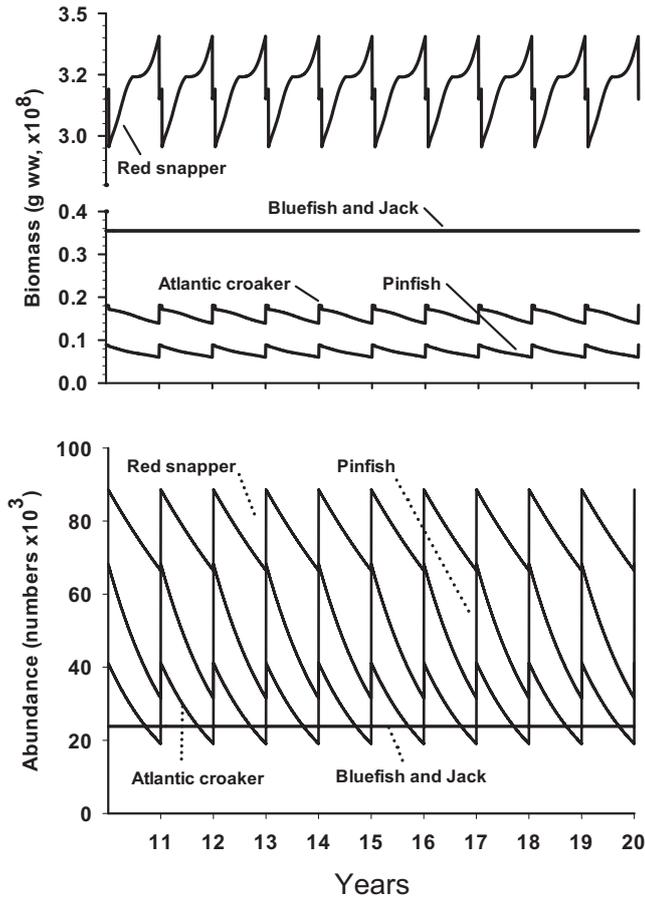


Fig. 4. Daily values of red snapper, pinfish, croaker, bluefish, and jack (a) biomass and (b) abundance during model years 10–20 of the calibration simulation.

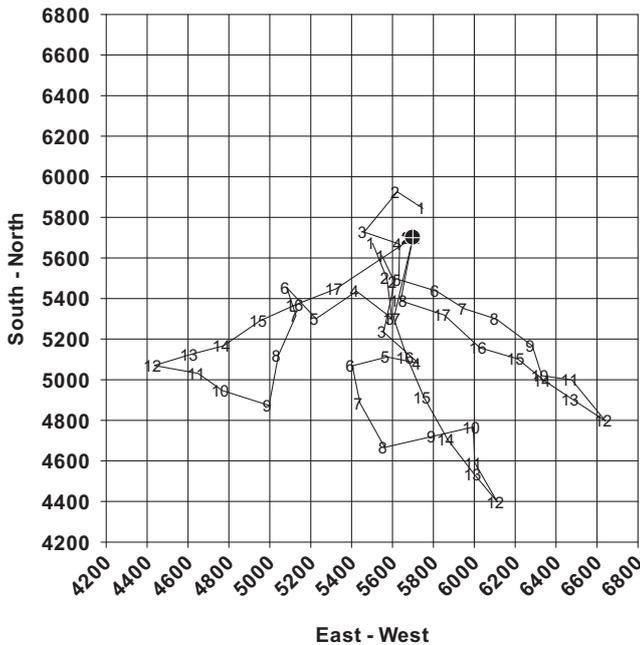


Fig. 5. Hourly position of an individual red snapper during four days in year 20 of the calibration simulation. The numbers on the track line are hours within each day (1–12 is nighttime and 13–24 is daylight). Reef cells are indicated with a black hexagon.

number of reefs resulted in less displacement from reefs while foraging and enabled individuals to return to refuge in approximately 2–4 h for the 49 reef case versus 5.5–8.5 h for the 4 reef case (Fig. 10c). Additionally, the number of unique reefs visited per week increased with the number of reefs available on the grid (Fig. 10d). Under fixed-grid recruitment increasing the number of reefs acted to disperse fish more evenly over the grid, allowing them to maximize resource use and grow more efficiently, while simultaneously displacing them less distance from reefs and minimizing time at risk.

4.3. Simulation experiment 1: increasing reefs under fixed-AR recruitment

Increasing reef number under fixed-AR recruitment resulted in decreasing mean weight at age-5 (Fig. 11a) but increased abundance (Fig. 11b) which in turn resulted in increasing biomass regardless of refuge treatment (Fig. 11c). The increase in biomass with increasing number of reefs is a direct effect of fixed-AR recruitment because growth was negative. If recruitment is in fact tied to available habitat then abundance increases linearly. Biomass appears to level off with increasing number of reefs which demonstrates the impact of reduced growth on biomass (Fig. 11c). There is a clear tradeoff under fixed-AR recruitment between growth and increased abundance.

