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Integrated Monitoring and Stock Assessment of Spatially Heterogeneous Reef Fisheries

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UNIVERSITY OF MIAMI

INTEGRATED MONITORING AND STOCK ASSESSMENT OF SPATIALLY
HETEROGENEOUS REEF FISHERIES

By

William John Harford

A DISSERTATION

Submitted to the Faculty
of the University of Miami
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INTEGRATED MONITORING AND STOCK ASSESSMENT OF SPATIALLY
HETEROGENEOUS REEF FISHERIES

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Managing coral reef fisheries can be complicated by spatial heterogeneity in the distribution of fish and in the distribution of fishing activities. Improving reef fish sampling can be addressed by evaluating linkages between data and their subsequent uses in population assessment and fisheries decision-making. In this dissertation, integrated approaches to sampling and assessment of coral reef fisheries were developed using a spatially explicit individual-based simulation framework. The simulation framework was used to evaluate whether and how precision of spatially-stratified surveys influenced assessment and decision-making performance for a black grouper (*Mycteroperca bonaci*) fishery within the Florida Keys reef tract. The simulation framework was also used to evaluate whether a spatially explicit mark-recovery approach could accurately estimate exploitation status of a spiny lobster (*Panulirus argus*) fishery in Belize that is managed in conjunction with a no-take marine reserve. The former simulations emphasized the effects of spatial heterogeneity of fish on population assessment, while the latter simulations emphasized the effects of spatial heterogeneity of fishing activity. Simulations attributed breakdowns in fishery management to bias and precision of sampling, but also illuminated strategies for moving beyond these breakdowns by integrating sampling designs with assessment and decision-making.

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CHAPTER 1: INTRODUCTION

Data limitations are pervasive in fisheries management and may affect whether decision-making leads to achievement of management goals, such as fishery sustainability and population rebuilding. Typically, data limitations are thought of as a lack of yield and fishing effort histories, biomass indices, or age composition data; all of which are used in population assessment procedures (Hilborn & Walters 1992). However, when data are available, more subtle aspects of data bias and precision can affect how useful data are for informing fisheries management. In ecosystems where highly heterogeneous habitats affect fish distributions, sampling designs and data collection must account for this complexity; otherwise, evaluations of population status and responses to management actions are likely to be inaccurate (Jennings 2001, Gerber et al. 2003, 2007, Smith et al. 2011, Ault et al. 2013). Accordingly, where spatial data collection is aimed at informing fisheries management, sampling designs can be improved by considering linkages between data and their subsequent uses in population assessment and management decision-making (Olsen et al. 1999, Walters & Martell 2004, Houk & van Woesik 2013).

The goal of this dissertation was to develop integrated approaches to sampling and assessment of coral reef fisheries to improve management of fisheries operating in heterogeneous habitats. To achieve this goal, a spatially explicit individual-based model framework was constructed that incorporated interconnections between fish populations, their habitat, data collection, population assessment, and decision making. Individual-based models (IBMs or agent-based models) are used to simulate many individuals and keep track of their biological characteristics and locations. Several IBMs have been

previously developed to describe fish population dynamics (DeAngelis et al. 1991, van Winkle et al. 1998, Rose et al. 1999) and have sometimes been used to evaluate fisheries monitoring and assessment procedures (Codling 2008, McDonald et al. 2008, Miethe et al. 2009, Saul et al. 2012). Of the advancements made in describing fish population dynamics, IBMs that simulate areal distribution and movement of fish hold considerable potential for supporting evaluations of spatial aspects of fisheries management (Tyler & Rose 1994, Huse & Giske 1998, Railsback et al. 1999, Huse 2001). However, spatially explicit IBMs are only beginning to be used to evaluate monitoring designs for spatially-structured fish stocks (Thorson et al. 2012).

Applications of the IBM framework developed in this dissertation emphasized two contemporary challenges facing coral reef management. The first application was motivated by the observation that considerable effort in sampling design and data collection are necessary to achieve precise survey indices of fishes in coral reef habitats (Smith et al. 2011, Ault et al. 2013). But, how well fish survey designs translate into information that can accurately inform fisheries management is not as well established. Thus, simulation-based analysis was conducted to understand how survey precision influenced assessment and decision-making performance for a black grouper (*Mycteroperca bonaci*) fishery within the Florida Keys reef tract. In developing this application, two analytical studies were first carried out. In chapter 2, the temporal exploitation patterns of black grouper were quantified as a means to investigate the effects of harvesting long-lived and late-maturing fishes. In chapter 3, a statistical estimation procedure was used to reveal previously uncertain patterns of habitat use by grouper species within the Florida Keys reef tract and to demonstrate the applicability of

diver-based surveys for understanding occupancy patterns of coral reef fishes. In chapter 4, the black grouper simulation framework was used to evaluate how the precision of biomass surveys can affect management decision-making. The analysis emphasized interconnections between the collection of biomass survey data, assessment procedures, and decision-making to identify circumstances when achieving fisheries management objectives can be robust to survey imprecision.

The second application was motivated by the observation that marine reserves have become widely implemented, but that their use can lead to inaccuracies in population assessments unless spatially explicit sampling and assessment procedures are implemented (Hilborn et al. 2004, Punt & Methot 2004, Field et al. 2006, Ton 2013). In this application, the IBM framework was representative of the spatial dynamics of spiny lobster (*Panulirus argus*) at Glover's Reef Atoll, Belize. Glover's Reef Atoll is currently managed by a network of spatial regulatory zones, including a no-take reserve that covers approximately 20% of the atoll (Belize Fisheries Department 2013). Consequently, the spatial distribution of fishing effort is heterogeneous relative to the distribution of spiny lobster that are partially protected by a marine reserve. Thus, spatially explicit design considerations for monitoring and population assessment are needed (Gerber et al. 2005, 2007). In chapter 5, simulation analysis was used to evaluate whether a mark-recovery sampling design could be used to accurately estimate fishing mortality rates for a spiny lobster fishery managed in conjunction with a marine reserve.

Simulation studies that incorporate spatial heterogeneity in habitat configuration and in fish distribution, like those presented in this dissertation, are uncommon (Meester et al. 2004, Thorson et al. 2012). Where previous evaluations of spatial management

actions have been conducted, simulation-based approaches have typically represented coastal environments as one-dimensional linear arrays (Hilborn et al. 2006, Kellner et al. 2007, Ralston & O'Farrell 2008, McGilliard et al. 2011, Babcock & MacCall 2011). Conversely, the simulation framework developed in this dissertation emphasized two-dimensional contiguous habitat distributions as well as additional details of fish movement in relation to habitat availability and heterogeneity in the distribution of fishing activities. This design enabled the simulation framework to be aimed at evaluating how bias and precision of spatially explicit sampling and assessment procedures could lead to breakdowns in fisheries management. The simulation framework was also aimed at illuminating strategies for moving beyond management breakdowns through improved integration of sampling, assessment, and decision-making. Notably, the use of simulation frameworks to evaluate strategies for fisheries management that link spatially explicit sampling, assessment, and decision-making is only beginning to be explored (Sainsbury 1991, Meester et al. 2001, McDonald et al. 2008).

CHAPTER 2: A PROBABILITY-BASED APPROACH TO FISHERIES ASSESSMENT USING PER-RECRUIT ANALYSIS

Summary

A Bayesian approach to error propagation was demonstrated in which life history parameters of a fish population were simultaneously estimated from data and estimation uncertainty was carried through into the estimation of exploitation rates using Markov Chain Monte Carlo methods. This approach was used to conduct a stochastic per-recruit analysis to explore the exploitation characteristics of a black grouper, *Mycteroperca bonaci*, a long-lived and late maturing species. Probabilistic trade-offs between yield and biomass protection supported comparisons of current minimum harvest length regulations with alternatives derived from life history characteristics. Increases in minimum harvest length or decreases in fishing mortality rate had minor effects on long-term yield, while considerably improving spawning biomass protection. Life history characteristics formed the basis for discussing why fishes with low natural mortality rates and delayed maturation may be particularly vulnerable to overexploitation. This analysis contributed to the overall research goal by expanding a low-data assessment approach to include probability-based statements about important management quantities, rather than relying on simple point estimates. This chapter also contributed to the specification of temporal dynamics of a spatially explicit simulated fish population representative of black grouper.

Background

      Per-recruit analysis is a widely used analytical method in fisheries science for estimating equilibrium yield and biological status of a cohort based on a specified combination of minimum harvest size and fishing mortality rate (Beverton & Holt 1957, Quinn & Deriso 1999). Per-recruit analysis can be applied to the problem of identifying optimal size at first capture and harvest rate that will maximize yield, prevent resource declines below reproductive thresholds, or otherwise optimize economic value (Die et al. 1988, Quinn & Deriso 1999, Haddon 2011). In general, per-recruit analysis provides a basis for determining optimality-based management targets based on harvest size and rate, which can be contrasted against actual fishery behavior. To carry out per-recruit of analysis, only basic descriptions of growth and survival are required, which are typically obtained from statistical models. Given reliable estimates of demographic parameters, per-recruit analysis provides a tractable low-data solution for determining fishery management targets (Weyl & Banda 2005, Ault et al. 2009).

      Despite its simple input requirements, per-recruit analysis relies on predictions of growth and survival processes that are obtained from statistical models, but such predictions cannot be made with certainty. Several sources of uncertainty affect the prediction of quantities used in fisheries management. Process uncertainty arises from natural variation in biological processes and observation uncertainty arises from sampling and measurement error. Both of these types of uncertainties contribute to residual error between observed and predicted values. Further, parameter estimation uncertainty is a consequence of sampling and measurement error and a consequence of model misspecification (Francis & Shotton 1997, Peterman & Peters 1998, Peterman 2004,

Mangel 2006, Haddon 2011). Uncertainty can be propagated to per-recruit metrics using Monte Carlo-based methods (Restrepo & Fox 1988, Chang et al. 2009, Hart 2013). In Monte Carlo simulation, uncertain input parameters are described by probability distributions. By sampling the distributions of input parameters, probability distributions of derived parameters, such as per-recruit metrics, can be approximated.

Bayesian methods offer an alternative approach for moving beyond point-estimates to making probability statements about predicted quantities. Recent literature trends highlight the adoption of Bayesian methods in ecology and fisheries science (Walters & Ludwig 1994, McAllister & Kirkwood 1998, Wade 2000, Ellison 2004). But importantly, propagating uncertainty to derived quantities is not an intrinsically Bayesian or non-Bayesian concept and alternate approaches have been developed (Håkanson 1998, Lo 2005, Halpern et al. 2006). This analysis falls under the Bayesian paradigm because probability statements take the form of posterior probability distributions that are estimated using prior distributions, observed data, and the mathematical rules of conditional probability (Ellison 1996).

The objective was to apply a Bayesian approach to uncertainty propagation in per-recruit analysis and to illustrate how low-data stock assessment methods can be extended to include probability statements about management quantities of interest. The Bayesian per-recruit analysis was applied to an investigation of the life history and exploitation characteristics of black grouper, *Mycteroperca bonaci*. Black grouper is widely distributed within the western Atlantic, but is commonly found within waters adjacent to the Florida Keys (Randall 1967, Smith et al. 1975, Bullock & Smith 1991). Black grouper is not currently deemed to be overfished or experiencing overfishing (SEDAR

2010a), but some evidence suggests otherwise (Ault, Smith, et al. 2005). The effects of harvesting on black grouper are of interest given its growth characteristics and because the current minimum harvest length (610 mm or 24 inches) appears to allow for the harvest of immature individuals. Black grouper in Florida waters attain maturity with a probability of 0.5 at a total length of 833 mm (33 inches; age ~6). Harvesting individuals before they have had a chance to reproduce is concerning because of the vulnerability of this near-shore species to open-access recreational fisheries (Coleman et al. 2004, Ault et al. 2009, 2013, McClenachan 2013). A Bayesian per-recruit analysis was used to determine the probabilistic trade-offs between yield and biomass protection. Probability statements supported comparisons between current minimum harvest length and alternatives derived from life history characteristics. Finally, sensitivity to assumptions about survival on calculation of per-recruit metrics was investigated.

Methods

Statistical models of black grouper life history

A collection of 2,141 individual length-otolith pairings, utilized in the 2010 assessment of the Gulf of Mexico and south Atlantic stocks were used in this analysis (Crabtree & Bullock 1998, SEDAR 2010a). Sectioned otoliths were aged by personnel from the Florida Fish and Wildlife Research Institute (O'Hop & Beaver 2009, SEDAR 2010a). Black grouper total lengths ranged from 26 mm (age 0 years) to 1518 mm (age 25 years), and the maximum observed age in the dataset was 33 years. Ten percent of the samples were aged to be older than 14 years. Fishery-dependent and fishery-independent sources contributed 70% and 30% of the samples, respectively. Of the fishery-dependent

samples, 96% were obtained from commercial gears. Data on length-at-maturity (n=260) and length versus whole weight (n=852) were available from Crabtree and Bullock (1998) and from the 2010 assessment (SEDAR 2010a). Only samples collected between January and March were used to estimate female length-at-maturity; this coincides with the period just prior to the onset of spawning within the south Atlantic region (O'Hop & Beaver 2009, SEDAR 2010a). Female maturity status was based on histological examinations reported in Crabtree and Bullock (1998).

Somatic growth was assumed to follow the von Bertalanffy growth function (von Bertalanffy 1938), $L_i = L_\infty \left(1 - \exp\left[-K\left(t_i - t_0\right)\right]\right)$, where L_i is length at age t_i for observation i, L_∞ is asymptotic length, K is the Brody growth coefficient, and t_0 is the theoretical age at which length equals zero. Error variance was assumed to follow a truncated normal distribution, with log-likelihood function ($\log \Lambda$):

$$\log \Lambda = \sum_i \log\left(\frac{1}{\sigma\sqrt{2\pi}} \exp\left\{-\frac{1}{2\sigma^2}(L_i - \hat{L}_i)^2\right\} \middle/ \left\{1 - \Phi((MIN_i - \hat{L}_i)/\sigma)\right\}\right), \qquad (2.1)$$

where $\hat{L}_i$ and σ are location and scale parameters, respectively, MIN_i is the minimum length limit assigned to observation i, and Φ denotes the cumulative density function of the standard normal distribution. The truncated normal distribution was used because it is useful in accounting for truncated length-at-age observations that arise from fishery-dependent sources that are subject to minimum size restrictions (Diaz et al. 2004; SEDAR 2006, 2010a,b). Fishery-dependent samples were assigned minimum length limits in accordance with state and federal regulations at the time of collection (SEDAR 2010a). Fishery-independent samples were assigned a minimum harvest length value of

zero (Diaz et al. 2004). Maturity was modeled for females only, as all males were assumed to be mature and transition from mature females. The smallest mature female was 565 mm, and largest immature female was 938 mm. Female maturity was modeled using logistic regression with proportion mature specified as

$$Mat(L_i) = \frac{1}{1 + \exp(-\kappa(L_i - L_{\mathrm{Mat}}))}, \text{ where } L_{\mathrm{Mat}} \text{ is the length at which black grouper}$$

attain maturity with a probability of 0.50. Length-whole weight conversion followed an allometric function ($W_i = a_W L_i^{b_W}$) with lognormal error variance.

A Bayesian approach was used to fit life history functions using the software OpenBUGS (Lunn et al. 2009). Diffuse priors were specified for all life history parameters and for error variances of growth and length-weight functions. Parameters for each life history model were evaluated to determine whether the Markov chain Monte Carlo (MCMC) algorithms converged on their target distributions. Convergence was checked for all model parameters against Geweke and Gelman-Rubin convergence criteria (Geweke 1992, Congdon 2003, Gelman et al. 2004). After discarding an initial burn-in period of 50,000 iterations, diagnostic tests indicated convergence and approximations of posterior distributions were based upon a subsequent 50,000 iterations from two parallel chains, for a total of 100,000 simulated draws.

Per-recruit analysis

Per-recruit calculations were specified similar to the formulation of Thompson and Bell (1934). The abundance equation was

$$N_t = N_{t-1} \exp(-(M_{t-1} + F_{t-1})), \tag{2.2}$$

where M_t is natural mortality, F_t is fishing mortality, N_t is abundance at age, t, and the age interval was specified as one year. At each age interval, fish age was converted to length and used to perform subsequent calculations. Selectivity was knife-edge, thus, fishing mortality rate, F_t, was constant for all lengths equal to or greater than a specified minimum length restriction. The number of deaths attributed to fishing, or yield in numbers, Y_t^N, was calculated :

$$Y_t^N = \frac{F_t}{M_t + F_t} N_t (1 - \exp(-(M_t + F_t))).$$ (2.3)

The yield equation is known as the Baranov catch equation and was also explored by Beverton and Holt (1957). Yield-per-recruit in weight (Y^W/R) was calculated as

$$Y^W/R = \frac{\sum_t Y_t^N W_t}{N_r}.$$ (2.4)

Yield-per-recruit was the expected total yield over the fishable life span of a cohort scaled to annual recruitment (Quinn & Deriso 1999). Weight (W_t) was calculated from predicted length and N_r is the number of recruits at age 1. The maximum age included in the analysis was 33, reflecting the oldest available age estimate for black grouper.

Since the per-recruit analysis included both juveniles and adults of this long-lived species, a single estimate for natural mortality was biologically unreasonable. Thus, natural mortality schedules for juveniles and adults were specified as an inverse function of length (Lorenzen 1996, SEDAR 2010a):

$$M_t(L_t) = M_{\text{Ref}} \frac{L_{\text{Ref}}}{L_t}$$ (2.5)

where M_{Ref} is the reference mortality rate at a specified reference length, L_{Ref}. An inverse relationship between mortality and body size is established among fish populations (Lorenzen 1996, 2000). M_{Ref} was scaled so that average lifetime natural mortality (M_{Avg}) was 0.140 year^{-1}, which was obtained using Alagaraga's (1984) maximum age method and assuming that 1% of all individuals achieved a longevity of 33 years. Reference length, L_{Ref}, was set equal to L_{Mat}.

Of interest in the analysis was the extent to which biomass was protected, given the specified management measures. Spawning-biomass-per-recruit (*SBR*) was calculated

$$B^s\Big/R = \frac{\sum_t N_t W_t \mathrm{Mat}_t}{N_r}, \tag{2.6}$$

where W_t and Mat_t are functions of predicted length at age t. Because black grouper is a protogynous hermaphrodite (Crabtree & Bullock 1998), spawning biomass was calculated as the sum of both sexes, rather than for females only. Brooks et al. (2008) demonstrated that when the dynamics of fertilization are not explicitly accounted for in an assessment procedure, including both sexes in estimates of biological reference points more closely approximates the true values than when only females are included. Spawning potential ratio, SPR, was also calculated and used as a proxy for spawning-biomass-per-recruit. SPR is the expected lifetime spawning biomass per-recruit of an exploited cohort scaled relative to that of an unexploited cohort (Goodyear 1993, Restrepo & Powers 1999).

Per-recruit calculations depended on statistical models of several life history characteristics whose parameter estimates were considered uncertain:

(i) von Bertalanffy growth – parameters K, L_∞, t_0 ;

(ii) Weight conversion – parameters a_W and b_W ;

(iii) Logistic maturity – parameters κ and L_{Mat}

(iv) Mortality-at-length – parameters $L_R = L_{\mathrm{Mat}}$.

In addition, predicted values were subject to residual error variance of the von Bertalanffy growth model and the length-weight conversion model. The statistical models describing (*i*) von Bertalanffy growth, (*ii*) weight conversion, and (*iii*) logistic maturity, were fit simultaneously using the same MCMC chains, but with separate log-likelihood functions. Log-likelihood functions were specified using the syntax of the OpenBUGS programming language as truncated normal, log-normal, and Bernoulli for von Bertalanffy, weight conversion and logistic maturity, respectively. Uncertainty in parameter estimates was quantified by posterior sampling. MCMC simulation iteratively produces vectors, $\boldsymbol{\theta}$, of all estimated parameters. A sample of the target posterior distribution consisted of a large number of successive MCMC iterations, which were summarized graphically and through simple statistics such as the posterior means of each parameter. Per-recruit metrics that were functions of estimated life history parameters were concurrently calculated from the simulated parameter vectors (Ntzoufras 2009).

The stochastic per-recruit analysis was also used to calculate probabilities pertaining to biomass protection (Fig 2.1). As a proxy for spawning biomass, SPR values between 0.2 and 0.4 have previously been assumed as thresholds for biomass protection for reef-associated fishes like black grouper (Ault, Bohnsack, et al. 2005). Selection of an appropriate biomass threshold depends on the life history of the species and knowledge of recruitment processes. Here, SPR threshold $= 0.3$ was selected to be as consistent as

possible with actual management reference points (SEDAR 2010a). The probability of SPR falling below the SPR threshold was approximated by the functions

$$D_j = \begin{cases} 1, & \text{if SPR}_j < 0.3 \\ 0, & \text{otherwise} \end{cases} \tag{2.7}$$

where D_j is an indicator function that is calculated for T total MCMC iterations, and

$$\Pr(SPR < 0.3) = \frac{\sum\limits_{j=1}^{T} D_j}{T} \tag{2.8}$$

Sensitivity to average lifetime natural mortality rate

Per-recruit analysis is sensitive to assumptions made about natural mortality. In the initial per-recruit analysis, average lifetime mortality (M_{Avg}) was calculated using Alagaraga's (1984) approach and assuming that 1% of individuals achieved the maximum age. Sensitivity analysis was conducted by making two alternative assumptions about natural mortality rate that was specified in the per-recruit analysis. First, an alternative estimate was based on the assumption that 5% of individuals achieved age 33, which resulted in $M_{Avg} = 0.090$ yr^{-1}. Estimates of M_{Avg} based on Alagaraga's (1984) approach were similar to estimates obtained using Hoenig's (1983) longevity-based estimators that ranged between $0.126 - 0.136$ yr^{-1}. Second, an alternative estimate was made using the approach developed by Pauly (1980) that relies on von Bertalanffy growth parameters, which resulted in a much higher natural mortality rate of 0.240 yr^{-1}.

Results

Statistical models of black grouper life history

Life history models converged on their target distributions and samples from each chain were considered sufficient to approximate posterior distributions. The von Bertalanffy growth model produced an asymptotic length, L_∞, of 1360 mm and a Brody growth coefficient, K, of 0.137 year^{-1}. Centered 95% ranges of predicted lengths-at-age were consistent with observed variation in length-at-age, with the exception of the oldest age classes for which only a small number of observations were available (Fig. 2.2A). Maturity-at-length and length-weight functions produced good fits to the data (Fig. 2.2B&C). The inflection point for female maturity-at-length (i.e. maturation probability of 0.5) was $L_{\mathrm{Mat}} = 832.7 \pm 15.1$ mm. Parameters of the allometric length (mm) to weight (kg) conversion were $a_W = 4.46 \times 10^{-9}$ and $b_W = 3.18$.

Per-recruit analysis

Growth overfishing is defined as harvesting fish below their optimal length at first capture, which reduces long-term yield (Haddon 2011). At the current minimum harvest length of 610 mm, growth overfishing is illustrated across a range of fishing morality rates approximately >0.1 yr^{-1} (Fig. 2.3). Lost yield potential could be addressed by increasing minimum allowable harvest length. To this end, changes in minimum harvest lengths were explored corresponding to different fishing mortality rates. Fishing mortality rates corresponded to (*i*) the rate that would produce an SPR of 0.30 ($F_{0.3SPR}$; minimum harvest length 610 mm), (*ii*) M_{AVG}, (*iii*) an arbitrarily low value (*F*=0.050) and (*iv*) a high value (*F*=0.600) estimated by Ault et al. (2005) for black grouper in Florida waters. For each fishing mortality rate, the percent increase in yield was

calculated between the current minimum harvest length (610 mm) and two alternatives. These two alternatives were the length at which black grouper attain maturity with a probability of 0.50 (833 mm on average) and the optimal minimum length at which yield-per-recruit in weight is maximized for each specified fishing mortality rate (Table 2.1). Despite current sub-optimal harvest lengths, only modest changes in yield-per-recruit of -3.0% to +6.4% were predicted across fishing mortality rates, with the exception of F=0.600. (Table 2.1).

In contrast to the modest changes in yield per recruit, changes to fishing mortality and minimum harvest lengths produces more notable changes to predicted SPR. Increasing minimum harvest length to length at 50% maturity or to optimal minimum length at each fishing mortality rate increased SPR between 0% and 540.8%. Under the current minimum harvest length, relatively small increases in fishing mortality rate caused considerable increase in the probability of SPR falling below the SPR threshold (Table 2.2 & Fig. 2.4). For instance, a modest increase in fishing mortality from a target of $F_{0.3SPR} = 0.125$ to $F_{MAvg} = 0.140$, only reduces mean SPR from 0.31 to 0.28, but creates a two-fold increase in the probability that SPR is below the chosen threshold.

Sensitivity to average lifetime natural mortality rate

Alternative assumptions about natural mortality modified the expected unfished age-structure, the SPR relationship with fishing mortality, and consequently the fishing mortality required to reduce SPR below an acceptable threshold (Fig. 2.5). Modifying M_{Avg} affected the fraction of the population expected to reach maturation and to reach the oldest age-class included in the analysis (Fig 2.5A, B, & C). Increases in M_{Avg} shifted the SPR curve, suggesting that correspondingly higher fishing mortality rates

could be sustained before undesirable spawning stock thresholds would be reached.

Conversely, reducing M_{Avg} produced SPR curves that suggested the population was of

increased vulnerability to exploitation (Fig. 2.5D). Natural mortality is often used in the

context of establishing fishing mortality benchmarks. For each alternative M_{Avg}, the

probability of SPR falling below the SPR threshold was calculated when fishing mortality

was set equal to the assumed M_{Avg}. For the minimum length restriction of 610 mm, the

initial per-recruit analysis ($F = M_{Avg} = 0.14$) had a high probability of SPR falling

below the threshold ($\Pr(SPR < 0.3) = 0.80$). A probability of 0.87 was obtained for SPR

falling below the threshold when $F = M_{Avg} = 0.240$. Conversely, the probability of

spawning biomass decline was 0.03 when $F = M_{Avg} = 0.090$.

Discussion

     A Bayesian approach to uncertainty propagation was used to conduct a stochastic

per-recruit analysis for black grouper. This approach utilized a Markov chain Monte

Carlo method for numerical sampling. The sampling routine fits all life history models

(e.g. growth, maturity, length-weight conversion) simultaneously, but with separate

likelihoods. Through an iterative process in the software OpenBUGS, samples from

posterior distributions of all life parameters were obtained at each sampling iteration

(Lunn et al. 2012). Per-recruit metrics were then calculated from all life history

parameters. This process was repeated over many iterations to approximate the

uncertainty associated with per-recruit metrics (Fig 2.1). Arguably, implementing a

Bayesian approach within a unified numerical framework may be less cumbersome than a

Monte Carlo routine that requires separate estimation of each statistical model, assignment of probability distributions to life history parameters, and then the use of a numerical routine to iteratively calculate per-recruit metrics. The Bayesian approach has the advantages of automatic inclusion of uncertainty in estimation of life history parameters and direct propagation of uncertainty to per-recruit metrics.

Current harvest length restrictions for black grouper in U.S. waters include multispecies commercial trip limits, recreational bag limits, gear restrictions, and protected areas (FKNMS 1997, SEDAR 2010a). Therefore, the effects of changes to length-based regulations on exploitation patterns can most reasonably be explored in the context of concurrent controls on fishing mortality. Fisheries regulated through the combined use of minimum harvest length restrictions and harvest rate restrictions are well suited for investigation using per-recruit analysis. Under the current minimum harvest length, a striking contrast between yield and biomass protection was predicted for changes in fishing mortality rate (Fig. 2.4). Small changes in fishing mortality rate, say from $F_{0.3SPR} = 0.125$ to $F_{Mavg} = 0.140$ had a negligible effect on long-term yield-per-recruit, but had a considerably larger effect on the probability of SPR falling below the chosen SPR threshold (Fig. 2.4). The evidence for this effect can be seen by comparing the rapidly descending limb of the SPR curve to the reasonably flat yield-per-recruit curve within proximity to fishing mortality rates near $F_{0.3SPR}$ (Fig. 2.4). This result reaffirms the common finding in analytical fisheries models that reducing fishing mortality will have minor effects on long-term yield, but will considerably improve biomass protection (Hilborn 2010, Hilborn & Stokes 2010).

The per-recruit analysis revealed that under the current minimum harvest length of 610 mm, only a narrow range of fishing mortalities would result in low or moderate probability of spawning biomass depletion below the specified threshold. This finding is important for fisheries management for two reasons. First, incorporating uncertainty in life history parameters revealed that implementing a management target, for example of $F_{0.3SPR} = 0.125$, could result in SPR that deviates from the expected target because of uncertainty associated with parameter values used in the calculations (Fig. 2.4). Second, the analysis emphasized the importance of accurate estimation of actual long-term average fishing mortality rate. If fishing mortality is estimated unreliably and particularly if it is subtly underestimated, overly optimistic advice about the current state of the fishery could result and lead to the false perception that management targets are being adequately met. Further, it is unlikely that fishing mortality can be controlled with sufficient precision in proximity to an optimal rate (say $F_{0.3SPR}$).

Probability-based statements about biomass protection reinforced the expectation that long-lived and late maturing fishes are generally vulnerable to becoming overfished at low levels of fishing mortality. That long-lived species require conservative management approaches can also be demonstrated through well-established theoretical and correlative evidence about relationships between natural mortality and reproductive investment. Theoretical work has suggested that natural mortality should be proportional to reproductive investment-per-unit-time (Charnov 1993, 2007, Jensen 1996). This proportionality has also been shown to be optimal in terms of an energy investment trade-off between growth and reproduction (Lester et al. 2004). Since natural mortality is lower in long-lived species, correspondingly low reproductive investment per unit time may

also be expected (Hoenig 1983, Lester et al. 2004). Low-reproductive investment per-unit-time, that results in many reproductive events over a long life, may confer an evolutionary advantage over life strategies consisting of one or few spawning events when there is considerable survival variability in early life stages (Murphy 1968). This theory is supported empirically by correlative evidence from fisheries science involving interrelationships between natural mortality, recruitment compensation, recruitment variability, and life history parameters that have been examined for determining fishing mortality reference points (Mace 1994, Rose et al. 2001, Beddington & Kirkwood 2005, Hutchings et al. 2012, Zhou et al. 2012).

Consequently, long-lived fishes may require management interventions that not only allow individuals to reach maturity, but to reproduce a sufficient number of times to enable replacement of spawning biomass. Common advice for fisheries management has been to allow fish to spawn at least once before capture (Walters & Martell 2004). Allowing contributions to the production of new recruits over more than one spawning opportunity appears to be an important management consideration for long-lived species like black grouper, but is at odds with current minimum length restrictions that are below benchmarks for length at maturation. However, a caveat to this conclusion is that release mortality or discard mortality associated with capture of undersized fish was not investigated and needs to be addressed before it is clear how changes in minimum harvest length will affect long-term yield and biomass protection. Optimistically, fishing mortality for black grouper appears to have stabilized during the past decade, and the current fishing mortality estimate is in proximity to the estimated $F_{0.3SPR}$ benchmark (SEDAR 2010a). Less optimistically, for many reef fishes, debate remains about whether

current fishing mortality rates can be kept at sustainable levels or reduced where already necessary, given the vulnerability of these near-shore fishes to the open-access nature of recreational fisheries (Coleman et al. 2004, Ault et al. 2009, 2013, McClenachan 2013).

Many harvested fishes within warm-temperate and tropical waters of the U.S. Atlantic are managed as a grouper-snapper complex. Several species in this complex are considered vulnerable to exploitation because they are long-lived and have late maturation schedules, including black grouper (Coleman et al. 2000, Ault, Bohnsack, et al. 2005, Ault, Smith, et al. 2005). Further, many members of this complex appear to be declining towards abundance thresholds that may compromise continued provision of ecosystem services (Ault, Bohnsack, et al. 2005, Ault et al. 2008, 2009). Concern that many grouper species are vulnerable to exploitation is global; and indeed, delayed maturation can contribute to declining abundance because reproductive success is inevitably reduced when management measures permit capture prior to maturation (Sadovy de Mitcheson et al. 2013).

Table 2.1. Yield-per-recruit (Y^W/R ; kg) predicted for fishing mortality and minimum harvest length. Optimal minimum length refers is the length at which yield-per-recruit is maximized for a given fishing mortality rate, $\Delta Y^W/R$ is the percent change in yield-per-recruit predicted relative to the current minimum length, $F_{0.3SPR}$ is fishing mortality producing spawning potential ratio of 0.3, and $F_{MAvg}=M_{Avg}= 0.14$ yr^{-1}.

Fishing mortality scenarios		Current minimum length		Length at 50% maturity			Optimal minimum length		
Description	Value	Length (mm)	Y^W/R	Length (mm)	Y^W/R	$\Delta Y^W/R$ (%)	Length (mm)	Y^W/R	$\Delta Y^W/R$ (%)
Low	0.050	610	1.31	833	1.27	-3.0	620	1.31	0.0
$F_{0.3SPR}$	0.125	610	1.86	833	1.95	5.0	790	1.95	4.9
F_{Mave}	0.140	610	1.89	833	2.01	6.4	810	2.01	6.3
High	0.600	610	1.85	833	2.40	32.1	970	2.57	42.2

Table 2.2. Spawning potential ratio (SPR) predicted for four fishing mortality levels (rows) and three minimum harvest lengths. Current minimum harvest length is 610 mm, length at 50% maturity is 833 mm, and optimal minimum length corresponds to the length at which yield-per-recruit is maximized for each fishing mortality rate. ΔSPR is the percent change in SPR relative to the current minimum length, $F_{0.3SPR}$ is fishing mortality rate that produces SPR=0.3 under the current minimum harvest length, $F_{Mavg}=M_{Avg}=0.14$ yr^{-1}, Prob. is the probability that SPR<0.3.

Fishing mortality		Current minimum length			Length at 50% maturity				Optimal minimum length			
Description	Value	Length (mm)	Mean *SPR*	Prob.	Length (mm)	Mean *SPR*	Prob.	ΔSPR (%)	Length (mm)	Mean *SPR*	Prob.	ΔSPR (%)
Low	0.050	610	0.58	0.00	833	0.65	0.00	13.5	620	0.58	0.00	0.0
$F_{0.3SPR}$	0.125	610	0.31	0.41	833	0.42	0.00	36.6	790	0.39	0.00	28.2
F_{Mave}	0.140	610	0.28	0.80	833	0.39	0.00	42.0	810	0.37	0.00	36.4
High	0.600	610	0.04	1.00	833	0.14	1.00	259.7	970	0.25	0.88	540.8
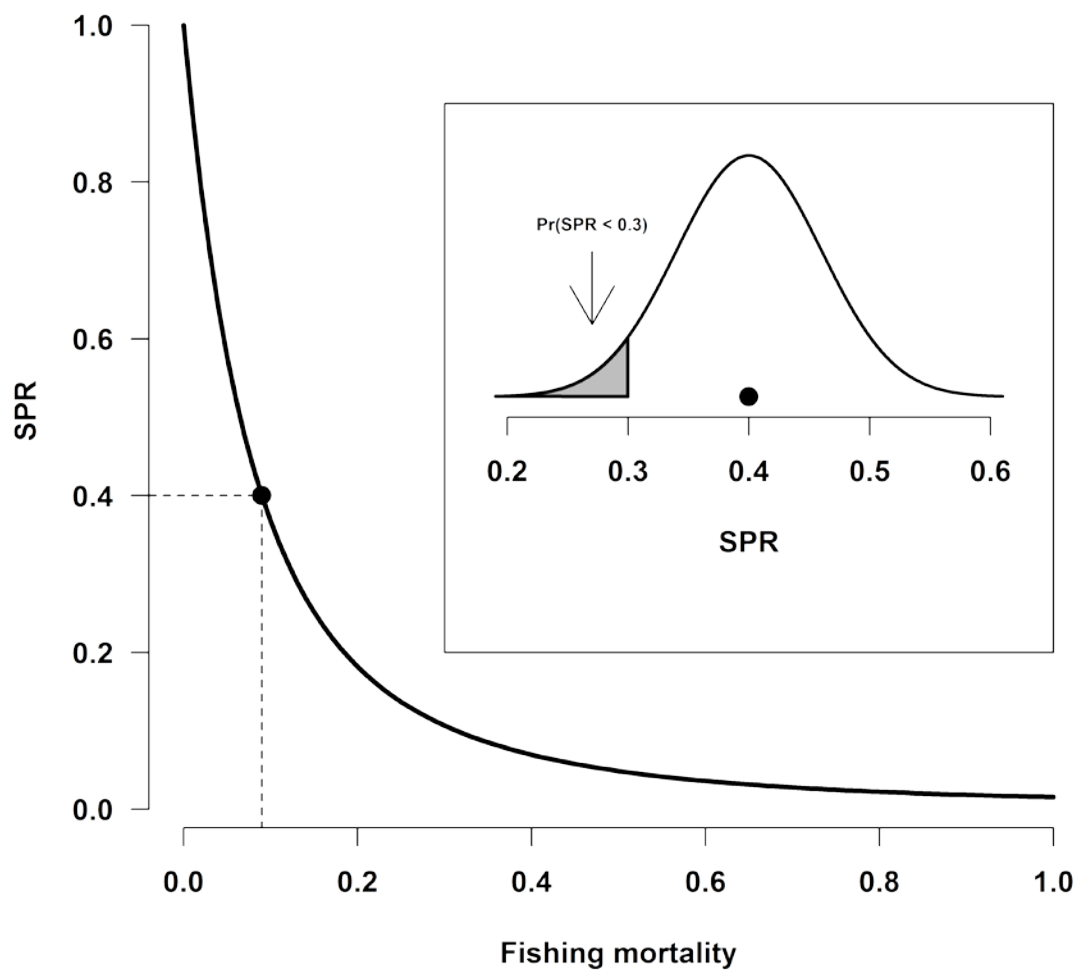
Figure 2.1. Spawning potential ratio (SPR) with respect to fishing mortality rate (year^{-1}). Dashed lines indicate fishing mortality rate corresponding to SPR of 0.4. Inset: probability distribution SPR with mean 0.4, shaded area shows area of the probability distribution falling below arbitrary SPR threshold 0.3.
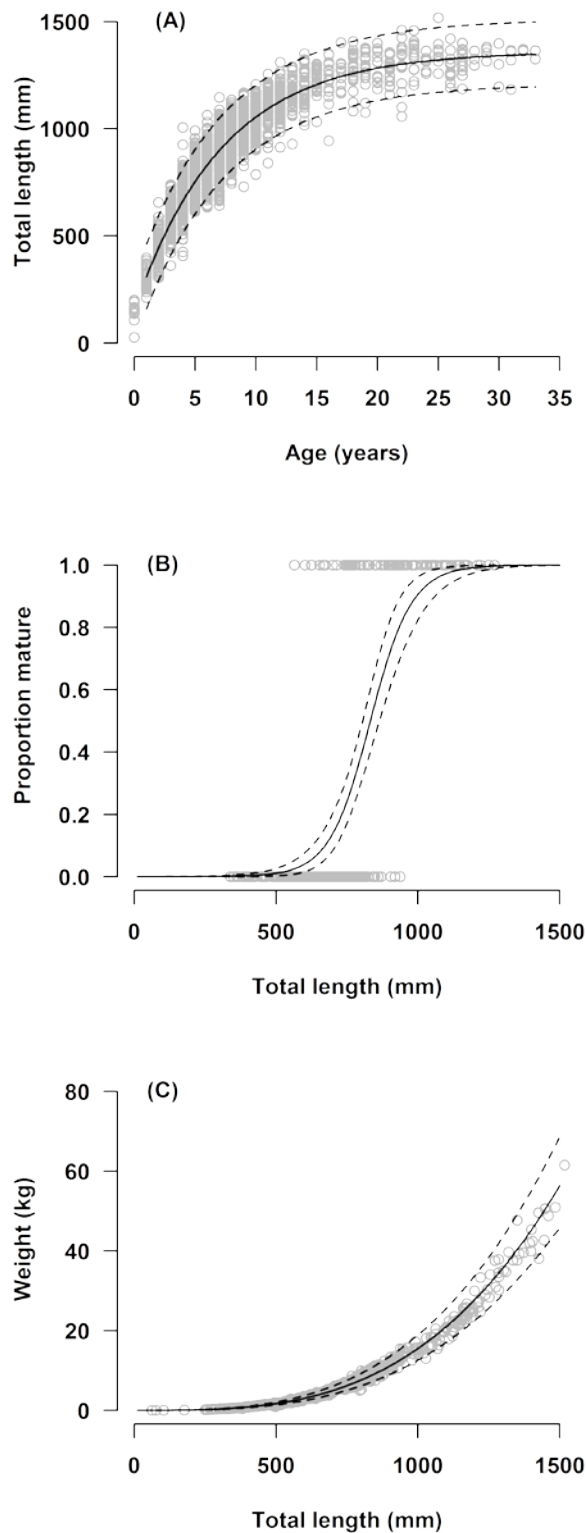
Figure 2.2. von Bertalanffy growth (A), maturation proportion (B) and whole weight (kg) (C) functions for black grouper *Mycteroperca bonaci*. Solid lines are mean responses, dashed lines are 95% credible intervals, and open circles are observed data.
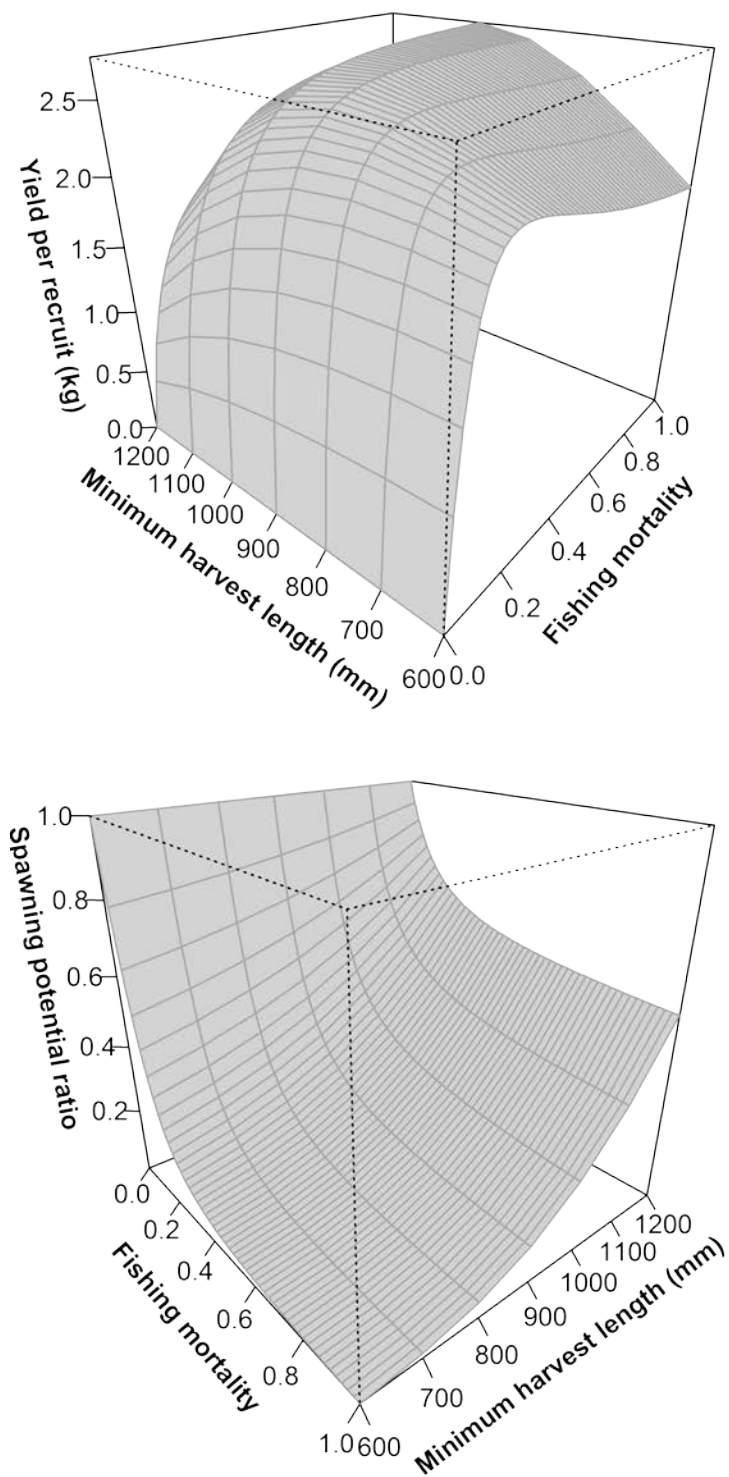
Figure 2.3. Surface plots of mean yield-in-weight-per-recruit (top panel) and spawning potential ratio (bottom panel) against fishing mortality rate and minimum harvest length.
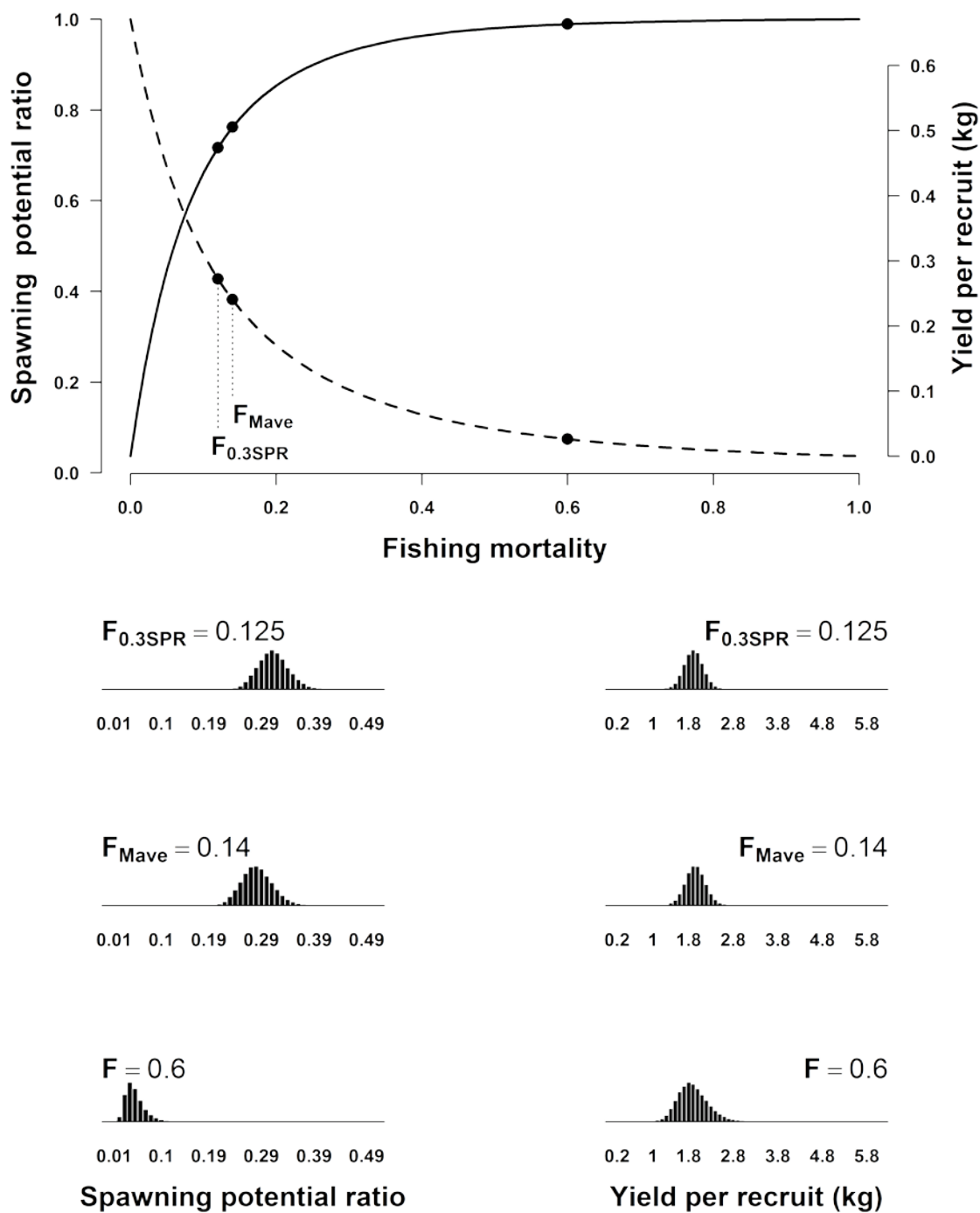
Figure 2.4. Yield-per-recruit in weight (kg) and spawning potential ratio relative to fishing mortality (year^{-1}). Curves calculated using a minimum harvest length of 610 mm (top panel). Histograms of uncertainty associated with yield-per-recruit and spawning potential ratio at fishing mortality rates of 0.125, 0.140, and 0.600.
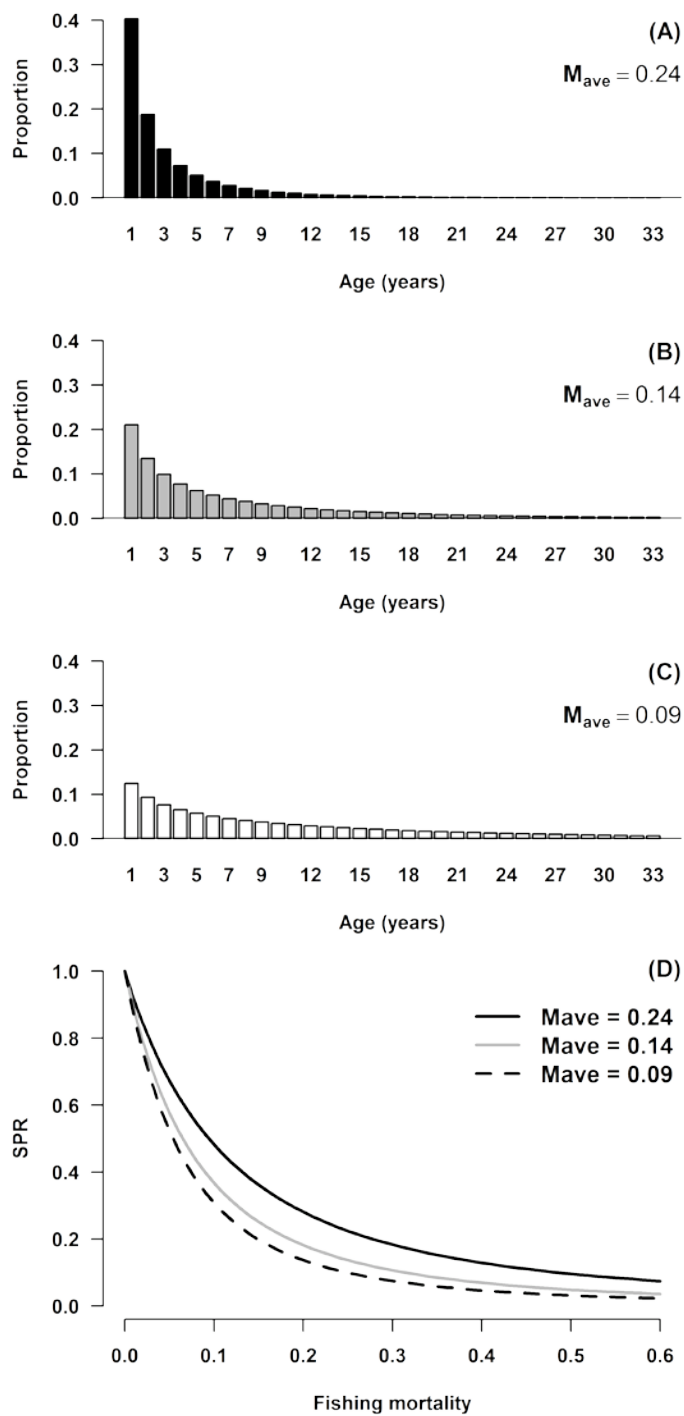
Figure 2.5. Unfished age structure (A, B & C) calculated under alternative assumptions about average lifetime natural mortality rate (M_{Avg}). Spawning potential ratio (*SPR*) with respect to fish fishing mortality rate (year^{-1}) for minimum allowable harvest length of 610 mm (D).