There was progressively more halo cells containing lower shrimp biomass as reef number increased from 4 to 49 (Fig. 9b). The amount of shrimp missing from the grid due to consumption by focal species and bluefish increased more than with the fixed-grid simulations: 0.41%, 2.7%, and 11.0% for 4, 16, and 49 reefs respectively. Increased abundance from recruitment resulted in increasing reductions in prey, despite red snapper and other species being distributed over more reef cells.

Under the fixed-AR simulations increasing reef number resulted in decreased distance traveled (Fig. 12a), displacement (Fig. 12b) and daylight hours spent off of the reef cells (Fig. 12c) while the number of reefs visited in a week increased (Fig. 12d). Primary community abundances per reef and the size of the resultant prey halos were fairly constant, which resulted in less difference in displacement and movement, despite increasing number of reefs. The small decrease observed in displacement and distance moved are the result of decreased interstitial spacing between reefs rather than an effect of decreasing competition. Number of unique reefs visited was similar between fixed-AR and fixed-grid because the reef layout was the same (Fig. 10d versus Fig. 12d). Under fixed-AR recruitment per-reef abundance and biomass was fairly constant and so the dispersal effect did not lessen local competition for resources but did allow for a larger portion of the grid to be utilized.

4.4. Simulation experiment 1: refuge effect

The effect of the maximum prey refuge treatment was to retain higher red snapper abundance and biomass in the model which resulted in slower growth and less available prey (Figs. 8 and 11, all subplots). Fish under maximum refuge conditions also moved longer distances, were displaced further from reef cells, spent more time at risk, and visited more unique reefs during a week (Figs. 10 and 12, all subplots). The obvious benefit of maximum refuge was that red snapper individuals were protected from predators and fishing while on reefs cells. Additionally retention of biomass in the model caused increased displacement from near-reef areas with high mortality rates, although the subsequent displacement increased time at risk which carried an associated respiration penalty (Figs. 10 and 12b).

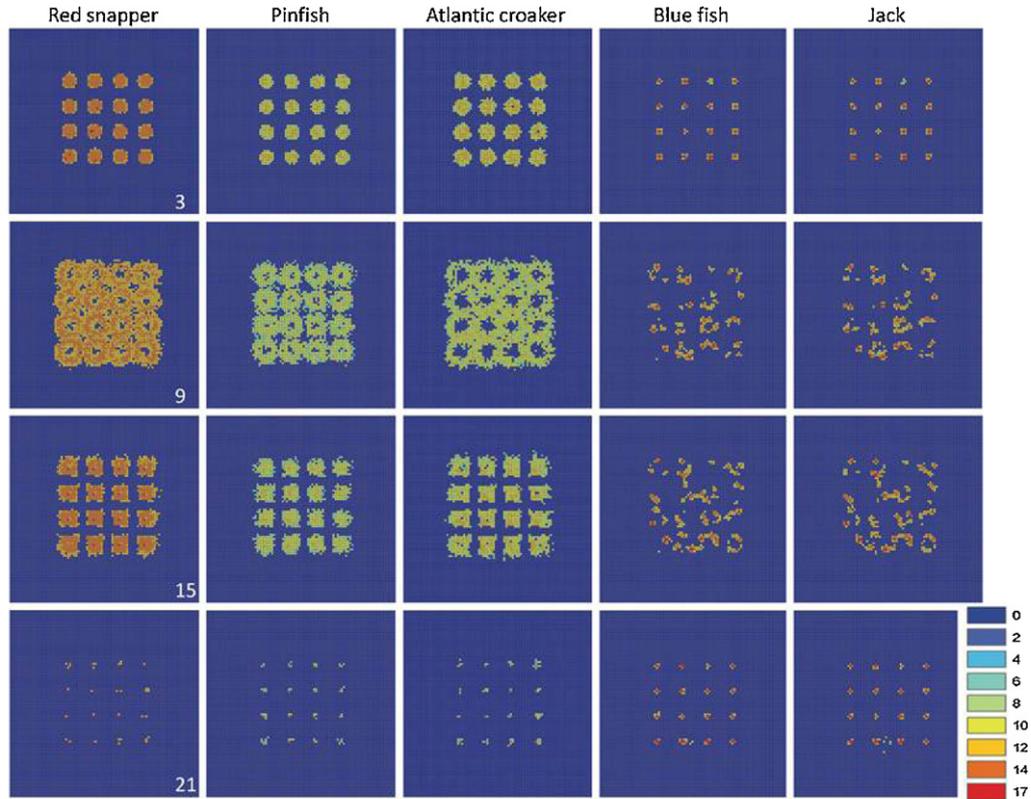


Fig. 6. Grid values of log-transformed red snapper, pinfish, croaker, bluefish, and jack biomasses at hours 3, 9, 15, and 21 during day 56 of year 20 in the calibration simulation.