CHAPTER 3: SPATIALLY-STRATIFIED REEF-FISH SURVEYS REVEAL CROSS-SHELF HABITAT USE IN THE FLORIDA KEYS REEF TRACT

Summary

Occupancy patterns of pre-exploitation sized black grouper (*Mycteroperca bonaci*) and red grouper (*Epinephelus morio*) within the Florida Keys reef tract were quantified using data from a diver visual survey that was implemented using a stratified random sampling design. Stratification was based on cross-shelf coral reef formation types and afforded the opportunity to evaluate whether site-scale occupancy patterns varied among strata. Among-strata variation in occupancy responses to physical environmental features was quantified using a mixed effects zero-inflated binomial statistical model. Four main findings were supported by the analysis. First, excess observations of non-detection (zero inflation) led to uncertainty about the effect of substrate vertical relief on occupancy responses. Second, red grouper occurrence probability was higher in nearer-to-shore patch reefs than in offshore fore reefs, indicative of a cross-shelf distribution gradient. Third, black grouper occurrence probability demonstrated a latitudinal gradient that appeared to support the Dry Tortugas and lower Florida Keys as potentially important recruitment sources. Fourth, black grouper occurrence responses to depth gradients varied among reef strata, suggesting speculatively that depth correlations may be overly simplistic surrogates for more complex ecological responses. These findings improved upon previous descriptions of pre-exploitation sized red grouper and black grouper distributions, which have been mainly qualitative. Findings were incorporated in the development of a spatially explicit individual-based simulation model of grouper distribution in the Florida Keys reef tract.

Background

Central in importance to understanding habitat requirements of substrate-associated fishes is uncovering spatial scales that connect environmental patterns to biological patterns (Turner 1989, Wiens 1989, Levin 1992). The spatial scales at which environmental processes shape fish distributions have been studied occasionally through multi-scale observation and modeling approaches. In freshwater riverine ecosystems, fish distributions can be described in relation to nested spatial hierarchies of environmental characteristics from watershed-scale climate patterns, to catchment-scale drivers of surface runoff and stream flow, and to stream-scale substrate characteristics (Harig & Fausch 2002, Harford & McLaughlin 2007). In coastal marine environments, distributions of coral reef-associated fishes can be described in relation to cross-shelf categorization of reef types and to localized environmental variation within reef landscapes (Done 1983, Williams 1991, Connell & Kingsford 1998, Aguilar-Perera & Appeldoorn 2008, Yeager et al. 2011). Uncovering biological and environmental linkages at multiple spatial scales requires data collection driven by principles of statistical sampling and a complementary analytical statistical framework.

During the past 30 years, a multispecies fisheries-independent survey has been conducted in the Florida Keys coral reef tract (Bohnsack & Bannerot 1986, Ault et al. 1998, Ault, Smith, et al. 2005, Smith et al. 2011). In its current form, a stratified random sampling scheme is implemented using a spatial hierarchy of cross-shelf and site-scale environmental characteristics (Smith et al. 2011). This design afforded the opportunity to evaluate whether site-scale patterns of reef fish distribution varied between cross-shelf zones describing reef formation types. When responses to environmental features vary

from place to place, researchers have pointed out that the underlying ecological processes that shape animal distributions may also vary (Rosenzweig 1991, Mysterud & Ims 1998, McLoughlin et al. 2010). Recognizing whether habitat requirements differ between locations, can lead to better informed predictions about animal occurrence patterns, but can also serve as a requisite for understanding how ecological processes influence distribution patterns (Boyce et al. 2002, McLoughlin et al. 2010).

Resource selection functions (RSFs) are analytical statistical models for delineating animal distribution patterns. RSFs comprise several statistical approaches, with one approach being the use of "presence-absence" data to assess habitat occupancy probability (Manly et al. 2002). Although RSFs are used increasingly to address a wide range of ecological questions, their application to marine ecosystems remains relatively rare (Robinson et al. 2011). This underutilization is unfortunate because RSFs hold potential for addressing a range of ecological concerns, including gauging responses to reef degradation and for informing marine reserve design (Lindeman et al. 2000, Sale et al. 2005, Grober-Dunsmore et al. 2006). In addition, RSFs that accommodate spatial and temporal differences in habitat use have produced improved understanding of how habitat requirements differ regionally or at different times of year in terrestrial environments (Boyce et al. 2002, Gillies et al. 2006, McLoughlin et al. 2010).

The objective of this chapter was to gain an improved understanding of the distributions of pre-exploitation sized red grouper (*Epinephelus morio*; <50 cm) and black grouper (*Mycteroperca bonaci*; <60 cm) in relation to cross-shelf variation in physical environmental features of the Florida Keys reef tract. Cross-shelf patterns of fish abundance and assemblage structure have been reported for several fish assemblages,

including groupers (Serranidae) of the Great Barrier Reef, the Bahamas islands, and the

Florida Keys reef tract (Alevizon et al. 1985, Sluka & Sullivan 1996, Sluka et al. 1996,

2001, Newman et al. 1997, Connell & Kingsford 1998). However, habitat-use has mainly

been reported for adult phase groupers, whereas descriptions of pre-exploitation or

juvenile distributions and habitat use remains mainly qualitative. Spatial patterns of

occurrence were quantified by developing RSFs at two spatial scales, which was viewed

as a prerequisite for understanding ecological drivers of reef fish distributions.

Methods

Coral reef surveys

The Florida Keys coral reef tract consists of a series of parallel low ridges and

connected valleys that influence coral reef formations (Hoffmeister 1974). Cross-shelf

reef formations consist of patch reefs along the inner shelf that form discontinuous linear

clusters or irregularly scattered clusters, and fore reefs occurring along the reef tract outer

edge (Hoffmeister 1974, Shinn et al. 1977, Lidz et al. 2006). Found within reef

formations are localized topographic features, disparate substrate types, variable coral

densities, and unique flow patterns and wave action (Hoffmeister 1974, Geister 1977,

Shinn et al. 1977). Beginning in 1979, a multispecies fisheries-independent diver visual

survey has been conducted between May and September in the 885 km^2 domain of the

Florida Keys coral reef tract (Fig. 3.1; Bohnsack & Bannerot 1986, Ault et al. 1998,

Smith et al. 2011). A two-stage stratified random sampling design consists of primary

sampling units (PSUs) defined as 200 m x 200 m map grid cells (40,000 km^2) and

second-stage units (SSUs) defined as 15 m diameter observation plots (177 m^2) (Smith et

al. 2011). At each SSU, closely-spaced pairs of SCUBA divers conducted a standardized observation process by listing all observed fish species during five minute sampling periods before recording abundance and fork length information.

Pre-exploitation phase grouper were individuals less than 50 cm and 60 cm fork lengths for red grouper and black grouper, respectively. Observed SSU abundance was re-coded as a binary indicator of "presence-absence", with a value of 1 indicating at least one individual was observed by a diver and a value of 0 indicating non-observation. The cross-shelf spatial stratification consisted of habitat strata that each occurred in <18 m water depth, but differed in terms of reef type, rugosity, and cross-shelf location (Table 3.1). Localized environmental variables measured at SSUs by divers were averaged to produce PSU-level estimates and were normalized by subtracting the mean and dividing the result by the standard deviation of the original values. Environmental variables were bottom depth (m), maximum vertical relief (m), percent coral cover, percent hard-bottom, and latitude. Maximum vertical relief was recorded as the height of the tallest structure, including hard structures (e.g. coral, coralline spur, rocky outcrop) and soft structures (e.g. octocorals, sponges, and macroalgae). Hard-bottom was considered the benthic area of the SSU and comprised solid substrates, consolidated lithogenic or biogenic substrates, including living coral, dead coral, or non-coral composition (Brandt et al. 2009).

Resource selection functions

Logistic regression was initially explored to describe habitat-use patterns, but extremely poor fits were obtained because the quantity of zeros in the dataset exceeded the binomial expectation. Hall (2000) introduced the zero-inflated binomial model for bounded count data to account for excess zeros or "absent" observations, which

subsequently led to the development of site-occupancy modeling of animal distributions (MacKenzie et al. 2002, Tyre et al. 2003). Site-occupancy models consist of several approaches similar to logistic regression, but where two binomial processes are jointly estimated (MacKenzie et al. 2002, 2006, Royle & Dorazio 2009). Occurrence patterns were modeled using a zero-inflated binomial distribution:

$$Z_i \sim \begin{cases} 0, & \text{with probability } 1\text{-}\psi_i \\ \text{binomial}(J_i, p_i) & \text{with probability } \psi_i \end{cases} \qquad (3.1)$$

where the number of observed detections, Z_i, at PSU i, was a function of the probability of occurrence in the first binomial process, ψ_i, and the conditional frequency of detections, p_i, arising from J_i SSU visits in second component. Interpretation of the probability of a zero observation at a PSU can be thought of as the sum two possible outcomes; either no individual occurred with probability $(1-\psi_i)$ or individuals occurred, but were not counted with probability $\psi_i (1- p_i)^{J_i}$. In site-occupancy modeling, this model formulation has allowed surveys consisting of repeated site visits to address the issue of false-zeros, or non-detection when sites are actually inhabited, which is known to have an effect on estimation of occupancy rates (Martin et al. 2005, MacKenzie et al. 2006, Royle & Dorazio 2009). Thus, predictions from site-occupancy models characterize sites as either inhabited or not and sites are estimated to be inhabited with an associated probability based on a joint probability distribution. The surveys used in this analysis consisted of repeat visits to PSUs, however, the survey design and the behavior and local abundance of red grouper and black grouper necessitate care in interpreting the conditional second component of the zero-inflated binomial. This issue is discussed in

detail later, but briefly, non-detections can be affected by: (i) the cryptic nature of the species, (ii) sampling smaller observation plots within a site (rather than repeat visits to the same observation plot), (iii) heterogeneity in fish distribution within sites not accounted for in the survey or the analysis, (iv) abundance-induced heterogeneity in detection probability, and (v) absence of an individual inhabiting a site due to movement within a home range (Martin et al. 2005, Royle & Dorazio 2009, Issaris et al. 2012).

Returning to the fisheries-independent surveys, two different datasets were used in the statistical analysis and are described as follows. For several periods of time, the fisheries-independent surveys differed with respect to the number of observation plots (SSUs) visited within sites (PSUs), but the diver-based observation procedure always remained the same. These differences in sampling allocation were considered a potential means to resolve ambiguity about the interpretation of p in relation to the excess zeros. Simulation-based guidance on survey effort allocation suggests that bias and precision in p and ψ are affected by the number of sites and repeat visits to sites, particularly when p corresponds to detection probability (Tyre et al. 2003, MacKenzie & Royle 2005, Guillera-Arroita et al. 2010). The first of the two datasets, termed the *late-1990s* dataset, was of interest for estimating p. The *late-1990s* dataset consisted of shallow water (<18 m) surveys conducted between 1994 and 1998 inside and outside of an anticipated network of marine reserves (Smith et al. 2011). Many of the PSUs selected during these surveys were visited up to nine times, and those visited at least three times were retained in the analysis (n=248 PSUs, black grouper dataset; n=249 PSUs, red grouper dataset). The second dataset, termed the *late-2000s* dataset, consisted of surveys conducted in 2003 and between 2005 and 2011 and were of interest for occupancy estimation. During

this sampling period, the number of SSUs visited was reduced to two per PSU, but the number of PSUs visited was greatly expanded and detailed measurements of environmental variables were taken by divers (n=2225; Smith et al. 2011).

Occupancy patterns at two spatial scales were evaluated using the *late-2000s* dataset, as the *late-1990s* dataset lacked detailed observations of local environmental variables. The logit-linear occurrence response, ψ_i', was:

$$\psi_i' = \mu + \alpha_{s[i]} + \sum_{j=1}^{5} \beta_{j,s[i]} X_{ij} \tag{3.2}$$

with probability of occurrence (ψ_i) written:

$$\psi_i = \exp(\psi_i') / (1 + \exp(\psi_i')). \tag{3.3}$$

The notation $s[i]$ referred to the habitat stratum that contained PSU i, μ was the mean intercept, and α_s referred to categorical habitat stratum coefficients. To investigate whether occurrence responses to PSU-level environmental variables differed among habitat strata, slope coefficients, $\beta_{j,s}$, were allowed to vary among strata:

$$\beta_{j,s[i]} = \mu_{\beta j} + \delta_{j,s[i]}, \tag{3.4}$$

where $\mu_{\beta j}$ was mean slope for coefficient j, and $\delta_{j,s[i]}$ were random coefficients describing deviations from the mean slope with variances, $\sigma_{\delta j}^2$. Since the *late-1990s* dataset lacked detailed information about environmental variables, its logit-linear response consisted only of categorical habitat stratum coefficients.

To construct resource selection functions, occurrence probability responses, ψ, were explored by systematically expressing p as a function of environmental variables.

First, a naïve site-occupancy formulation (i.e. logistic regression) that assumed *p=1* was developed. Second, *p* was assumed to be constant, and estimated from *J*=2 visits to each site in the *late-2000s* dataset. Third, heterogeneity in *p* was fit to the *late-2000s* dataset and expressed as a logit-linear function of PSU-level environmental variables:

$$p_i' = v + \sum_{j=1}^{3} \omega_j X_{ij}, \tag{3.5}$$

with mean intercept v, and expressed as a probability (p_i):

$$p_i = \exp(p_i') / (1 + \exp(p_i')). \tag{3.6}$$

Coefficients, ω_j, corresponded to maximum vertical relief, depth, and coral cover. Habitat stratum-level differences in *p* were initially considered, but had poor support. Finally, occurrence patterns for the *late-2000s* dataset were estimated using constant *p* that was estimated from the *late-1990s* dataset. The fourth formulation can be thought of as using the *late-1990s* dataset as a pilot study to inform estimation of *p*.