4.5. Simulation experiment 2: actual versus regularly spaced grid

Model results appeared robust when we using an actual reef layout in place of the regularly spaced layouts used in simulation

experiment 1. For the fixed-grid recruitment, predicted mean weight at age-5 was similar to mean weight for the regularly spaced 9-reef results (Fig. 13a), while overall abundance was moderately higher than both the 9-reef and 16-reef results (Fig. 13b). The net

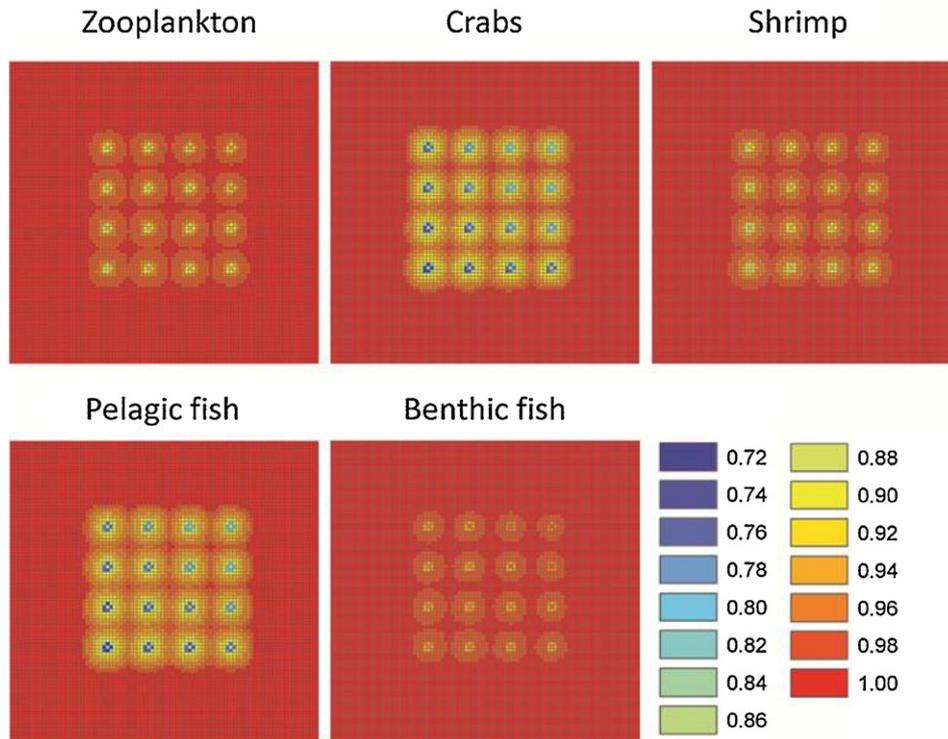


Fig. 7. Grid values prey biomass (proportion of carrying capacity) for the five prey types at hour 12 (post-foraging) on day 56 of year 20 in the calibration simulation.

effect of these differences was that biomass for the actual 14-reef layout was very similar to the 9 and 16-reef results (Fig. 13c). Under the fixed-AR conditions, mean weight at age-5 red snapper were smaller than the 9 and 16-reef results (Fig. 13a) because abundances were slightly higher than the 16-reef results (Fig. 13b). Again, the net effect was averaged biomass for the 14-reefs that was intermediate to the 9 and 16-reefs (Fig. 13c). Thus, while the actual layout with 14-reefs did distort the model predictions (i.e., all results were not always intermediate to the results with 9 and 16 reefs), the results with the actual layout were similar in magnitude and showed the same patterns as with the regularly spaced grids.

5. Discussion

Our model analysis suggests that red snapper (age-1–10) are habitat limited, although increasing artificial reef habitat does not simply result in more and larger red snapper. Increasing reefs in a fixed area increases red snapper biomass, although the increases become progressively smaller with increasing number of reefs as growth of individuals is reduced. Across equivalent increases in the number of reefs deployed the net return in production is not equivalent. Use of an actual grid, while a limited test, showed that our results based on regularly spaced reefs were likely indicative of the more irregularly spaced reefs seen in the Gulf of Mexico. Also, although not shown, pinfish and croaker showed very similar relationships of growth, abundance, and biomass with increasing reefs as red snapper.

The answer to the simple question of whether more reefs mean more red snapper is complicated and not a simple yes or no. Increasing the number of reefs in an area can result in more red snapper but they will be smaller in size and under some conditions, the incremental increases in red snapper biomass can be quite small even for large increases in the number of reefs. For fixed-grid recruitment, biomass quickly leveled off beyond about 20 reefs, while biomass was still increasing at 50 reefs when recruits were in proportion to the number of reefs. However, the crowding with fixed-AR recruitment resulted in mean weight-at-age 5 actually decreasing with increasing number of reefs. Whether reefs serve as refuge or not further complicate the responses by modifying the magnitude of the response; maximum refuge increased abundance but reduced individual growth. Depending on the recruitment pattern and the role of reefs as refuge, increasing reefs can result in mean weight at age-5 of red snapper increasing or decreasing, and abundance and biomass of red snapper remaining the same or increasing.