The four model formulations were fit using a Bayesian approach in the software OpenBUGS. (Lunn et al. 2009, Kéry & Schaub 2012).The fourth model was implemented in OpenBUGS by simultaneously fitting both datasets, with the *late-1990s* dataset used to predict *p* and the *late-2000s* dataset used to predict ψ. Simultaneously fitting both datasets allowed uncertainty in *p* to be propagated to occupancy estimation, while preventing the *late-2000s* dataset from contributing to *p* estimation through the use of the OpenBUGS "cut" function (Lunn et al. 2012). For each of the four model formulations, a Gibbs sampler-based variable selection technique was used to identify the most probable set of environmental variables to describe heterogeneity in occurrence probability (Kuo & Mallick 1998, Congdon 2003, Ntzoufras 2009). For the model

formulation that allowed for heterogeneity in p (model 3), support for covariates was also explored using the variable selection technique. Logit-linear responses were modified such that coefficients were multiplied by a binary indicator parameter. When indicator parameters took on a value of 1, the associated coefficient was included in the model, while a value of 0 excluded the coefficient. Indicator parameters had Bernoulli priors with probabilities of 0.5 to give each variable an equal prior probability of inclusion. Posterior means of binary indicators determined the inclusion probabilities of their associated parameters, with those having probabilities > 0.50 retained in the RSF (Ntzoufras 2009).

Model fits were assessed for convergence and model adequacy. Logit-scale intercept and categorical habitat stratum coefficients were assigned diffuse normal priors with means zero and variances 2.7 (Lunn et al. 2012). Mean slope coefficients were assigned diffuse normal priors, and among-strata slope variances, $\sigma_{\delta j}^2$, were assigned priors of $\sqrt{\sigma_{\delta,j}^2} \sim \text{Uniform}(0,5)$. After discarding an initial burn-in period of 150,000 iterations, the Markov chain Monte Carlo (MCMC) algorithm converged on its target distribution, based on Geweke and Gelman-Rubin convergence criteria (Geweke 1992, Congdon 2003, Gelman et al. 2004). Approximation of the posterior distribution was obtained from a subsequent 150,000 samples from two parallel chains. Model adequacy was assessed by calculating squared Pearson residuals to compare the lack of model fit to the data against the lack of fit that would be expected from replicated datasets that conformed exactly to model assumptions (Gelman et al. 2004, Gelman & Hill 2007, Kéry 2010). A graphical comparison revealed whether the distributions of observed and replicated discrepancy measures were symmetrical (Brooks et al. 2000, Gelman et al.

2004). The Bayesian *p*-value was defined as the proportion of times the discrepancy

measure for the replicated discrepancy was greater than the observed discrepancy

measure with values near 0.5 indicating a good fit (Gelman et al. 2004, Ntzoufras 2009).

Results

Coral reef surveys

In the *late-1990s* dataset, between 20 and 105 PSUs were visited annually by

divers from 1994 to 1998. The *late-2000s* dataset was much larger, consisting of between

213 and 457 PSUs visited annually by divers during the period of 2003 to 2011 (Table

3.1). Across all PSUs of the *late-2000s* dataset, bottom depth ranged between 1.5 m and

18.0 m, and maximum vertical relief ranged between 0.10 m and 4.42 m (Table 3.1).

PSUs were sampled between the latitudes of 24.431ºN and 25.749ºN, which corresponds

approximately to reef formations occurring between Key West and Miami. Coral cover

did not exceed 45.6% and hard bottom habitat ranged from 0% to 100% (Table 3.1).

Observed within-habitat-strata ranges for environmental variables corresponded well with

the cross-shelf stratification of PSUs selected from digital map layers (Table 3.1). There

was some evidence for correlation between standardized variables used in site-occupancy

models (Pearson's $|r|<0.38$, all pair-wise comparisons). For the *late-2000s* dataset,

abundance at the scale of the SSU ranged, on average, between zero and eight individuals

per diver for black grouper and between zero and 2.5 individuals per diver for red

grouper, thus, relatively little information loss about habitat use patterns was expected by

re-coding abundance as binary observations.

Resource selection functions - red grouper

Posterior inclusion probabilities indicated support for a negative occupancy

relationship with maximum vertical relief in the naïve logistic regression model and in

each of the site-occupancy models that assumed constant p (Tables 3.2). When p was

allowed to vary in relation to environmental variables, inclusion probabilities suggested

that presence-absence observations were a function of vertical relief-induced

heterogeneity in p and that ψ did not vary with any of the environmental variables

(Table 3.2 model 3: linear detection). There was weak support for differences in

occurrence response to latitude among habitat strata, but latitude coefficients were mostly

non-significant and were not considered further. In each of the four model formulations,

inclusion probabilities supported habitat-stratum-level intercepts (a_s; Table 3.2).

However, estimated stratum-level intercepts were non-significant, with the exception of

high rugosity offshore fore reefs (habitat strata vi). Habitat-stratum-level intercepts were

retained in the model because of the strong effect of high rugosity offshore fore reefs and

because predicted occurrence probabilities, expressed as odds ratios, were consistently

suggestive of an onshore-to-offshore trend in red grouper distribution (Fig. 3.2).

Fits of the zero-inflated binomial models were quite variable. The naïve logistic

regression had a poor fit to the data with a Bayesian *p-value* of 0.99, as did the site-

occupancy model that incorporated p obtained from the *late-1990s* dataset, suggesting

that these two models had low support as plausible descriptors of red grouper habitat use

(Fig 3.3). Both site-occupancy models based solely on the *late-2000s* dataset fit

appreciably better with Bayesian *p-values* between 0.61 and 0.65. Estimates of constant p

obtained from the *late-1990s* and *late-2000s* datasets were 0.25 and 0.34, respectively; however these estimates were disparate enough to strongly influence model fit (Fig 3.3).

All four model formulations included habitat-stratum-level intercept terms (Table 3.2). Habitat-stratum-level intercepts can be interpreted as conditional categorical responses, thus, odds ratios for intercept coefficients were calculated using habitat stratum (i) – low-medium relief inshore patch reefs – as a reference category (Fig. 3.2). Intercept odds ratios greater than 1 indicated better odds of red grouper occurrence relative to the reference category and odds ratios less than 1 indicated worse odds of occurrence relative to the reference category. While most coefficient values were not significant, a cross-shelf decline in occurrence odds was evident (Fig. 3.2). Next, for each model formulation, predicted responses from zero-inflated model components p and ψ were plotted against maximum vertical relief (Fig 3.4). Trends illustrate how the predicted source (p or ψ) of a negative response to vertical relief changed based on whether heterogeneity in p was allowed in model structure.

Resource selection functions - black grouper

Posterior inclusion of maximum vertical relief and latitude were supported in the naïve model formulation and in each of the site-occupancy formulations that assumed constant p (Tables 3.3). Like red grouper, when p was allowed to vary in relation to environmental variables, inclusion probabilities supported vertical relief-induced heterogeneity in p, and no corresponding occurrence probability response (Table 3.3). However, unlike the case for red grouper, p varied positively with maximum vertical relief. There was also support for habitat-stratum-level differences in occurrence probability in response to depth and maximum vertical relief, but support for inclusion of

these random slope coefficients varied among model formulations (Tables 3.3). In each model formulation, inclusion probabilities did not support habitat-stratum intercepts (Table 3.3).

Fits of each model formulation to the black grouper data followed a pattern similar to that of red grouper. Fit of the naïve logistic regression to the data was poor and had a Bayesian *p-value* of 1.0. Similarly, the site-occupancy model that incorporated constant p obtained from the *late-1990s* dataset also demonstrated a poor fit to the data, and thus had low support as plausible descriptors of black grouper habitat use. The site-occupancy models based solely on the *late-2000s* dataset fit appreciably better with Bayesian *p-values* between 0.6 and 0.7. Estimates of constant p were lower in the *late-1990s* dataset than the *late-2000s* dataset, with values of 0.17 and 0.29, respectively.

For each black grouper model formulation, predicted occurrence probability was plotted against latitude, with maximum vertical relief fixed at its observed mean, and vice versa (Fig 3.5A & 3.5B). In all formulations, a negative occurrence probability response to latitudinal change was predicted (Fig. 3.5A). Conversely, occurrence probability responded positively to maximum vertical relief in each of the three constant p formulations (Fig. 3.5B). The analysis also revealed mixed support for cross-shelf differences in occurrence probability response to depth gradients (Table 3.3 & Fig. 3.6). Two model formulations (naïve logistic regression and heterogeneous p) suggested that occurrence probability responses to depth were disparate among habitat strata (Fig. 3.6). Logit-scale slope coefficients for depth in each habitat strata were consistently negative for the nearest-to-shore strata and positive for the offshore fore reef strata (Fig. 3.6).

Unique responses to maximum vertical relief were supported in the constant detection probability formulation based on the *late-2000s* dataset, but no obvious cross-shelf trend was evident (Fig. 3.6).

Discussion

Fisheries-independent surveys that adhere to statistical sampling principles potentially avoid biases associated with fisheries-dependent sampling and offer the advantage of observation at spatial scales relevant to ecological investigation (Cochran 1977, Wiens 1989, Johnson et al. 2012). Occurrence modeling of pre-exploitation phase grouper was feasible due to the stratified random design, sampling domain, and sampling intensity of the fishery-independent diver visual survey (Smith et al. 2011, Ault et al. 2013). This design enabled the effects of covariates on the conditional probability component, p, to be illuminated, which was an important aspect of resource selection function development. However, the context-specific meaning of p requires some careful consideration. It may seem intuitive to interpret p as detection probability, as is commonly inferred from site-occupancy modeling of repeat survey designs, but characteristics of the fisheries-independent survey and of grouper ecology make this an untenable conclusion for several reasons. With respect to grouper ecology, false-zeros could have occurred in the data if individual fish inhabiting a PSU moved into or out of the SSU, altering the probability of it being observed by a diver. While many reef-associated fishes tend to exhibit low mobility, large groupers appear to maintain home ranges considerably larger than the 200 m by 200 m PSU (Chapman & Kramer 2000, Farmer & Ault 2011). A separate, but not mutually exclusive possibility is that an

individual fish could be present within the SSU when being observed by a diver, but not detected. In this context, it is plausible that p could pertain to detection as a confounding of the probability of movement among SSUs and the probability of observation given presence; however, this definition of p is incomplete.

Given the survey design of visiting observation plots (SSUs) that covered a small areal extent of larger PSUs, the meaning of p may alternatively reflect sampling considerations. Although sampling designs that achieve replication by conducting surveys in multiple plots within each sampling unit are common in the context of occupancy modeling (MacKenzie & Royle 2005, MacKenzie et al. 2006), these designs may exaggerate abundance-induced heterogeneity in detection probability. Abundance-induced detection heterogeneity arises in most sampling situations, as higher local (site) abundance is expected to yield more net detections (Royle & Dorazio 2009). A simple motivating example will illustrate how this problem may affect interpretation of occurrence patterns. Consider two PSUs, each too large to sample completely, and divide these PSUs into a grid of 100 smaller rectangular observation plots. The first PSU will consist of high quality habitat that is uniform across all observation plots and the second will consist of low quality habitat that is also uniform across observation plots. The first PSU will naturally have higher abundance than the second because of its higher quality, and it will be assumed that individuals are assigned randomly to observation plots within PSUs. Both PSUs are thus truly occupied, but fewer observation plots are expected to be occupied in the second PSU because abundance is lower and those few individuals are randomly assigned to observation plots. Now, observing (counting individuals) in any randomly selected two observation plots in the first PSU will, on average, result in higher

perceived detection probability than in the second PSU. That is, given presence, the probability of detection will be affected by local abundance. Importantly, detection heterogeneity is induced in this example by abundance and not by observation processes like observer experience or sightline obstruction.

Interpretation of predicted habitat-use patterns from the zero-inflated binomial models must reflect uncertainty about the underlying causes of zero inflation in the datasets. Predicted occurrence responses to environmental variables for both red grouper and black grouper were affected by whether p was also allowed to vary with the environmental covariates. Red grouper appeared to occur in locations with lower vertical relief when p was assumed to be constant. When p was allowed to vary with vertical relief, a similarly negative trend was predicted, but a corresponding trend in ψ was no longer evident (Fig 3.4). If p is interpreted as detection probability, the declining trend with increasing vertical relief could suggest that individuals are more difficult to observe in highly rugose habitats, but this conclusion is inconsistent with the gregarious and possibly territorial responses of red grouper that are reported by approaching divers (S. G. Smith personal communication). Alternatively, correlation between p and vertical relief could reflect correlation between abundance and vertical relief through apparent abundance-induced detection heterogeneity. Model fitting for black grouper produced a predicted positive relationship between p and vertical relief. In this instance, interpreting p as detection probability leads to the counter-intuitive prediction that black grouper are more difficult to observe in less rugose habitats. Speculatively, black grouper could be more transient in less rugose habitats, thus reducing detection probability, or their typically dark grey blotches could contribute to their cryptic nature among octocoral-

dominated flats of the Florida Keys reef tract (S.G. Smith personal communication). But, it is also perhaps not coincidental that slope direction of ψ in response to vertical relief was the same as that of p, when p was allowed to vary with vertical relief, again suggesting p could reflect abundance (Fig 3.5). This trend is also evident for red grouper, thus suggesting that the predicted heterogeneity in p may be related to abundance trends.

Uncertainty associated with the interpretation of p and ψ was most problematic for extracting trends about occurrence with respect to vertical relief. This uncertainty is clearly problematic in the applied sense of relying on apparent habitat-use relationships for stratifying future survey effort or for marine reserve design if those relationships do not in fact reflect occurrence patterns. For red grouper, if positive responses to vertical relief that were estimated for both p and ψ do reflect occurrence patterns, this may be consistent with existing studies. Like other members of the genera *Epinephelus*, red grouper probably utilize crevices in hard substrates for shelter and are ambush predators that consume almost exclusively benthic prey (Smith 1961, Cailliet et al. 1986, Parrish 1987, Brulé & Rodriguez Canché 1993, Coleman et al. 2010). Use of benthic habitats is continued as individuals grow and undergo characteristic ontogenetic migrations to offshore waters (Moe 1969, Burgos et al. 2007, López-Rocha & Arreguín-Sanchez 2008, Coleman et al. 2010). For black grouper, if negative responses to vertical relief estimated for both p and ψ reflect occurrence patterns the similarities between this study and previous studies appear more ambiguous. Black grouper tend to forage higher above the bottom, are more slender, have a tapering body form, and appear to be more agile swimmers (Parrish 1987). In addition, they maintain a fish-dominated diet, including fast-swimming and pelagic species (Randall 1967, Parrish 1987, Brulé et al. 2005). Within the

Florida Keys reef tract, adult black grouper have been associated with several types of reef formations, including *Acropora* and *Montastrea* dominated high-relief spur-and-grove reefs and octocoral dominated low-relief relic reefs (Sullivan & Sluka 1996). Nevertheless, interpreting these statistical relationships as evidence for vertical relief-induced occurrence patterns remains difficult and still requires a more complete understanding of the influence of detection probability on the observation process.

Given the subtleties of model interpretation, three conclusions are supported by this analysis. The first conclusion was that pre-exploitation red grouper occurrence appears to vary systematically with reef habitat proximity to the coastline. Occurrence probability was predicted to be higher in nearer-to-shore patch reef habitats than in offshore fore reefs. The strength of this pattern was somewhat inconsistent; however, the four near-shore patch reef strata were, on average, occupied with higher probability than the remaining two offshore fore reef strata (Fig. 3.2). Onshore-to-offshore occurrence patterns were observed across all four model formulations. Positive occurrence nearer-to-shore confirms previous observations that pre-exploitation stage red grouper inhabit inshore waters of the Florida Keys (Moe 1969, Sluka et al. 1994). Based on previous studies, pre-exploitation red grouper habitat use may vary geographically. Moe (1969) reported that juvenile red grouper were rare in shallow water habitats of the west Florida shelf; rather, that they were spread over rocky substrates of the shelf as deep as 36 m. Differential habitat use may reflect the relative availability of hard substrates, as for instance, the narrow shelf of the Florida Keys may compress the areal extent of juvenile habitats, whereas suitable habitats may be more expansive on the west Florida shelf.

The second conclusion was that pre-exploitation phase black grouper occurrence was correlated with latitude, which suggested a trend of decreasing occurrence probability from Key West (24.5º N) to Key Largo (25.07º N) and to Miami. This southwest-to-northeast occurrence decline along the Florida Keys is striking in the context of the related distribution of the spawning abundance of black grouper. Using the same intensive diver surveys analyzed in this study, Ault et al. (2013) reported on the recovery of exploited reef fishes in marine reserves of the Dry Tortugas, located 115 km west of Key West, Florida. While the Tortugas region contains about 22% of the broader Florida Keys – Dry Tortugas coral reef habitat, it accounts for over 50% of black grouper spawning abundance (Ault et al. 2013). The potential importance of the Dry Tortugas as a source of recruitment for the Florida Keys is also supported by regional directionality of currents that potentially transport larval fish (Lee et al. 1994, Domeier 2004). Thus, the latitudinal occurrence gradient of pre-exploitation phase black grouper appears to support the importance of the Dry Tortugas region as a potential recruitment source for the Florida Keys – Dry Tortugas coral reef ecosystem.

The third conclusion was that black grouper occurrence varied in response to depth gradients, but responses differed among habitat strata. Within inshore and mid-channel patch reefs, model outcomes suggested that black grouper occurred with higher probability in the shallowest of available depths, while in outer fore reefs occurrence was highest in the deepest available habitats (Fig 3.6). This result was somewhat perplexing, but could suggest that black grouper are not cueing on depth at all; rather, depth may be correlated with more important ecological influences on habitat selection. Fishes are the dominant diet item of black grouper and include families considered inshore pelagic

diurnal (Carangidae), demersal diurnal (Scaridae and Labridae), and nocturnal (Lutjanidae) (Brulé et al. 2005). For black grouper, significant dietary overlap exists among juvenile size classes (between 10.5 cm and 45.5 cm; Brulé et al. 2005). Many reef fishes, including plausible black grouper prey of families Scaridae and Labridae, display preferences as juveniles for near-shore habitats (Williams 1991, Overholtzer & Motta 1999, Collins & McBride 2011). Additionally, Aguilar-Perera and Appeldoorn (2008) reported higher densities of Pomacentridae, Scaridae, and Labridae relative to other reef fishes inhabiting the deeper areas of fore reefs (3 to 10 m depth) surrounding southwestern Puerto Rico. However, any such implications about prey-induced distribution patterns are speculative without direct comparative data on prey densities within the sampling domain of this study. An alternative, but not mutually exclusive explanation for disparate occurrence responses to depth involves ontogenetic habitat shifts from shallow to deep habitats. Currently, little evidence is available to suggest that black grouper move from shallower to deeper habitats, although trends in population size structure suggest that individuals inhabiting shallower waters are commonly smaller than those found in deeper water (Crabtree & Bullock 1998, Brulé et al. 2003). Although size structured habitat use was not investigated in this study, differential responses to depth could indicate size-specific habitat responses within the range of pre-exploitation sizes (~10 cm to 60 cm) included in this study. More detailed investigation of size structure could improve understanding of black grouper distribution.

A limitation of this study was the inability to resolve uncertainty about the interpretation of p, particularly in the context of imperfect detection. Imperfect detection arises when an observer fails to detect a cryptic species, or when a species occurs at a

site, but is absent during sampling (Martin et al. 2005, Issaris et al. 2012). When detection probability is ignored in RSF development, occupancy probability will often be underestimated (MacKenzie et al. 2006, Royle & Dorazio 2009, Kéry 2010). In other words the naïve use of species distribution models that ignore detection probability describe where species can be *found* by observers, rather than describing occupancy patterns (MacKenzie et al. 2006, Kéry 2011, Monk 2013). This inaccuracy may be acceptable as long as comparisons of occupancy patterns between habitat types are interpreted in relative terms. However, complications can arise when detection probability varies systematically among sites. This situation can lead to overstating of occupancy probability when detection and occupancy are positively correlated and understating of occupancy probability when the two are negatively correlated (Gu & Swihart 2004, MacKenzie 2006, Kéry & Schaub 2012).

Designing occupancy studies to account for imperfect detection requires multiple site visits to resolve ambiguity about whether an observed absence reflects a true absence or an undetected occurrence (Field et al. 2005, MacKenzie & Royle 2005, Guillera-Arroita et al. 2010, Wintle et al. 2012, Monk 2013). Studies of marine fishes have revealed that detection probability varies systematically with body size, schooling behavior, cryptic nature, distance from divers, and survey method (Byerly & Bechtol 2005, MacNeil, Tyler, et al. 2008, MacNeil, Graham, et al. 2008, Bozec et al. 2011, Dickens et al. 2011). However, taking the subsequent analytical step of incorporating heterogeneity in detection probability in statistical occupancy modeling has not yet been achieved for any marine organism (Monk 2013). The challenges faced in this study in

addressing the source(s) of excess zeros exemplified the recommendation of Gu and Swihart (2004) that correct interpretation of species distribution will require doing so.

Evaluating multi-scale habitat-occupancy patterns as a requisite to better understanding of how ecological processes that shape fish distributions was demonstrated by this study, and indeed has also been demonstrated elsewhere (Sluka et al. 1994, Aguilar-Perera & Appeldoorn 2008). Quantifying benthic and pelagic prey distributions should be viewed as an essential next step in illuminating the dynamics of habitat selection by predatory reef fishes (Williams 1991, Sluka et al. 1994). In addition, advances in species distribution modeling position these techniques as important tools for continuing to delineate habitat requirements of marine species (MacKenzie et al. 2006, Royle & Dorazio 2009, Kéry 2011). Understanding habitat requirements of fishes continues to be essential for fisheries management in places like the Florida Keys coral reef ecosystem where it is necessary to address fishing and non-fishing stressors on marine resources (Lindeman et al. 2000, Ault et al. 2009, Sadovy de Mitcheson et al. 2013). Delineating habitat use patterns is essential for fisheries management because marine reserves are becoming widely implemented as a priority management measure and because monitoring substrate-associated fish populations relies on habitat-use patterns for informing how survey sampling should be spatially distributed (FKNMS 1997, Lindeman et al. 2000, Smith et al. 2011).