Production of biomass is associated with the extent to which the community maximizes prey resources and refuge habitat on the spatial grid. In this model production was inextricably linked to the dispersal function of the reefs and those were dependent on the recruitment treatment applied. Fixed-grid recruitment showed that increasing the number of reefs caused wider dispersal of biomass over the entire grid, and reduced per-reef biomass. Increasing number of reefs related to increased efficiency of prey resource use on the grid, decreased distance traveled and displacement from reefs while foraging, lowered time spent off the reef during daylight, and increased the number of new reefs visited during a week. Fixed-reef recruitment resulted in essentially equivalent per-reef biomass and abundance regardless of the number of reefs placed on the grid, and resulted in negative growth but improved abundance. In both recruitment treatments the overall effect was to spread biomass over a larger area, increase habitat connectivity resulting in more efficient use of prey resources. Analysis of the relationship between habitat quantity, recruitment, and population abundance in field studies is needed to fully understand which of these recruitment treatments is most representative.

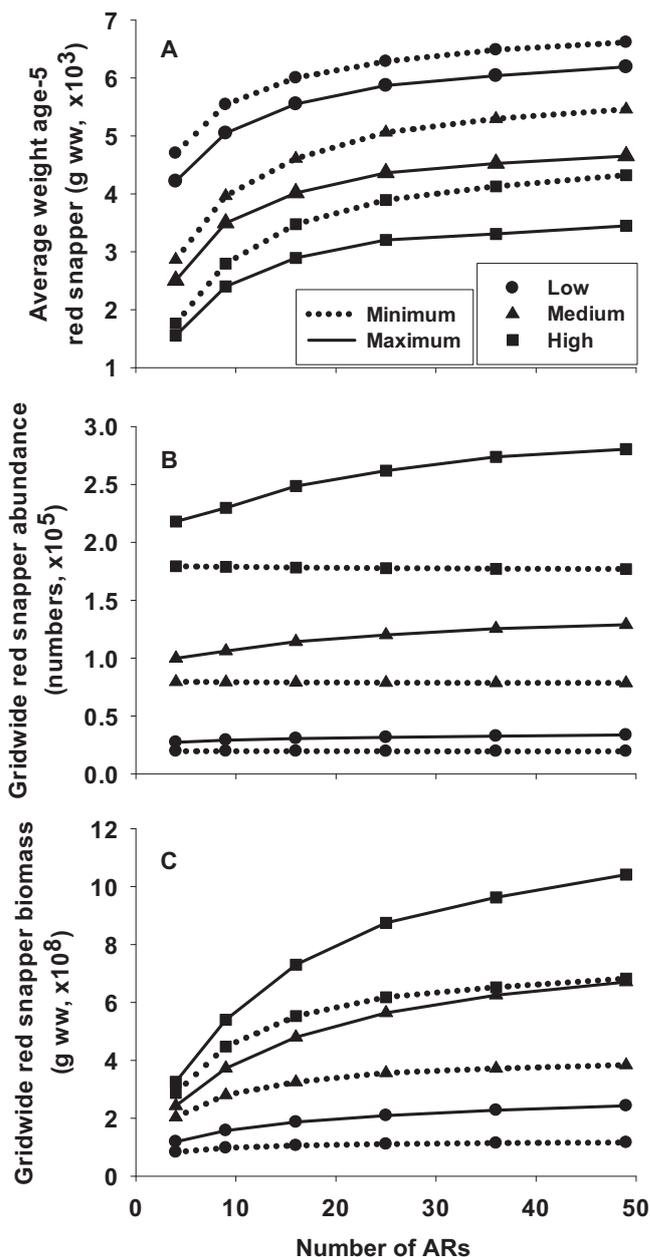


Fig. 8. Red snapper (a) average weight at age-5, (b) abundance, and (c) biomass with increasing number of reefs for the fixed-grid recruitment for the low, medium, and high recruitment levels and minimum and maximum refuge.

The model is capable of generating diurnal movement patterns and prey halo distributions that are based on and are consistent with the resource mosaic hypothesis (Lindberg et al., 1990). This movement pattern implies a high degree of site fidelity and that long distance movement to new areas is dependent on the number and connectivity of reef habitats available on the grid. Studies pertaining to site fidelity of red snapper on artificial reefs show mixed results concerning site fidelity and range from <25% to >60% year<sup>-1</sup>, and demonstrated that high site fidelity may not be the rule (Szedlmayer and Shipp, 1994; Patterson et al., 2001, 2003). Long distance, explorative behavior, demonstrated from field studies can take place within days (McDonough, 2009), can be long in duration and distance (Szedlmayer and Shipp, 1994; Patterson et al., 2001), and has unclear or unknown motivations. Future iterations of the model should include a component to model these wide scale movement patterns, and field studies should continue to