Table 3.1. Physical and biological characteristics of primary sampling units (PSUs) for the *late-2000s* dataset. n is number of PSUs sampled. Min is minimum value, Max is maximum value, Ave is mean value, and DD is decimal degrees.

Habitat Stratum			Environmental variables					
			Bottom depth (m)			Vertical relief (m)		
	Rugosity	n	Min	Ave	Max	Min	Ave	Max
i. Inshore patch	Low-med	99	1.8	3.5	7.8	0.10	1.16	3.12
ii. Mid-channel patch	Low-med	390	1.5	5.3	12.6	0.12	1.37	4.27
iii. Offshore patch	Low-med	228	2.1	7.0	13.5	0.10	1.08	4.00
iv. Offshore patch	High	45	2.2	6.2	12.4	0.90	2.41	3.97
v. Outer fore reef	Low-med	1184	2.1	9.0	18.0	0.10	0.79	3.20
vi. Outer fore reef	High	279	2.8	6.6	17.1	0.32	2.19	4.42

Table 3.1 continued.

Habitat Stratum	Environmental variables								
	% Coral cover			Latitude (DD)			% Hard bottom		
	Min	Ave	Max	Min	Ave	Max	Min	Ave	Max
i. Inshore patch	0	13.8	45.6	24.51	24.96	25.74	17.5	75.6	100
ii. Mid-channel patch	0	10.7	52.2	24.46	25.03	25.52	10.7	77.1	100
iii. Offshore patch	0.2	6.2	32.2	24.44	24.91	25.55	12.5	73.2	100
iv. Offshore patch	2.2	9.0	26.0	25.10	25.11	25.29	35.0	79.2	98.2
v. Outer fore reef	0	3.3	25.0	24.43	24.97	25.74	0	70.6	100
vi. Outer fore reef	0.6	5.3	36.8	24.43	24.76	25.58	23.7	74.2	100

Table 3.2. Variable inclusion probabilities for red grouper (*Epinephelus morio*) site-occupancy models with alternative conditional probability formulations. *p* is conditional probability, * indicates variable included in resource selection function.

Parameters	Conditional probability formulation			
	1. Naïve logistic regression (*p=1*)	2. Constant conditional probability (*p<1*)	3. Linear conditional probability	4. Constant conditional probability (*p<1*)
		late-2000s detection	*late-2000s* detection	*late-1990s* detection
Occurrence parameters				
Mean slope coefficients ($w_{\mu j}$)				
Depth	0.02	0.02	0.13	0.02
Vertical relief	0.91*	0.97*	0.27	0.93*
% coral cover	0.01	0.01	0.03	0.02
Latitude	0.01	0.02	0.03	0.02
% hard bottom	0.00	0.01	0.02	0.02
Random slopes coefficients ($w_{\delta j}$)				
Depth	0.14	0.11	0.16	0.09
Vertical relief	0.16	0.09	0.27	0.17
% coral cover	0.11	0.23	0.44	0.34
Latitude	0.61	0.24	0.57	0.20
% hard bottom	0.02	0.06	0.07	0.07
Habitat stratum coefficient (W_a)	1.00*	1.00*	1.00*	1.00*
Conditional probability parameters				
Mean slope coefficients ($w_{\omega j}$)				
Depth	-	-	0.13	-
Vertical relief	-	-	0.78*	-
% coral cover	-	-	0.01	-

Table 3.3. Variable inclusion probabilities for black grouper (*Mycteroperca bonaci*) site-occupancy models with alternative conditional probability formulations. *p* is conditional probability, * indicates variable included in resource selection function.

Parameters	Conditional probability formulation			
	1. Naïve logistic regression (*p=1*)	2. Constant conditional probability (*p<1*)	3. Linear conditional probability	4. Constant conditional probability (*p<1*)
		late-2000s detection	*late-2000s* detection	*late-1990s* detection
Occurrence parameters				
Mean slope coefficients ($w_{\mu j}$)				
Depth	0.02	0.02	0.09	0.03
Vertical relief	0.90*	0.68*	0.04	0.91*
% coral cover	0.29	0.07	0.04	0.10
Latitude	0.98*	0.98*	0.80*	0.93*
% hard bottom	0.01	0.04	0.10	0.10
Random slopes coefficients ($w_{\delta j}$)				
Depth	0.99*	0.42	1.00*	0.12
Vertical relief	0.36	0.63*	0.11	0.35
% coral cover	0.05	0.07	0.05	0.18
Latitude	0.05	0.06	0.39	0.22
% hard bottom	0.03	0.06	0.18	0.16
Habitat stratum coefficient (w_a)	0.31	0.46	0.05	0.49
Conditional probability parameters				
Mean slope coefficients ($w_{\omega j}$)				
Depth	-	-	0.06	-
Vertical relief	-	-	1.00*	-
% coral cover	-	-	0.04	-
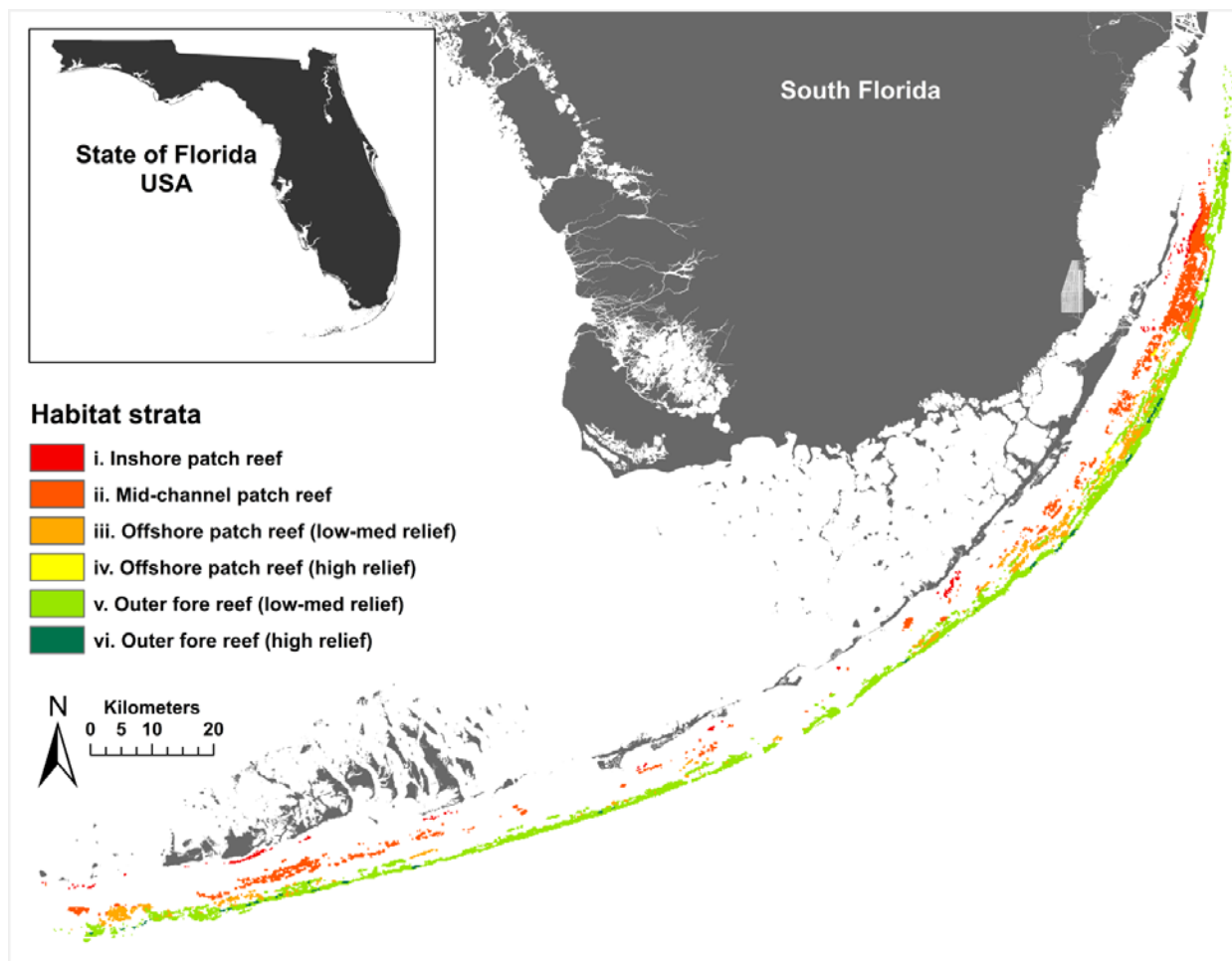
Figure 3.1. Florida Keys coral reef tract, Florida, USA.
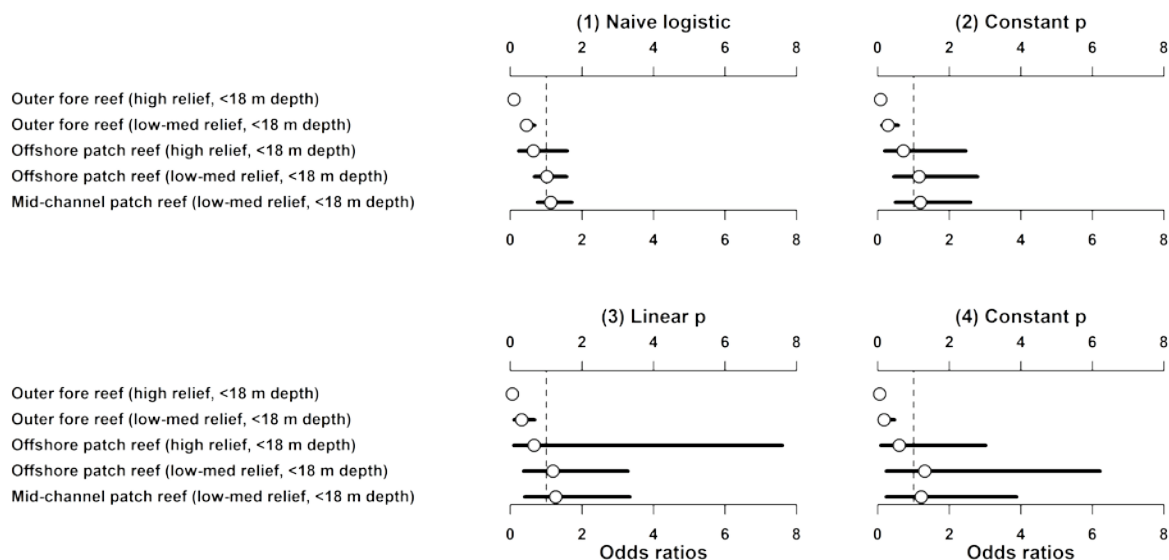
Figure 3.2. Intercept odds ratios of red grouper occurrence in each habitat stratum. Plots were produced for each of four zero-inflated binomial model formulations: (1) naïve logistic regression, (2) constant conditional probability (*p*) estimated from the *late-2000s* dataset, (3) heterogeneous *p*, and (4) constant *p* estimated from the *late-1990ss* dataset. Habitat strata are described in Table 1.1. Odds ratios were calculated relative to reference habitat stratum (i) defined as low-medium relief inshore patch reefs. Circles are means and lines are centered 95% intervals.
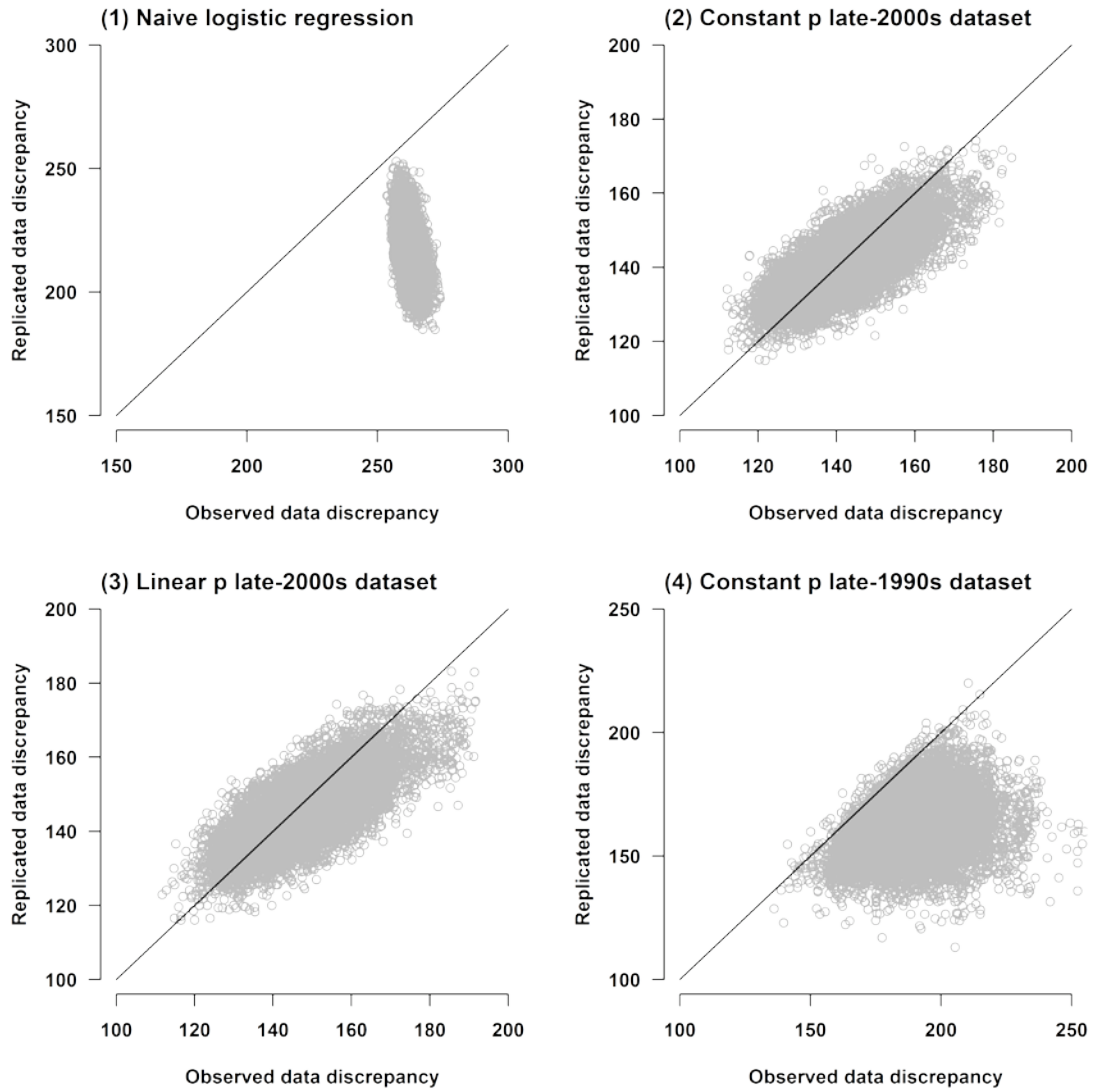
Figure 3.3. Goodness-of-fit plots for red grouper resource selection functions. Shown are observed and replicated discrepancy measures calculated from squared Pearson residuals produced for each of four zero-inflated binomial model formulations: (1) naïve logistic regression, (2) constant conditional probability (*p*) estimated from the *late-2000s* dataset, (3) heterogeneous *p*, and (4) constant *p* estimated from the *late-1990ss* dataset.
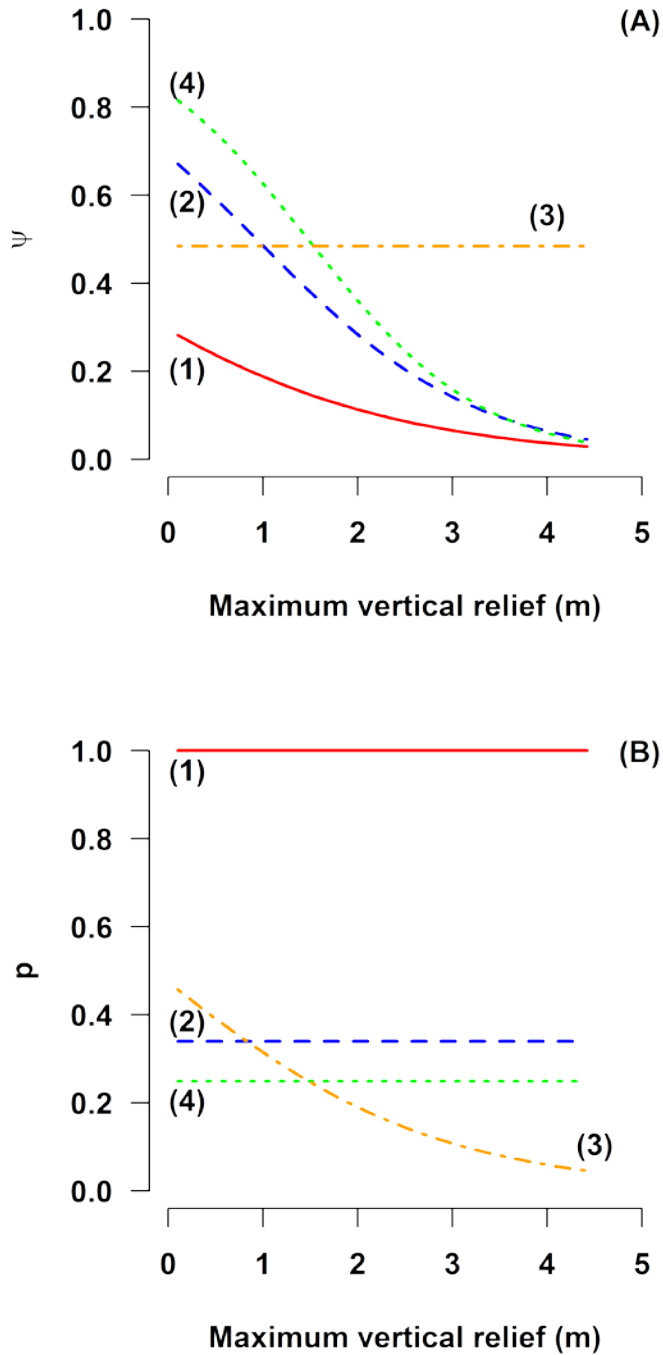
Figure 3.4. Predicted responses in red grouper occurrence probability, ψ, (A) and conditional probability, p, (B) to maximum vertical relief. Lines correspond to zero-inflated binomial model formulations: (1) naïve logistic regression, (2) constant p estimated from the *late-2000s* dataset, (3) heterogeneous p, and (4) constant p estimated from the *late-1990ss* dataset.
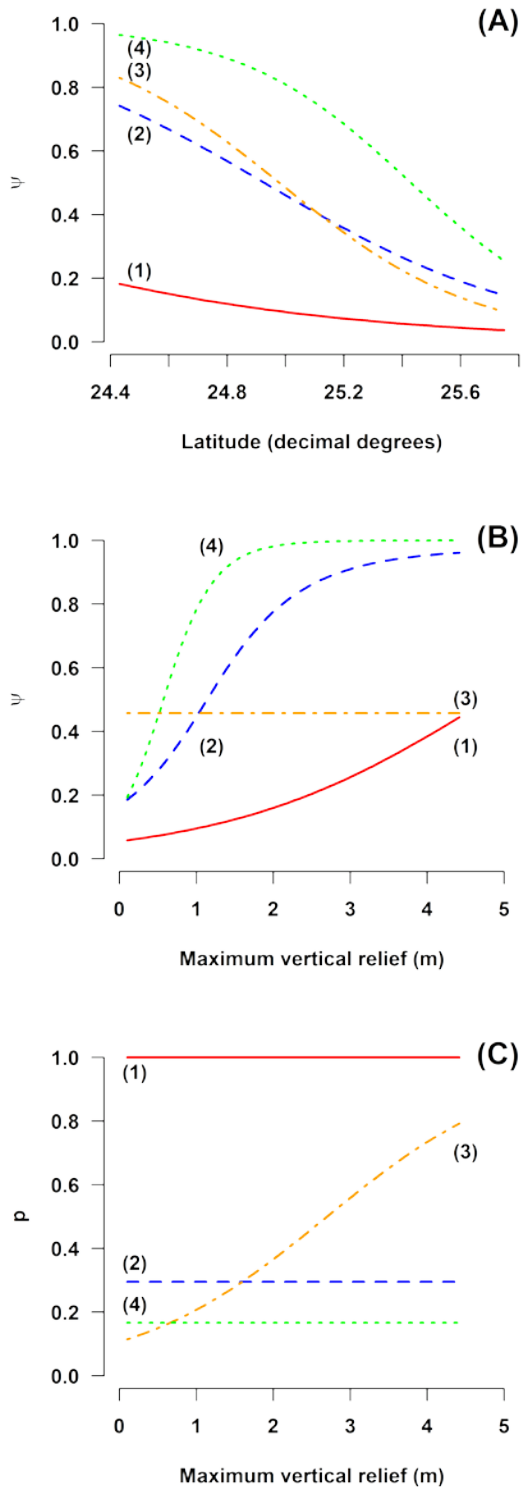
Figure 3.5. Predicted mean responses in black grouper occurrence probability, ψ, to latitude (A) and maximum vertical relief (B), and response in conditional probability, p, to maximum vertical relief (C). Lines correspond to zero-inflated binomial model formulations: (1) naïve logistic regression, (2) constant p estimated from the *late-2000s* dataset, (3) heterogeneous p, and (4) constant p estimated from the *late-1990ss* dataset.
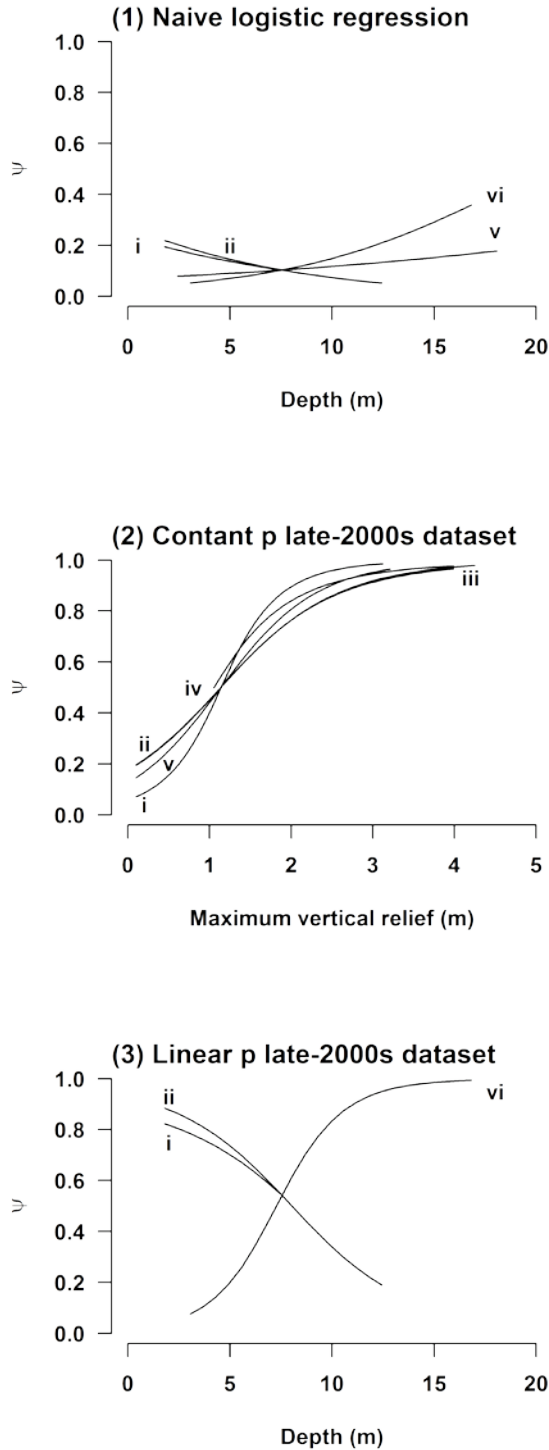
Figure 3.6. Conditional responses in black grouper occurrence probability, ψ, to depth and maximum vertical relief within each habitat stratum. Plots were produced for three of the zero-inflated binomial model formulations in which random slope coefficients (for depth or maximum vertical relief) were supported in model fitting. Habitat strata are described in Table 1.1. Only habitat strata with statistically significant coefficients are shown.