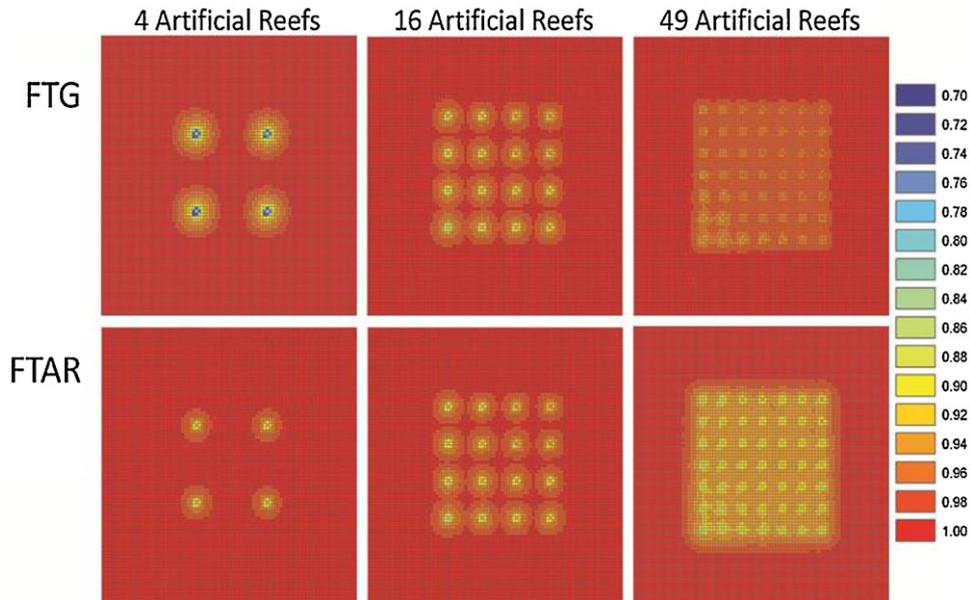


Fig. 9. Prey density plots of the number of halo cells with different values of shrimp biomass (expressed as fraction of carrying capacity) for 4, 16, and 49 reefs on hour 12 of day 56 in year 20 for (a) fixed-grid recruitment and (b) fixed-AR recruitment. Results are for minimum prey refuge condition.

investigate site fidelity with particular focus on age-related movement behavior and ontogenetic shifts.

Prey species distributions showed a distinct halo effect in which prey densities were depressed closest to the reef cells, increased in a radial fashion from the reef cell, and persisted throughout the

simulations. All prey species showed prey halos, and the extent and magnitude of the halos depended on the concentration of primary community biomass, which in turn, was related to recruitment and refuge treatments. In general any treatment that concentrates focal community biomass (e.g., increasing recruits, or decreasing

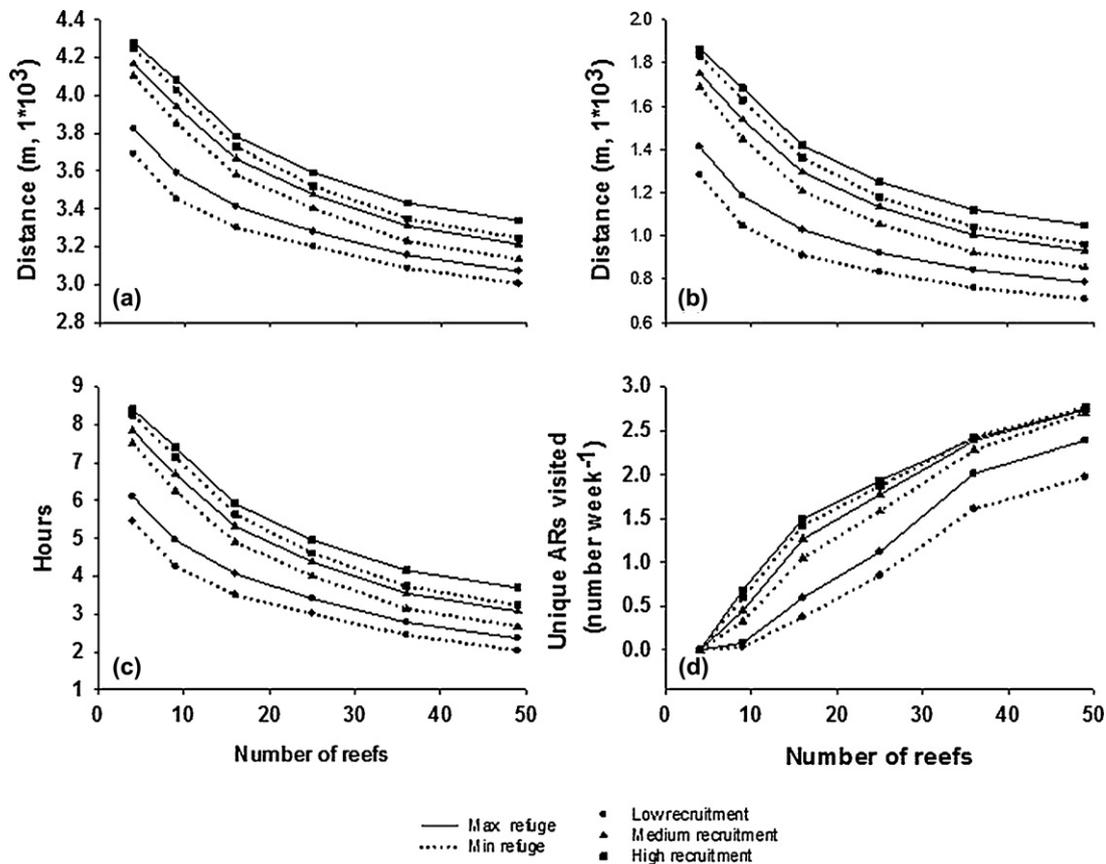


Fig. 10. Red snapper averaged (a) distance moved, (b) displacement, (c) hours spent off the reef during daylight, and (d) unique reefs visited with increasing number of reefs for the fixed-grid recruitment for the low, medium, and high recruitment levels and minimum and maximum refuge.

reef number) caused decreased prey biomass. Conversely treatments that dispersed individuals over a greater area reduced the impact on prey resources. Prey halos have been demonstrated to develop on small artificial reefs (Lindberg et al., 1990); however, evidence for their development on large artificial reefs is inconclusive. Recent measurements from an ongoing study in the Gulf of Mexico only detected obvious halos at one of four oil platforms for the prey communities utilized by red snapper (Daigle, 2011). However, lack of evidence of prey halos from the Daigle (2011) study may have been the result of sampling sufficiently to detect halos within the patchy spatial distributions typical of benthic communities.

Depending on the role played by reefs as refuge, the consequences of returning to a reef cell can be positive or negative. Under the minimum refuge assumption, the reef becomes a death trap because the movement rules concentrate biomass on the reef where distance-from-reef mortality is at a maximum and fishing and predation mortalities occur. Under the maximum refuge assumption, all sources except basal mortality were set to zero on the reefs. Investigation of the role of reefs as refuge relative to off-reef habitat is needed, particularly because reefs tend to concentrate biomass and possibly elevate fishing mortality (Powers et al., 2003). Movement rules applied in the model are simplistic in regards to predation because predation risk on or off the artificial reef is not considered as a factor in how an individual moves. The result is that high mortality, regardless of the source, results in lower competition and higher growth rates. In opposition to our model, many studies on the topic of predation risk have shown that behaviors such as food acquisition are frequently modified when predation risk increases and can result in decreased growth rates (Werner et al., 1983; Werner and Hall, 1988; Halpin, 2000). Most importantly it has been shown that habitats offering slower growth rates but lower predation risk are preferred over those with high predation risk at all levels of growth rates (Halpin, 2000). Future iterations of the model would benefit by inclusion of a function that is able to evaluate predation risk as well as growth simultaneously, rather than only evaluating growth.

Our alternative assumptions about recruitment (fixed-grid versus fixed-AR) affected red snapper responses to increasing number of reefs. If reefs not only provide habitat but also act as attractors for settling juveniles (fixed-AR recruitment), then increasing reefs results in almost continuous increases in red snapper biomass. More recruits could result from higher survival during and just after settlement (reef habitat effect), or from reefs acting as attractors and simply taking recruits from other areas, which over broad spatial scales, would redistribute rather than create new red snapper biomass. We can also envision a situation where our grids are so small that the same number juveniles settle onto the grid regardless of the number of reefs (fixed-to-grid recruitment); under this recruitment mode the model simulations showed rapidly leveling off red snapper biomass with increasing number of reefs.

Spatially explicit mortality was critical to our model results, and those were more impacted by the distance-from-reef mortality than by the predation mortality. We represent bluefish and jack similarly, and they had relatively small effects in our simulation experiments. Because they had the same movement parameters (Table 1), we could simply double bluefish abundance and eliminate jack or eliminate bluefish and double jack abundance to see if their effects were symmetrical. If bluefish and jack had the same effects, then we could have modeled them as a single predator species. Doubled jack had small effects on biomass (<10% different from baseline), but doubled bluefish resulted in a red snapper mean weight at age-5 of 4094 g ww versus 4608 in baseline and doubled jack resulted in an average red snapper abundance of 76,478 versus