CHAPTER 4: SURVEY PRECISION AFFECTS PERFORMANCE OF CORAL REEF FISHERIES MANAGEMENT

Summary

Simulations were conducted to evaluate how management strategies that rely on biomass surveys as inputs to population assessments perform under varying degrees of survey precision. Evaluations were carried out by simulating the entire management cycle to understand how data inputs affect fishery analyses and decision-making, and the cumulative effects of this process through time on the sustainability of a fish population. Simulation analysis emphasized management of fisheries that target long-lived fishes in coral reef environments and management actions that are informed by simple model-based population assessment and model-free population assessment procedures. The simulation framework was representative of black grouper *Mycteroperca bonaci* inhabiting a simulated environment with substrate properties similar to those of the Florida Keys reef tract. Findings suggested that precautionary management actions are necessary when biomass surveys were imprecise. In addition, model-free control rules that did not rely on an underlying description of population dynamics produced promising results, but more detailed analyses of these approaches are needed. The findings of the analysis framed discussions about the types of management objectives that can be achieved under data-limited circumstances.

Background

Resource surveys that support estimation of population status and management reference points should be designed to produce correct information with sufficient precision to support decision-making (Olsen et al. 1999, Walters & Martell 2004, Smith et al. 2011, Houk & van Woesik 2013). Resource management difficulties can arise when information needs are not met by the available data. Limitations in data availability are common in fisheries management and affect whether and how population assessment procedures are carried out (Hilborn & Walters 1992). Poor data quality can also hinder population assessment and management decision-making, including for instance, when data are available but are biased or imprecise (high variance). Understanding how informative different kinds of data will be for decision-making remains a priority for fisheries management (Magnusson & Hilborn 2007). Of related concern is the question of whether available data are sufficiently precise to inform estimation of population status and management reference points.

Of fundamental importance in understanding how data collection affects fisheries management are the interconnections between monitoring, population assessment, and decision-making. A simulation-testing approach that emphasizes these interconnections is known as management strategy evaluation (Hertz & Thomas 1983, MSE; Butterworth & Punt 1999, Sainsbury et al. 2000). Fisheries management strategies consist of the specifications for: monitoring that describes how data are collected; scientific analysis that typically consists of a population assessment procedure; decision rules that determine how the analysis will be used in decision-making; and, regulatory measures that describe how decisions are implemented (Sainsbury et al. 2000). MSE simulates a management

system in its entirety, which can consist of a fish population that is connected to a fishery and an associated management strategy (Sainsbury et al. 2000, Butterworth et al. 2010). Performance of simulated management strategies are usually evaluated in terms of whether pre-stated management objectives are likely to be achieved (Sainsbury et al. 2000). MSE can be used to investigate how data limitations affect management strategy performance because the effects of changes in data inputs are propagated through the management system. In addition, feedback provided by monitoring, however unreliable, can reveal whether and how outcomes of previous management actions are detected and how this information influences subsequent decisions. Through this type of analysis, management strategies that are robust to data reliability issues may be identified.

For example, a management strategy could involve (1) monitoring of total catches and relative population biomass, (2) a population assessment procedure that uses these data inputs to estimate current biomass, and (3) a decision rule that uses current biomass to specify the total allowable catch (Hilborn & Walters 1992, Walters & Martell 2004). Issues that can arise include inadequacy of the biomass index in capturing true biomass trends and inadequacy of the assessment procedure in capturing true population dynamics. MSE can help to evaluate whether issues like these are likely to lead to substantial errors in decision-making or whether decision-making will be reasonably successful despite inadequacies of the management strategy.

In this chapter, simulations were conducted to evaluate how management strategies that rely on biomass surveys as inputs to population assessments perform under varying degrees of survey precision. The role of survey precision was presented in the context of managing fisheries that target long-lived fishes in coral reef environments. The

simulation framework was representative of black grouper *Mycteroperca bonaci*; a coral reef associated species having its center of range within the Florida Keys reef tract. Black grouper's long-lived and late-maturing life history characteristics are representative of coral reef fishes that are harvested globally and at unsustainable rates (Coleman et al. 2004, Ault, Bohnsack, et al. 2005, Ault et al. 2009, Sadovy de Mitcheson et al. 2013). The Florida Keys reef tract is a data-rich ecosystem among tropical and sub-tropical locales and actual population assessments utilize an array of data inputs and statistical analytical methods (Ault et al. 2008, SEDAR 2010a). For brevity, simulation analysis was focused on evaluating management strategies that relied upon biomass surveys as inputs to simple model-based population assessment and model-free population assessment procedures. Advancement of simple population assessment procedures has been rapid (Hilborn & Walters 1992, Ault et al. 1998, Froese 2004, Cope & Punt 2009, Martell & Froese 2012). But there remains uncertainty about how data inputs, assessment procedures, and decision-making function collectively in supporting science-based decision-making. Therefore, this modeling exercise is intended to trace the implications of data quality through the entire fishery management cycle over time. The simulation framework was informed by empirical data from the data-rich Florida Keys region, but was used to evaluate management strategies that could be used in a data-limited ecosystem with similar biology, ecology, and fisheries.

Methods

Spatially explicit simulation framework

     Purpose – An individual-based model (IBM) was developed that could be used to simulate an age-structured fish population that was distributed within a spatially-heterogeneous coral reef environment. The IBM was used to evaluate the effects of survey data quality on fishery management. A sufficiently detailed representation of fish population dynamics was required because contrasting fisheries management strategies against an overly simplified simulated fish population was viewed as unlikely to be informative. In the following sections, the simulation framework is summarized according to a protocol for communicating the development of IBMs that is known as Overview, Design concepts, and Details, or ODD (Grimm et al. 2006).

     State variables and scales – The simulation framework comprised three main components: a coral reef environment, individual fish, and a fishery. The coral reef environment was generated by creating artificial landscapes with substrate properties similar to those of the Florida Keys reef tract. Artificial landscapes represented patterns in vertical relief (i.e. reef height and complexity) across the 885 km^2 spatial domain of the Florida Keys reef tract as a grid of contiguous 200 m by 200 m rectangular cells. Vertical relief (m) describes the height of benthic structures, including hard structures (e.g. coral and rocky outcrops) and soft structures (e.g. octocorals, sponges, and macroalgae) (Brandt et al. 2009). Vertical relief was chosen as representative characteristic of the coral reef environment because reef fish distributions are generally known to be correlated with substrate complexity (Chapman & Kramer 1999, Sluka et al. 2001, Farmer & Ault 2011). Individual fish were characterized by: age, total length,

whole weight, and location. Fish movement was not included for brevity and because it was not essential for achieving the stated purpose of the model. The simulated fishery was subject to a minimum harvest length and total effort restriction.

Process overview and scheduling – The model operated on a monthly time step. During each monthly time step, model processes occurred in the following order: growth, recruitment (when month equaled January), spawning (when month equaled January), and mortality. Some model processes were seasonal. Spawning occurred at the beginning of the year, at which time the number of recruits to be added the following year was determined. Addition of newly recruiting individuals generated in the previous year also occurred in the first month of the year. The simulated fishery operated during the last eight months of each year. Simulations were constructed in the Java programming language using the multi-individual simulation library MASON (Luke et al. 2005, Sullivan et al. 2013). With the exception of spawning and recruitment, monthly processes were carried out through synchronous updating of state variables.

Design concepts – Population dynamics emerged from the state variables of individuals; however, individual states were imposed through deterministic functions and through probability-based rules that produced stochastic outcomes. Stochastic elements included: inter-annual recruitment variability, individual-level differences in growth trajectories, and mortality. Stochastic recruitment reflected natural temporal variability in abundance that is inherent to fish populations. Stochastic growth was incorporated by assigning unique growth trajectories to new recruits. Assigning individuals unique growth trajectories was not intended to imply that individual-level growth variation arose strictly from intrinsic factors; rather, the approach was intended to reproduce an empirical

pattern of growth variation. Incorporating individual growth variation was useful because simulations included a fishery that was regulated, in part, through minimum harvest length restrictions. Minimum harvest length restrictions are characteristic of actual grouper fisheries, and thus incorporating individual variation was expected to result in more realistic exploitation patterns (SEDAR 2010a).

Initialization – Each simulation run was initialized with a different random seed. At the beginning of each simulation run, a unique realization of the coral reef environment was generated and used for the duration of the simulation. Prior to using the simulated fish population in the analyses, model processes were initially stepped forward for 100 years and fishing mortality was held constant at a rate that would generate exploitation characteristics of a population that was reduced to ~50% of its unfished spawning biomass.

Inputs – Model inputs were (1) statistical properties of vertical relief of the Florida Keys Reef tract (Appendix A), (2) statistical properties of black grouper growth in length and weight (Appendix B), (3) a stochastic stock-recruitment function and its parameter values, (4) a target annual fishing mortality rate, and (6) a schedule of natural mortality rates at length.

Submodels – Artificial landscapes were generated, rather than being obtained from actual mapping data because actual mapping data of fine spatial resolution was only available for parts of the Florida Keys reef tract that had been previously sampled by divers (Smith et al. 2011). A detailed description of the algorithm for generating artificial landscapes is provided in appendix A. Briefly, simulated landscapes consisted of 13,630 grid cells (545.2 km^2) denoting reef habitat that were interspersed among other habitat

types, which were considered not to be inhabited by fish in the simulations. Reef habitat

grid cells had three spatial properties that were consistent with actual statistical properties

of substrate vertical relief within the Florida Keys Reef tract. First, the spatial distribution

of contiguous grid cells was consistent with the narrow, but irregularly shaped cross-shelf

distribution of reef habitats that extend approximately 250 km between Key West and

Miami, Florida (Fig 4.1). Second, the simulated spatial distribution of vertical relief

patterns reflected empirical measures of spatial autocorrelation among neighboring grid

cells. Third, the irregularly shaped grid was divided into cross-shelf habitat strata

reflecting measured means and variances of vertical relief patterns within different reef

formation types, such as inshore patch reefs and offshore fore reefs (Appendix A).

The total number of new 1-year old individuals added to the population was a

Beverton and Holt function of mature female biomass with additional lognormally-

distributed process error (σ_R; Table 4.1). Spawning biomass was calculated by summing

the fractional contribution of each individual to the pool of mature spawning biomass

based on logistic maturity curve that was a function of fish length. Since black grouper is

a protogynous hermaphrodite (Crabtree & Bullock 1998), it was necessary to calculate

the proportional contribution of each individual as being a female, which was similarly

calculated as a decreasing logistic function of length (SEDAR 2010a). Beverton-Holt

stock-recruitment parameters were reparametrized in terms of steepness, z, recruitment at

unfished equilibrium, R_0, and unfished spawner biomass per recruit, $\tilde{S}$ (Table 4.1). The

value of R_0 scales the unfished population size and z is defined as the proportion of

unfished recruitment produced when the spawning stock is reduced to 20% of its

unfished biomass (Mace & Doonan 1988, Hilborn & Liermann 1998). The value of

steepness, which describes the shape of the stock-recruitment function, was specified as 0.75 to reflect expected values for demersal marine species tending to be and late-maturing broadcast spawners and to reflect empirical values that have been previously estimated for black grouper and for other reef fishes (Rose et al. 2001, Goodwin, Grant, et al. 2006, SEDAR 2009, 2010a). Values of $\tilde{S}$ and σ_R were obtained from per-recruit simulations in the absence of fishing and from published meta-analyses of stock-recruitment relationships, respectively (Table 4.1; Myers et al. 1999, Rose et al. 2001). Newly recruiting individuals were distributed to the artificial landscape grid in proportion to vertical relief, V, in each cell, c, using a discrete choice logit model (Train 2002):

$$p_c = \frac{\exp(\beta V_c)}{\sum\limits_{c} \exp(\beta V_c)}, \tag{4.1}$$

where β was a coefficient describing the slope of the relationship between occupancy probability and vertical relief. Coefficient values, β, were estimated in chapter 3, but owing to the statistical complexities involved in model fitting, there remains uncertainty about appropriate values. For brevity, a value of $\beta = 0.5$ was specified, which was similar to the occupancy relationship reported for black grouper in chapter 3.

Growth in length occurred according to the function described by von Bertalanffy (1938). Individuals were assigned unique growth trajectories at time of recruitment by varying assigned values for asymptotic length, L_∞, and the Brody growth coefficient, K (Table 4.2). The values of L_∞ and K for each individual were randomly drawn from normal and gamma distributions, respectively, with the mean and variance parameters estimated from empirical length-at-age data of black grouper (Appendix B).

Survival was a function of instantaneous rates of natural mortality, M, and fishing mortality, F, and was converted into a probability, $S = EXP(-M(L) - F)$. Monthly natural mortality ($M(L)$) was specified as an inverse function of length (Table 4.2; Lorenzen 1996, SEDAR 2010a). Parameters of the natural mortality function were scaled so that average lifetime natural mortality was 0.09 year^{-1}, which was obtained using Alagaraga's (1984) maximum age method and assuming that 5% of all individuals achieved a longevity of 33 years, which is the reported maximum known age for black grouper (SEDAR 2010a). Reference length, L_{Ref}, was specified as the length at which black grouper obtain maturity with a probability of 0.50 (Table 4.2). Individuals survived to the following month if their individual survival probabilities were greater than randomly generated numbers between 0 and 1. When an individual did not survive, mortality was attributed to fishing (F) if a second randomly generated number was less than the harvest fraction, $F / (F + M(L))$ (Table 4.2).

The population-level properties of the simulations were recorded as follows. Abundance was recorded by counting all individuals. Total biomass was calculated by summing individual weights. Exploitable biomass was calculated by summing individual weights for individuals with lengths greater than >610 mm. Monthly yield in numbers and weight were tallied from summing the individuals that were probabilistically removed from the population through fishing. Population-level processes produced by the IBM were compared to those that were expected from a traditional age-structured population simulator (Appendix C).

Simulation-based analyses

Having built a spatially explicit individual-based simulation framework of the environment and the dynamics of the fish population, simulation-based analyses were carried out by adding the following components to the simulation framework: (1) fisheries-independent surveys of relative population biomass, (2) population assessment procedures, and (3) decision-rules aimed at achieving pre-stated management objectives. Two types of simulations were carried out. First, simulated surveys and model-based population assessment procedures were used to calculate bias associated with estimation of maximum sustainable yield-based reference points. These simulations were conducted to elucidate the capabilities and limitations of surplus production model performance before introducing the additional complexity of connecting population assessments to rules for decision-making (Fig 4.2). Schaefer surplus production was used as a model-based assessment procedure because the Schaefer model allows simple data of annual yields and a biomass survey index to be used to estimate maximum sustainable yield (MSY) and biological status of a population. Second, management strategy evaluation (MSE) was used to link biomass surveys, population assessment, and rules for decision-making, thus enabling the performance of management strategies as whole to be evaluated under circumstances of imprecise biomass surveys. MSE was useful for addressing questions like: can biased and imprecise management quantities still be "good enough" for achieving management objectives or will there be considerable risk of management failure? And, can management advice based on surplus production modeling guide the fishery towards a management target despite its simplicity?

Fisheries independent monitoring – Relative biomass surveys were generated by simulating stratified random sampling of the fish population inhabiting the artificial landscape. The survey was designed using an optimality procedure for allocating survey effort among grid cells (Cochran 1977, Thompson 2012). The optimality procedure allowed the degree of observation error associated with observed relative biomass density of the fish population to be controlled directly through spatial allocation of sampling and total sampling effort. Sampling effort consisted of the total number of 200 m by 200 m grid cells that were visited. Using the cross-shelf habitat strata of the artificial landscape as sampling strata, inputs to the optimality procedure were: a running average of within-strata density variances from the previous three years of sampling, the size of each stratum in number of grid cells, and the target observation error of the mean density estimator of the fish population. From these inputs, the total survey effort and the allocation of effort among strata that would achieve the target observation error were calculated (Table 4.3; Cochran 1977, Thompson 2012). Observation error was defined as the coefficient of variation (CV) of the mean density estimator; that is, the survey design maintained a target CV across changes in true population biomass by adjusting sampling effort and spatial allocation of effort among strata. Consequently, the survey did not randomly add observation noise to true population density; rather, realistic aspects of survey design were simulated, including calculating future sampling effort based on previous (and potentially imprecise) surveys (e.g. Smith et al. 2011). Simulated surveys of exploitation-sized individuals were carried out in June of each year. The probability of observing an individual within a grid cell selected for sampling was specified as 0.01. Taken together, an individual fish was observed and had its weight recorded if the 200 m

by 200 m grid cell it inhabited was selected in the stratified random allocation of sampling effort and if the fish was subsequently randomly selected with a probability (or survey catchability) of 0.01.

Population assessment procedures – The assessment procedures were carried out using Schaefer (1954) surplus production, which predicts exploitable biomass (B^E) at time (*t*):

$$B_{t+1}^E = B_t^E + rB_t^E \left(1 - \frac{B_t^E}{B_0} \right) - Y_t^w \qquad (4.2)$$

where r is intrinsic rate of increase, and B_0 is unfished biomass, and Y^w is yield in weight. Two approaches to parameter estimation and management reference point estimation were used: (1) the catch-MSY approach developed by Martell and Froese (2012), which did not require a statistical fitting routine and only required a yield history (Y_t^w), and (2) a statistical fitting routine that required a biomass survey and yield as data inputs. The catch-MSY approach was used to contrast survey-based parameter and reference point estimates with an approach that did not rely on a biomass survey. The catch-MSY approach uses a numerical algorithm to identify plausible values of r and B_0, based on prior parameter ranges (Martell & Froese 2012). Input value ranges of r and initial biomass as a fraction of B_0 along with observed catch history are used to calculate annual biomasses from repeated draws from input value ranges (Equation (4.2)). Parameter values that are biologically plausible are retained and point-estimates are calculated as geometric means of retained values (Martell & Froese 2012). Based on the life history characteristics of simulated black grouper, r was specified from 0.05 to 0.5

and B_0 ranged between 10 times and 50 times the maximum catch (Martell & Froese

2012). A range for initial biomass as a fraction of B_0 was calculated as follows. If catch

in the first year of the times series divided by the maximum catch was <0.5, then the

initial biomass fraction was between 0.5-0.9, otherwise the initial biomass fraction was

between 0.3-0.6 (Martell & Froese 2012). Final biomass as a fraction of B_0 was assigned

a range of 0.1 to 0.9. An algorithm for the catch-MSY approach was available online

(http://www.fishbase.de/rfroese/) and was implemented in the statistical computing

software R (R Development Core Team 2012).

The statistical fitting routine to fit the Schaefer model to the biomass survey index

was implemented using AD Model Builder (Fournier et al. 2012). It was assumed that

observed survey biomass (U_i) was log-normally distributed:

$$U_t \sim \text{lognormal}\left(qB_t^E, \sigma_U^2\right) \tag{4.3}$$

where q is a proportionality constant and σ_U^2 is residual variance. The model was fit

annual estimates of population-wide mean density (i.e. parameter $\overline{U}_d$ in Table 4.3) for n

total years of collected data by minimizing a concentrated negative log-likelihood

function ($-\log \Lambda$),

$$-\log \Lambda = \frac{n}{2}\log\left(\frac{1}{n}\sum\left(\log\left(\frac{U_t}{B_t^E}\right) - \frac{1}{n}\sum\log\left(\frac{U_t}{B_t^E}\right)\right)^2\right), \tag{4.4}$$

where q and σ_U^2 were concentrated out of the log-likelihood by specifying these

parameters at their maximum likelihood estimators (Walters & Ludwig 1994, Fournier et

al. 2012). In statistical fitting, survey indices were assumed proportional to biomass, catches were recorded without error and treated as data inputs, and r, B_0 and initial biomass as a fraction of B_0 were estimated as free parameters. Bounds were placed on these three model parameters using the same ranges as the catch-MSY approach to aid in model fitting, but also to facilitate comparison between approaches. Parameter bounding assumptions were initially tested using simulated time series and were deemed to be appropriate for the life history of the simulated fish population.