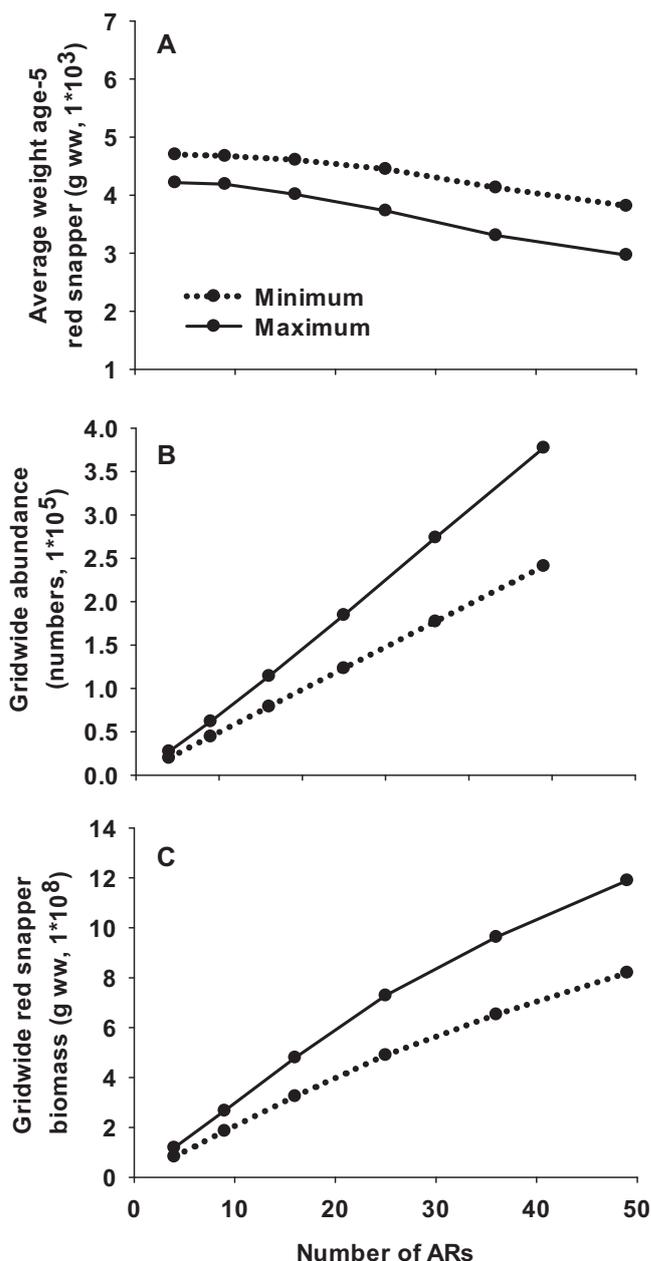
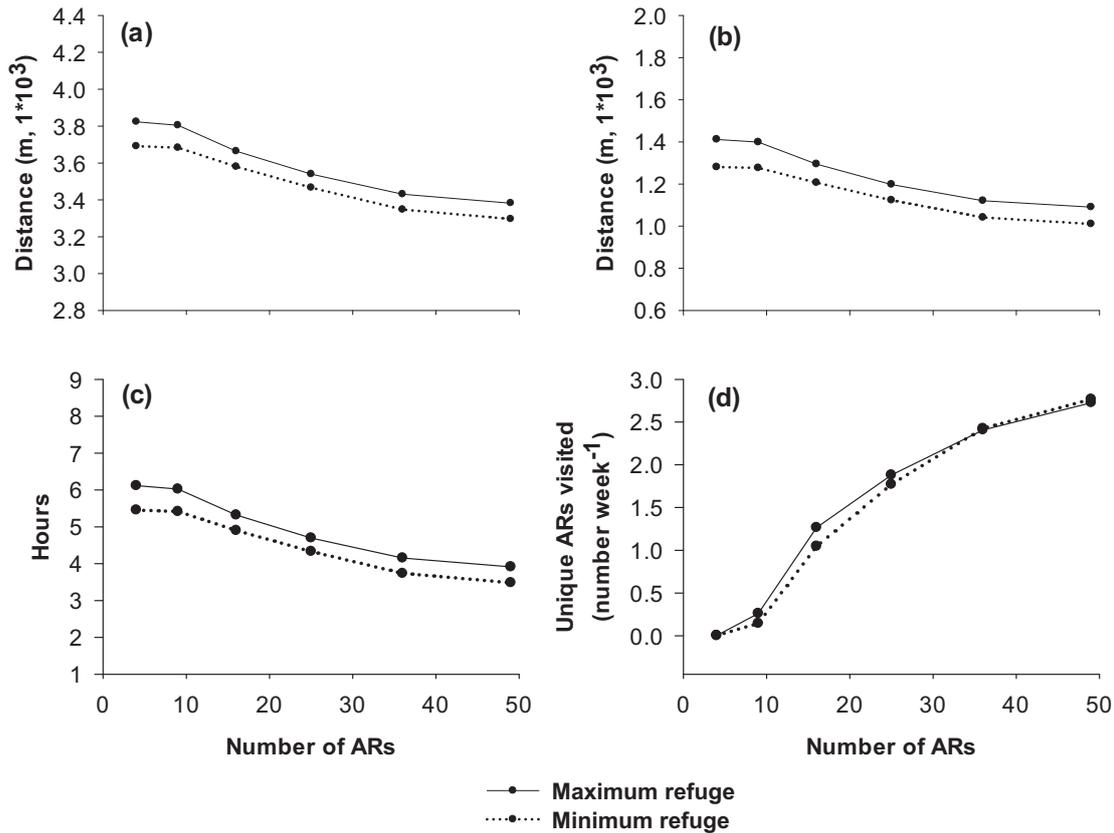


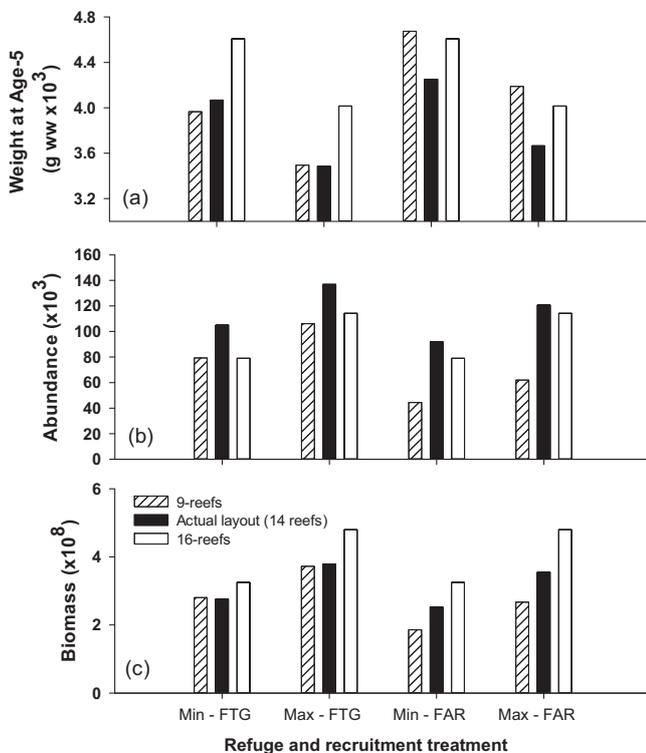
Fig. 11. Red snapper (a) average weight at age-5, (b) abundance, and (c) biomass with increasing number of reefs for the fixed-AR recruitment with minimum and maximum refuge.