Reference point estimation – Two factors were evaluated in reference point estimation: observation error of biomass surveys and the type of population assessment procedure. Relative biomass surveys were simulated with target CVs of 0.1, 0.3, and 0.5. Values of target CVs reflected variability of actual observation error associated with fish population surveys and reflected the ranges of observation error that have been previously assumed in simulation studies (Patterson 1998, Smith et al. 2011, Karnauskas, McClellan, et al. 2011, McCauley et al. 2012, Zhang 2013). The surplus production-based assessment procedures were: (1) a statistical fitting routine that required time series of yield and relative biomass, and (2) the catch-MSY approach that required yield, but no time series of relative biomass. For each combination of factor levels, two hundred datasets were simulated. The fishery was subject to a minimum harvest length restriction of 610 mm, which is consistent with actual regulations for black grouper in U.S. jurisdictions (SEDAR 2010a). After initialization of the simulation framework, 50-year biomass depletion-recovery scenarios were simulated by increasing fishing effort sequentially to 3.4-times its initial level over a 20 year period, followed by a rapid (10 year) reduction of effort to 1.4-times its initial level for the remaining 30 years (Fig 4.3).

This exploitation pattern caused population depletion, followed by recovery, and was implemented because a time series with both depletion and recovery is likely to provide the information needed to estimate both unfished biomass and the intrinsic rate of increase (Hilborn & Walters 1992, Walters & Martell 2004). Each simulation concurrently implemented three independent surveys of the simulated fish population, producing biomass indices with target CVs of 0.1, 0.3, and 0.5. Prior to analysis, the first five years were discarded from each 50-year depletion-recovery biomass time series. Discarding removed the initial adaptive phase of fisheries-independent monitoring procedure in which biomass surveys were adapting to achieve their target precisions. The simulation framework was also used to generate the "true" surplus production curve and management reference points for the simulated age-structured fish population. The true surplus production curve was generated by numerically determining the long-term (equilibrium) yield and population biomass for constant fishing mortality rates across a range of values. Plotting corresponding long-term population biomass against yield produces the true surplus production curve for the simulated population.

Management strategy evaluation – A harvest control rule consists of a pre-determined decision process that connects information about population assessment to fishery management tactics (Sainsbury et al. 2000). Changes to management tactics resulting from the control rule are aimed at achieving pre-stated management objectives. Two model-based control rules were implemented: (1) an MSY control rule was specified to guide the fishery towards the fishing mortality rate that would produce MSY and (2) a more precautionary control rule with a lower fishing mortality target. The MSY control rule assumed that the target fishing mortality rate was $F_{\text{target}} = F_{MSY} = 0.5r$, which was

based on the Schaefer surplus production model used to assess the population. Annual

adjustments to total fishing effort (f) in the current year (t) were based on parameter

estimates r and B_{t-1}^E, Y_{t-1}^W and f_{t-1}, and the target fishing mortality rate, F_{target}.

Annual effort adjustment was achieved by assuming that fishing effort was proportional

to fishing mortality:

$$F_{\text{target}} = qf_{\text{target}}, \tag{4.5}$$

and that fishing mortality in the previous year could be estimated as

$$F_{t-1} = -\log\left(1 - \frac{Y_{t-1}^W}{B_{t-1}^E}\right) = qf_{t-1}. \tag{4.6}$$

Solving for q in each of the two previous equations leads to the ratio

$$\frac{F_{t-1}}{f_{t-1}} = \frac{F_{\text{target}}}{f_{\text{target}}}, \tag{4.7}$$

which can be solved for the value of f_{target}. Total annual effort was then set to the

resulting target effort. Total annual effort was divided equally among the 8 month of the

fishing season. The precautionary control rule was implemented to investigate a situation

where uncertainty in relative biomass trends (low precision surveys) could be deemed by

managers as carrying excessive risk of contributing to undesirable management

outcomes. Instead of $F_{MSY} = 0.5r$, a more precautionary target of $F_{\text{target}} = 0.5F_{MSY}$ was

used. Fishing mortality rates that are more conservative than F_{MSY} have been widely

proposed (Quinn & Deriso 1999).

Two additional conditions were added to the use of each model-based control

rule: (1) effort was not increased by more than 20% between consecutive years to avoid

large effort fluctuations; and, (2) in instances of model fitting failure, effort was held

constant at the previous year's value as a status quo decision until fitting could be

attempted again in the following year. Some additional assumptions were required to use

the catch-MSY approach in conjunction with the optimal yield control rule. The catch-

MSY approach searches over parameter combinations to identify biologically plausible

combinations of r, B_0, and initial biomass. For each set of parameters and the observed

catch history, equation (4.2) can be used to estimate biomass in the terminal year in the

time series. By making these calculations over all plausible parameter combinations, and

taking the geometric mean of terminal biomass estimates, the catch-MSY approach

theoretically provides all necessary parameter values for calculation of the MSY control

rule (Equation (4.7)).

For contrast with the model-based control rules, a model-free control rule was

implemented, which relied on relative biomass surveys to inform decision-making

without using historical catch data or a model of population dynamics to provide

estimates of management reference points or population status. Model-free control rules

are often based on relative biomass trends because they do not incorporate yield data,

which would be necessary to scale trends to absolute biomass (Apostolaki & Hillary

2009). Accordingly, a simple control rule was formulated that maintained current relative

biomass with respect to a historical relative biomass reference point. Similar approaches

have been implemented elsewhere (Hilborn et al. 2002, Apostolaki & Hillary 2009). The

model-free control rule reflected the idea that data limitations (i.e. no catch data) could

restrict the use of MSY-based reference points in decision-making. Annual effort

adjustments were made following a general approach developed by Apostolaki and

Hillary (2009):

$$f_t = \left(\frac{1}{10} \sum_{j=t-10}^{t-1} f_j \right) \gamma_t,$$ (4.8)

where a moving-average of the previous 10 years effort levels was adjusted using a

multiplicative factor, γ_t. The multiplicative factor was calculated as:

$$\gamma_t = \frac{\frac{1}{10} \sum_{i=t-10}^{t-1} U_i}{U_{historic}}$$ (4.9)

where U is the moving average relative biomass survey over a period of the previous 10

years, and $U_{historic}$ is the historical relative biomass reference point. A ten year moving

average was selected to control inter-annual effort variation. In applying the model-free

control rule, effort was not increased by more than 20% between consecutive years to

impart consistency with model-based control rules.

In summary, MSE was used to evaluate management strategy performance in

circumstances where: (1) relative biomass surveys varied in terms of estimation error and

were used along with yield time series to inform model-based control rules based on

reference points derived from MSY; (2) relative biomass surveys were not available and

only yield time series were used to inform MSY-based control rules; and (3) relative

biomass surveys varied in terms of estimation error and were used to directly inform a

model-free control rules. In the procedure for reference point estimation, target CVs of

0.1 and 0.3 performed similarly, thus MSE was performed with a survey target CVs of

0.2 in addition to the more extreme CV of 0.5. In addition, because natural variation in

population dynamics was built into the simulations, it was important to first identify the

extent to which biomass changes could be expected to be controlled based on perfect

information about the population and its fishery. Consequently, a perfect information

version of the MSY control rule was simulated where fishing effort was specified directly

and without error at the level associated with maintaining the fish population at $1/2B_0$,

which corresponds to the biomass that produces MSY in the Schaefer model.

Simulations were carried out as follows. After model initialization, 50 year

depletion-rebuilding scenarios were constructed (discarding the first five years a survey

adaptive phase.). The resulting 45-year catch, effort, and relative biomass survey time

series were used in assessment procedures and control rules to adjustment of annual

fishing effort. The adjusted effort level was implemented and the simulation was stepped

ahead one year (in one month increments). Then, the time series of catch, effort, and

survey biomass were updated with the preceding year's values and assessment and

controls rule procedures were again carried out with the now longer time series. Each

control rule was implemented in this manner for 50 years.

Results

Reference point estimation

In fitting surplus production models in AD Model Builder, parameter estimates

could not be obtained for all simulated datasets. Model fitting was considered to have

failed when either no solution could be obtained or when parameter estimates were

within close proximity to parameter bounds. When relative biomass surveys having target

CVs of 0.1 were used in model fitting, 21% of simulated datasets failed the fitting

process, and failure rate increased as survey precision declined (Fig. 4.4C, E & G). This

failure rate may be indicative of general fitting challenges associated with biomass

dynamics modeling, but failures were also subject to limited scrutiny in batch-processing,

which could have otherwise been given more attention by an analyst.

Mean MSY estimates obtained from all levels of survey precision tended to be

overestimated (Figs. 4.4A, C, E & G). Under simulations using surveys with target CVs

of 0.1, MSY was least biased, although the magnitude of the bias was still concerning

(mean bias=32%, range:-4% to 104%; bias equation: *% bias=(estimate-true)/true*100*).

Further, plotted surplus production curves illustrate the potential for unreliable metrics

about the population under evaluation in any individual data realization (Fig. 4.5). In

addition to overestimating MSY, biomass expected to produce MSY was also

overestimated. This result was attributed to differences in the shape of the surplus

production function between true and predicted curves (Fig 4.5). That is, true biomass

expected to produce MSY was $\cong 0.3B_0$ and not $= 0.5B_0$ that is predicted by the Schaefer

surplus production model.

The effect of survey observation error on parameter estimation uncertainty was

also a cause for concern. As survey indices became less precise (i.e. target CVs

increased), MSY was estimated with less certainty (Fig 4.4B, D, F, H). This result

suggested that imprecise surveys will inflate estimation uncertainty associated with MSY.

Across all simulated surveys, estimation precision of MSY was not strongly correlated

with mean bias (Pearson's *r=0.09*), suggesting that biased estimates were not necessarily

imprecise and vice versa. Since $MSY = rB_0 / 4$, it was also instructive to examine

whether estimation uncertainty in r, B_0, or both, was contributing to estimation uncertainty in MSY. Correlation between estimation precision (as CV) of B_0 and r was high (Pearson's correlation coefficient=*0.85*). Accordingly, precision of MSY was affected by precision of r (Pearson's correlation coefficient =*0.54*) and by precision of B_0 (Pearson's correlation coefficient =*0.84*).

Using the catch-MSY approach, mean MSY was routinely overestimated, but MSY tended to be less variable among simulations than when using the fitting-based estimation routine (Fig. 4.6B). Thus, similar MSY estimates among simulations were obtained without reliance on survey indices. Further, MSY estimates from the catch-MSY approach were the least biased relative to true MSY (mean bias=31%, range: 0% to 72%). The performance of the catch-MSY approach may have been enhanced by the fact that simulated catches were reported without error and parameter input ranges were known to be reasonable for the life history of the simulated population.

Management strategy evaluation

Perfect information – In the Schaefer surplus production model, MSY is produced when a population is fished to reduce biomass to ½ of the biomass expected in the unfished state. Carrying out simulations that were given perfect information about the level of fishing effort that would guide biomass towards ½ of the unfished exploitable biomass was useful for establishing properties of the MSE (Fig 4.7). Perfect information simulations illustrated that, given the properties of the simulation framework, fishing at F_{MSY} could be expected to result in population recovery to $1/2B_0$ over the 50 timeframe used in the simulations. Also, perfect information resulted in fluctuations above and below the target biomass ($1/2B_0$). This result was expected and reflected

natural fluctuations in recruitment that prevent fish populations from being precisely controlled at target biomass levels (Larkin 1977, Hatton et al. 2006). These simulations also revealed that despite perfect information about effort levels, yield would fluctuate because of natural recruitment variation. During the final 10 years of each simulation, inter-annual variation in yield had a mean CV of 0.04.

MSY control rule – The MSY control rule was not effective in guiding population biomass towards $1/2B_0$, but protection of the population from undesirable biomass declines was reasonably good (Fig 4.8). The MSY control rule resulted in 10% and 12% of simulated biomass trends being greater than $1/2B_0$ after 50 years under target survey CVs of 0.2 and 0.5, respectively; rather than fluctuating in proximity to $1/2B_0$ like the perfect information control rule. The MSY control rule fared better at avoiding low biomass levels, with 6% and 13% of simulation runs falling below $0.2B_0$ under survey target CVs of 0.2 and 0.5, respectively. In simulations that fell below $0.2B_0$, the cause of population collapse was underestimation of the true fishing mortality rate. Underestimation of fishing mortality rate occurred because the fitting routine grossly overestimated current exploitable biomass; in some instances by an order of magnitude. Consequently, the control rule increased fishing effort – and this often occurred in consecutive years – because fishing mortality was incorrectly perceived to be much lower than F_{MSY}. Population declines were also accelerated by overestimation of F_{MSY}, which was caused by overestimation of r (noting that $F_{MSY} = 0.5r$). Inter-annual variation in catches during the final 10 years of each simulation had mean CVs of 0.13 and 0.17 for fitting routines with survey target CVs of 0.2 and 0.5, respectively.

In reference point estimation, the catch-MSY approach produced quite consistent MSY estimates among simulations. However, when the catch-MSY approach was coupled with the control rule aimed at adjusting fishing effort, management strategy performance was poor (Fig 4.6C). This management strategy did not perform well at avoiding low biomass levels, with 27% of simulations falling below $0.2B_0$. The difficulty in using the catch-MSY approach to adjust fishing effort was that biomass estimates were highly unreliable; however, this estimation procedure was designed to estimate MSY and not necessarily to estimate current biomass. There was no clear directionality in bias of biomass estimated, simply that a control rule dependent on current biomass estimates did not function well when biomass estimates were derived from the catch-MSY approach. In fact, Martell and Froese (2012) propose an alternative MSY-based control rule for total allowable catch regulation that may preform much better than the effort-based control rule used in these simulations.

Precautionary control rule – In contrast to the MSY control rule, the precautionary control rule ($F_{\text{target}} = 0.5F_{MSY}$) resulted in higher average exploitable biomass (Fig. 4.9). The precautionary control rule resulted in 70% and 65% of simulated biomass trends being greater than $1/2B_0$ after 50 simulated years under target survey CVs of 0.2 and 0.5, respectively; whereas the MSY control rule resulted in <15% of simulations above this biomass level. Not surprisingly, biomass protection was also improved with only 1% and 4% of simulation runs falling below $0.2B_0$ under survey target CVs of 0.2 and 0.5, respectively. Inter-annual variation in catches was more in-line with the variation expected from the perfect information control rule (catch CVs 0.05 and 0.07 for survey target CVs of 0.2 and 0.5, respectively).

Model-free control rule – The model-free control rule performed well even when surveys had target CVs of 0.5, as biomass fluctuations associated with effort changes were not extreme and rarely trended towards population collapse (Fig 4.10). Slightly poorer biomass stability was associated with surveys with higher target CV, but this control rule fared well at avoiding low biomass levels, with 0% and 0.5% of simulations falling below $0.2B_0$ under survey CVs of 0.2 and 0.5, respectively. Inter-annual variation in catches during the final 10 years of each simulation run had mean CVs of 0.08 and 0.11 for surveys with CVs of 0.2 and 0.5, respectively.

Discussion

Simulations revealed how management strategies of long-lived reef fishes functioned as a whole when faced with imprecise data. This study revealed three specific considerations about using data-limited management strategies to support fisheries management of reef-associated species. First, simulations revealed a trade-off between survey biomass precision and precautionary decision-making. Second, simulations confirmed existing knowledge about the use of surplus production modeling in assessing population status of long-lived fishes with life history characteristics like those of black grouper. Third, simulations revealed a trade-off between the types of management objectives that can be achieved and the data inputs that would be required to do so.

Simulations suggested that balancing survey precision, population assessment, and the degree of precaution taken in decision-making are important and interconnected considerations in fisheries management. In the fitting-based estimation routine that used a surplus production model, survey precision had a clear role in instances of undesirable

biomass declines, as the number of simulation runs where biomass fell below $0.2B_0$ was twice as high for surveys with target CVs of 0.5 as it was for surveys with CVs of 0.2. Simulations also suggested that surplus production modeling itself, regardless of survey precision, contributed to biases in parameter estimation. Fitting the surplus production model to relative biomass recorded without observation error revealed assessment model inadequacy (Fig 4.4A). Taken together, survey precision combined with the fitting-based estimation routine led to frequent failure to achieve the pre-stated biomass target. When increasingly noisy survey data were used as inputs to a potentially inadequate assessment model, erosion of signals about population trajectories occurred, and thus, bias and estimation error of population parameters was amplified. Contrasting the perfect information MSY control rule against the MSY control rule estimated parameters demonstrates that imprecise surveys coupled with surplus production performed modestly, at best, in achieving target biomass and at preventing undesirable biomass declines (Fig. 4.7 & 4.8). Further, inter-annual variation in catches under the estimated MSY control rule were higher than expected from the perfect information MSY control rule. This result exemplifies the instability of annual effort estimates produced by the fitting routine and control rule, despite long time series of yield and relative biomass being available to the fitting routine. When more precautionary management targets were chosen in conjunction with the use of the surplus production-based fitting routine, undesirable biomass declines were largely avoided. Thus, management strategies aimed at ensuring biomass protection, and which rely on surplus production modeling coupled with imprecise biomass surveys, can be reasonably successful if precautionary management targets are chosen.

An additional dimension to the use of surplus production in informing decision-making was the suitability of surplus production modeling in describing the temporal dynamics of the simulated fish population. Surplus production modeling is sometimes considered an overly simplistic representation of population dynamics; however, its simplicity contributes to its importance in fisheries management (Zhang 2013). Simulations confirmed the expectation that surplus production modeling may produce biased outcomes for long-lived and low-productivity species like black grouper. In reference point estimation, surplus production-based assessment procedures led to overestimation of MSY regardless of survey precision (Fig. 4.4). Overestimates of MSY have been previously obtained using surplus production modeling for long-lived species with low intrinsic rates of population increase (Hilborn 1979, Mohn 1980, Zhang 2013). It is thus important to consider whether MSY-based reference points obtained from surplus production modeling could be risk-prone in circumstances of low intrinsic growth rates; which was the case for the simulated black grouper in this study. For long-lived species that are generally vulnerable to overexploitation, fishing mortality targets that are substantially lower than F_{MSY} may be necessary to address this uncertainty when reference points are obtained from surplus production modeling.

In addition, several additional issues related to the use of surplus production modeling were not addressed in this study. Surplus production models assume stationarity of the production process and simulated datasets were consistent with this assumption. However, production stationarity is unlikely to be reasonable assumption for actual fish populations. Under the condition of non-stationarity, it would be interesting to contrast the performance of surplus production modeling against more complex

assessment procedures (Walters et al. 2008, Martell & Froese 2012). Simulation modeling could also be used to address uncertainties associated with fitting surplus production models to age-structured fish populations, such as whether allowing for asymmetry in the surplus production curve could provide improved estimation of MSY and population productivity (Pella & Tomlinson 1969, Fox 1970).

Contrasting outcomes between model-based and model-free assessment procedures was instructive about potential conflicts that may arise between what is achievable in data limited situations and what is intended to be achieved by stated management objectives. In the absence of a population dynamics model, the model-free control performed as well at avoiding undesirable biomass declines. However, performance of the model-free control rule was evaluated against the objective of maintaining historical relative biomass, rather than against MSY-based reference points. Model-based approaches are usually necessary for estimating population status and MSY-based reference points. This situation illustrates that management objectives and data availability are interconnected, with each potentially influencing the other. Thus, in addressing data limitations, legislative mandates may determine management objectives, and consequently, data collection priorities. Conversely, limited data availability may constrain the management objectives that can be achieved. For instance, approaches for population assessment are needed for data-poor fisheries that conform to the operational guidelines of the United States Magnusson-Stevens Fisheries Conservation and Management Act (Restrepo & Powers 1999, NOAA 2007). This may be particularly true for the grouper-snapper species complex as many members of this complex, including

recreational species, lack data inputs necessary to support assessment procedures (Ault, Bohnsack, et al. 2005, Porch et al. 2006, Ault et al. 2013).

MSE can be generally useful for addressing questions related to data limitations, like: can existing sampling designs be informative enough to avoid the need for additional data collection? And, what management objectives are achievable, given the data that is available? MSE could be used to tailor management strategies subject to data reliability concerns for specific fish populations. Design of model-free control rules remains on open research area where simulation modeling can be valuable (Hilborn et al. 2002, De Oliveira & Butterworth 2004, Prince et al. 2011). Model-free control rules have been developed for fish stocks in northern latitudes, but their remains a paucity of model-free control rule development for tropical fisheries (Pomarede et al. 2010, Cook 2013). Similarly, instances where unreliable yield data are not useful in population assessment call for novel approaches to population assessment and harvest regulation (Porch et al. 2006, Mesnil et al. 2009). In addition, the frequency of population assessments and time lags between data collection, assessment, and subsequent implementation of control rules are dimensions of MSE that need further exploration (Kell et al. 2003).

Constructing a spatially explicit IBM was particularly useful for addressing the effects of noisy survey biomass indices on management performance because several sources of the stochastic behavior of natural systems could be uniquely specified. For instance, natural process variation was incorporated in the simulations through individual growth heterogeneity and through recruitment deviations. Variation among individuals is inherent to fish populations and IBMs are well suited to incorporating biological characteristics that are otherwise difficult to incorporate in numerical simulations, like

individual variation in size and growth rate (Hart 2001, Bunnell & Miller 2005, Russo et al. 2009, Alós et al. 2010). In addition, anomalous events like strong recruitment deviations produce a signal in survey indices that persists over several years as a large/small cohort ages. Observation error was controlled in simulations through sampling intensity among disparate habitat types, but importantly, decisions about sampling intensity were themselves dependent on previous sampling events, which were subject to imprecision. Consequently, simulated noisy biomass surveys represented biological and sampling processes that separately and successively introduced process and observation error into observed data. This approach better represents the data and conditions faced by scientists and managers and avoided the unrealistic presumption that simulated survey trends fluctuate in a simple manner consistent with a single statistical distribution (Walters & Martell 2004). Spatially explicit simulations of fish populations that incorporate habitat heterogeneity are uncommon as are simulations that integrate survey design considerations with population assessment procedures and decision-making (Sainsbury 1991, Meester et al. 2001, 2004, McDonald et al. 2008, Thorson et al. 2012). Thus, simulation models of this type appear to be particularly useful for addressing design considerations for monitoring substrate associated fishes (Smith et al. 2011, Richards et al. 2011). Clearly though, understanding of the connections between the subtleties of survey design, statistical fitting routines used in population assessment, and harvest control rules remains an important research priority. This is one example of where simulation-based analyses will continue to be an essential to fisheries science.