79,008 in baseline. Thus, their effects were not identical but both had relatively small effects.

To explore the sensitivity of our results to stronger bluefish and jack predation, we made several additional simulations. We repeated the 4-reef, 16-reef, and 49-reef simulations from experiment 1 under fixed-grid (medium recruitment) and minimum prey refuge, but with bluefish and jack abundances increased 5-fold. As expected, mean abundances of red snapper were much lower than compared to the results of experiment 1: 13,726 versus 77,563 for 4-reefs, 13,856 versus 77,002 for 16-reefs, and 15,834 versus 76,532 for 49-reefs. Lower abundance resulted in higher mean weight at age-5 of red snapper under high predation (5402 g ww versus 2921 for 4-reef, 6522 g ww versus 4703 for 16-reef, and 7006 g ww versus 5585 for 49-reef). Average biomasses were similar between the high bluefish and jack predation and the lower predation levels in



**Fig. 12.** Red snapper averaged (a) distance moved, (b) displacement, (c) hours spent off the reef during daylight, and (d) unique reefs visited with increasing number of reefs for the fixed-AR recruitment with minimum and maximum refuge.



**Fig. 13.** Red snapper (a) average weight at age-5, (b) abundance, and (c) biomass for the real 14-reef layout and the 9-reef and 16-reef regularly spaced layouts (from simulation experiment 1) for the medium level fixed-grid recruitment and the fixed-AR recruitment, each with the minimum or maximum refuge.

experiment 1, and in both cases, increased with increasing number of reefs. Mean biomass of red snapper from 4 to 9 to 49 reefs under high predation increased from 23.8 MT to 28.1 MT to 36.7 MT versus 19.0 to 31.2 to 37.2 under experiment 1. The general result of higher red snapper biomass with increasing reefs was robust to higher predation by mobile piscivorous predators; however, different levels of predation and likely different mixes of predators will affect the magnitude of the increased biomass. As was pointed out earlier, the fitness movement algorithm optimized growth without taking into account predation risk. Hypothetically under increased predation risk (e.g., doubling predators in the model) foraging would be depressed and growth might decrease rather than increase. Comparison of model results which optimize either growth, lower predation risk, or both would be useful.

To explore the sensitivity of our results to stochasticity in the environment we made several simulations that allowed for variation on prey density, temperature, and distance mortality. Simulations were performed using uniform artificial reef configurations of 4, 16, and 36, fixed-to-grid recruitment, and no refuge conditions. For each individual, in every hour, each of the five prey densities, water temperature, and distance mortality were allowed to vary by drawing values for those parameters from folded-normal distributions with means set to the daily values and standard deviations then determined by the mean and assumed CV. We applied the normal deviate drawn to the prey density of the current cell location for each individual (assumed CV=20%), to the daily grid-wide temperature (assumed CV=5%), and to the instantaneous mortality rate experienced in the current cell location for each individual (assumed CV=20%). Model performance and results appear to be robust to environmental stochasticity and the effects of stochasticity weakened as more reefs were added to those simulations.

Modeling results showed that increasing the number of reefs generally produced higher biomass, but sometimes with smaller individuals and higher abundance, or with larger individuals and no change in abundance. Thus, more reefs are not simply better. Our modeling identified four major areas for further field data collection to refine the model and reduce the uncertainty in our predictions of the effects of increasing numbers of reefs. These are: the effects of reefs within a small area on juvenile settlement, quantification of prey halos to confirm model-generated levels of competition, measurement of predation risk in the vicinity of reefs, and the determination of the role of the reef as refuge. While such information needs may be apparent from common sense, the model provides a very specific framework for exactly what relationships are needed and then a quantitative method for scaling the pieces of information up to the population and simple community levels. Management strategies for determining the habitat-value of reefs in the Gulf of Mexico should consider the number of reefs and the local spatial layout of the reefs to ensure they are arranged close enough to allow for a high degree of dispersal of the red snapper among reefs, while far enough apart to avoid extensive overlap of prey halos. Additional data collection, with further model analyses, will provide more specific advice on the optimal number and distances between reefs. Finally, while the model is parameterized using species and habitats found from the Gulf of Mexico, the model is generally useful as an example of how to evaluate spatial patterns of habitat use, evaluating the use of fitness to incorporate behavior in models, incorporation of density dependent mechanisms of population control, and evaluation of methods to include predator-prey interactions in spatially explicit models.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2011.10.009.

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