Table 4.1. Population-level processes. Recruitment parameters based on life history information (Rose et al. 2001, SEDAR 2009), maturity and sex transition data estimated in chapter 2 and using data from SEDAR (2010a). Dashes indicate derived quantities, i is individual identifier, and t is annual time step.

Processes	Equations and algorithms		Parameters	Values
Annual recruitment	$R_t = \dfrac{B_{t-1}}{a+bB_{t-1}} \exp\left(\text{Normal}\left(0,\sigma_R^2\right)\right)$ $a = \tilde{S}\dfrac{(1-z)}{4z}$ $b = \dfrac{5z-1}{4zR_0}$	R_t	Annual recruits	-
		B_t	Spawning biomass	-
		a, b	Stock-recruitment parameters	-
		R_0	Unfished recruitment	50,000
		z	Steepness	0.75
		$\tilde{S}$	Unfished SBR	45
		σ_R	Log-scale standard deviation	0.6
Spawning biomass (kg)	$B_t^s = \sum_i W_i \text{Mat}_i \text{Female}_i$	B_t^s	Spawning biomass	-
Proportion mature	$\text{Mat}_i(L_i) = \dfrac{1}{1+\exp\left(-\kappa\left(L_i - L_{\text{mat}}\right)\right)}$	κ	Curvature	0.0139
		L_{mat}	Inflection (mm)	832.7
Sex transition	$\text{Female}_i(L_i) = \dfrac{1}{1+\exp\left(-\theta\left(L_i - L_f\right)\right)}$	θ	Curvature	-0.0158
		L_f	Inflection (mm)	1213.7

Table 4.2. Individual-level processes. Growth parameters estimated in Appendix B, weight parameters estimated in chapter 2, mortality parameters obtained from longevity and functions developed by Lorenzen (2000) and Alagaraja (1984). Dashes indicate derived quantities, i is individual identifier, and t is annual time step

Processes	Equations and algorithms	Parameters		Values
Growth in total length (mm)	$L_i(t) = L_{\infty,i}\left(1-\exp\left(-K_i\left(t_i - t_0\right)\right)\right)$ $L_{\infty,i} \sim N\left(\mu_\infty, \sigma_\infty^2\right)$ $K_i \sim \Gamma\left(s_K, r_K\right)$	$L_i(a)$	Total length	-
		$L_{\infty,i}$	Asymptotic length	-
		K_i	Brody growth coefficient (yr^{-1})	-
		μ_∞	Mean asymptotic length (mm)	1362
		σ_∞	Variance asymptotic length	38
		s_K / r_K	Mean growth coefficient (t^{-1})	0.138
		s_K / r_K^2	Variance growth coefficient	0.014
		t_0	Coefficient	-0.87
Whole weight conversion (kg)	$W_i = a_W L_i^{b_W}$	W_i	Total weight	-
		a_W	Factor	4.46 x 10^{-9}
		b_W	Factor	3.18
Mortality (year$^{-1)}$)	$M_i(L_i) = M_{\text{Ref}} \dfrac{L_{\text{Ref}}}{L_i}$	M_{Ref}	Reference mortality (t^{-1})	0.12
		L_{Ref}	Reference length	832.7

Table 4.3. Equations used in optimality procedure for survey effort allocation for stratified random sampling, described by Cochran (1977) and Thompson (2012). h is cross-shelf habitat strata, d is sampling-domain-wide estimate, T is the number of strata.

Parameter	Equation	Definition
$\overline{U}_h$	$\overline{U}_h = \dfrac{1}{g_h} \sum\limits_{i=1}^{g_h} U_{h,i}$	Sample mean for stratum h
g_h		Grid cells sampled in stratum h
var_h	$\mathrm{var}_h = \dfrac{1}{g_h - 1} \sum\limits_{i=1}^{g_h} \left(U_{h,i} - \overline{U}_h \right)^2$	Sample variance for stratum h
$\overline{U}_d$	$\overline{U}_d = \sum\limits_{h=1}^{T} w_h \overline{U}_h$	Sampling-domain-wide mean biomass density
w_h	$w_h = \dfrac{G_h}{\sum\limits_{h=1}^{T} G_h}$	Stratum weight
G_h		Total number of grid cells in stratum h
$\mathrm{var}\left[\overline{U}_d\right]$	$\mathrm{var}\left[\overline{U}_d\right] = \sum\limits_{h=1}^{T} w_h^2 \left(\dfrac{G_h - g_h}{G_h} \right) \dfrac{\mathrm{var}_h}{g_h}$	Domain wide variance of mean biomass density
g^*	$g^* = \dfrac{\left(\sum\limits_{h=1}^{T} w_h \sqrt{\mathrm{var}_h} \right)^2}{\mathrm{var}^* + \dfrac{1}{\sum\limits_{h=1}^{T} G_h} \dfrac{1}{T} \sum\limits_{h=1}^{T} w_h\, \mathrm{var}_h}$	Total number of samples required to achieve target variance
var^*	$\mathrm{var}^* = CV^* \overline{U}_d$	Target variance
CV^*		Target coefficient of variation of domain wide biomass density estimate
g_h^*	$g_h^* = g^* \dfrac{w_h \sqrt{\mathrm{var}_h}}{\sum\limits_{h=1}^{T} w_h \sqrt{\mathrm{var}_h}}$	Optimal allocation of total samples among strata
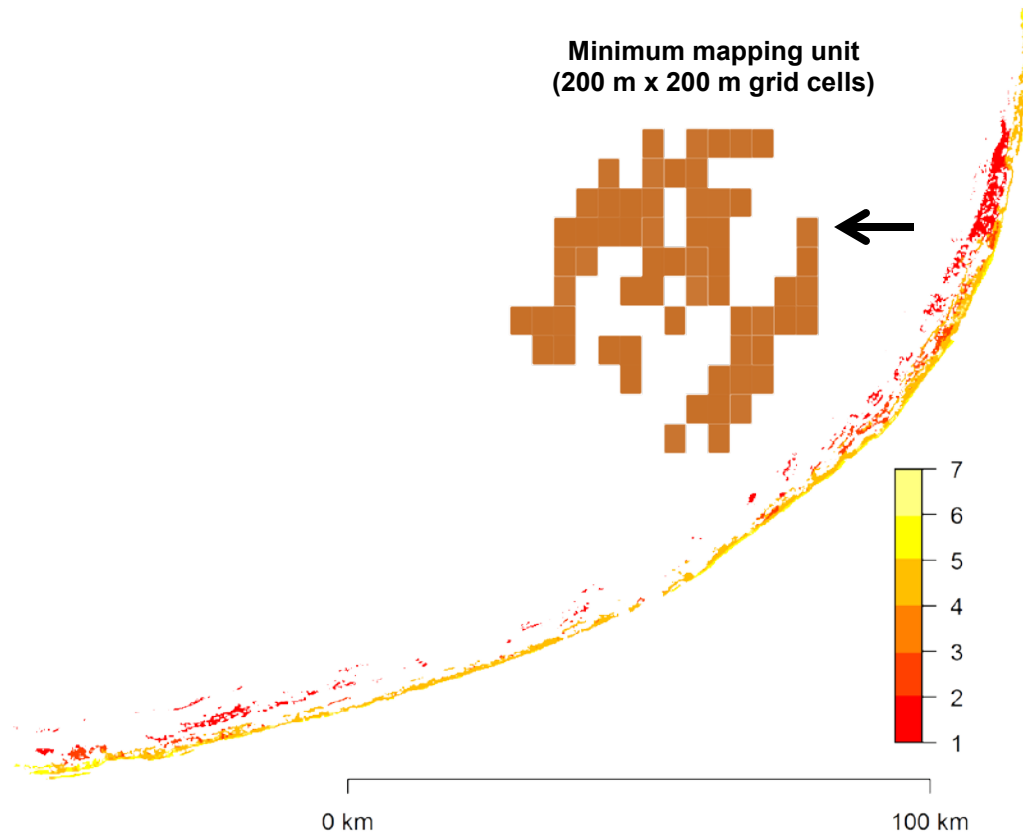
Figure 4.1. Spatial hierarchy of the artificially-generated reef-scape of the Florida Keys coral reef ecosystem. Scale (numbers 1 to 7) refer to the cross-shelf habitat strata used to distribute individual fish and to stratify survey effort. Cross-shelf habitat strata were: (1) low-medium rugosity inshore patch reefs, (2) low-medium rugosity mid-channel patch reefs, (3) low-medium rugosity offshore patch reefs, (4) high rugosity offshore patch reefs, (5) low-medium rugosity outer fore reef, (6) low-medium rugosity outer fore reef, and (7) high rugosity outer fore reef.
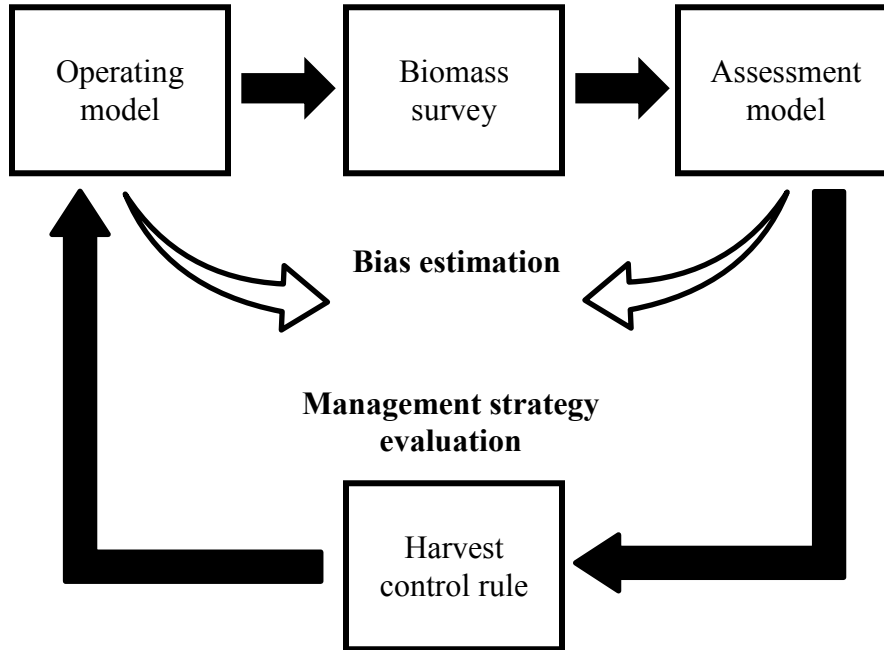
Figure 4.2. Simulation framework for bias estimation and management strategy evaluation. The operating model consists of the simulated fish population and its fishery.
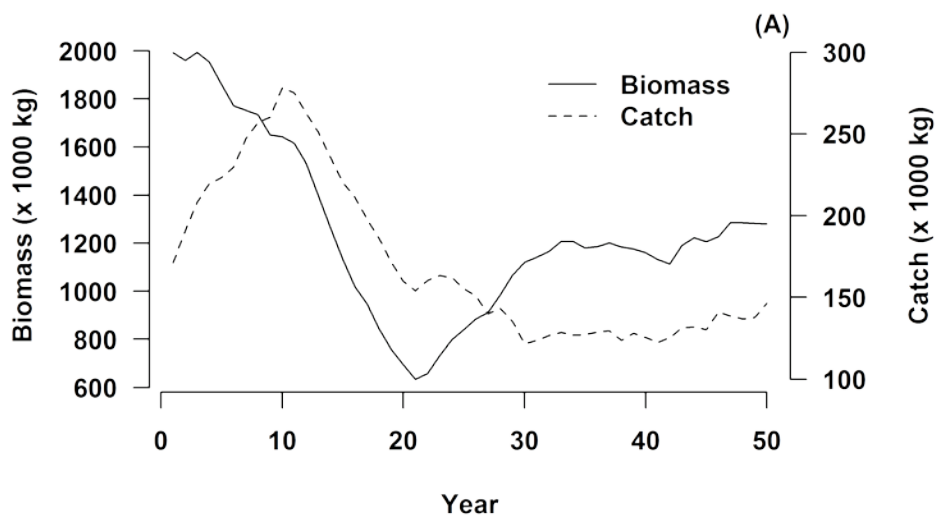
Figure 4.3. Example simulated time series of exploitable biomass and catch.
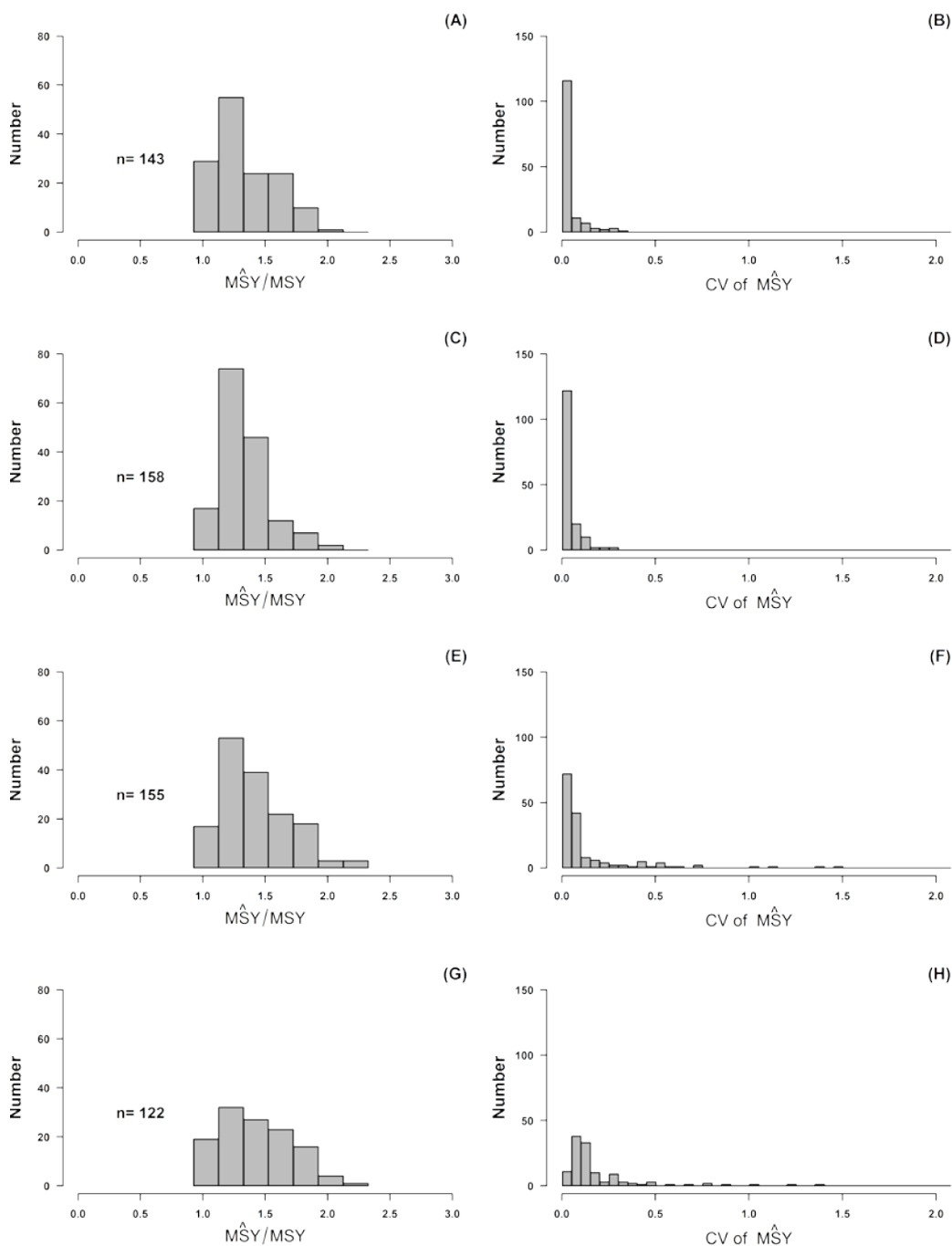
Figure 4.4. Estimated maximum sustainable yield ($\widehat{MSY}$), divided by the true value with associated estimator precision reported as coefficient of variation (CV). Shown are estimates obtained from fitting a Schaefer production model to population density recorded without observation error (A,B), and survey target CV of 0.1 (C,D), survey target CV of 0.3 (E,F), and survey target CV of 0.5 (G, H). n refers to the number of successful fits obtained from 200 simulated datasets.
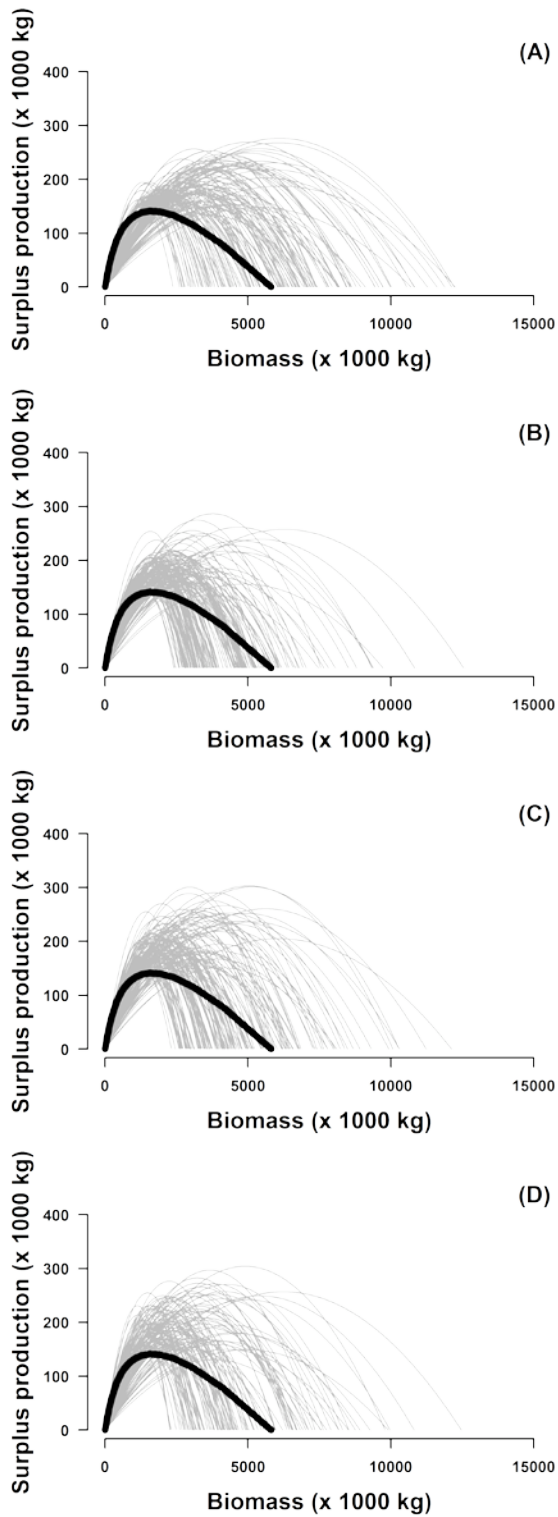
Figure 4.5. True surplus production (thick lines) and estimated surplus production (thin lines) obtained from fitting a Schaefer production model to population density recorded without observation error (A) and from survey indices with target CVs of 0.1, (B), 0.3 (C) and 0.5 (D).
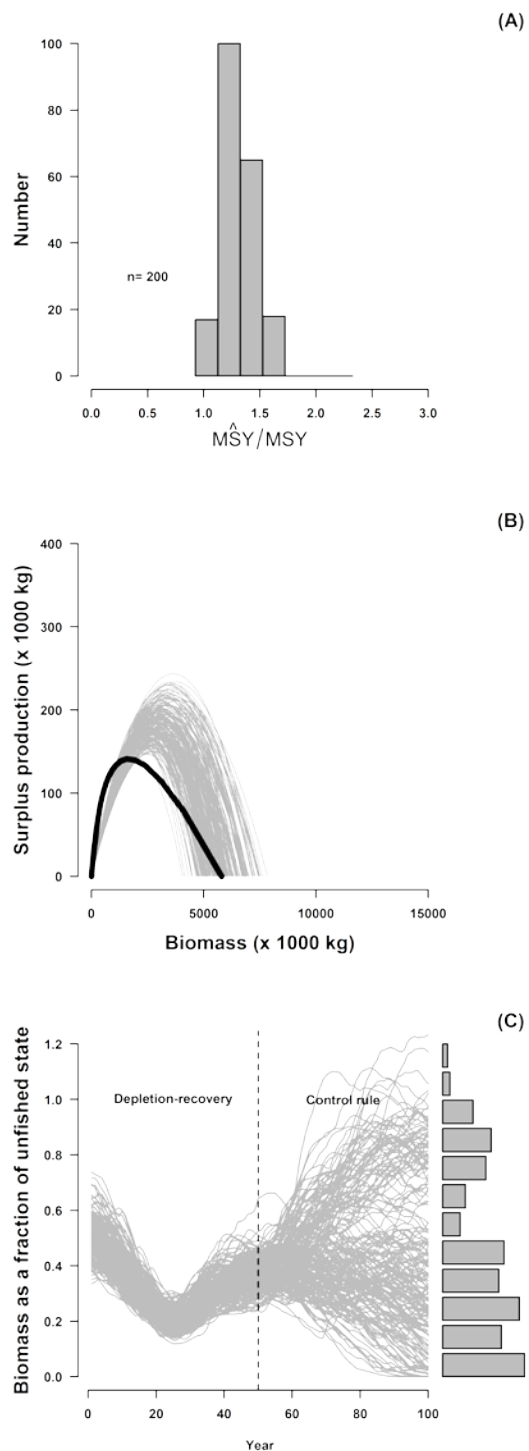
Figure 4.6. Estimated maximum sustainable yield ($\widehat{MSY}$) divided by the true value (A) based on the catch-MSY approach. Surplus production curves (B; thick line is expected curve, thin lines are predicted curves) and MSY control rule (C). Histogram shows distribution of terminal biomass as fractions of unfished state for 200 simulation runs.
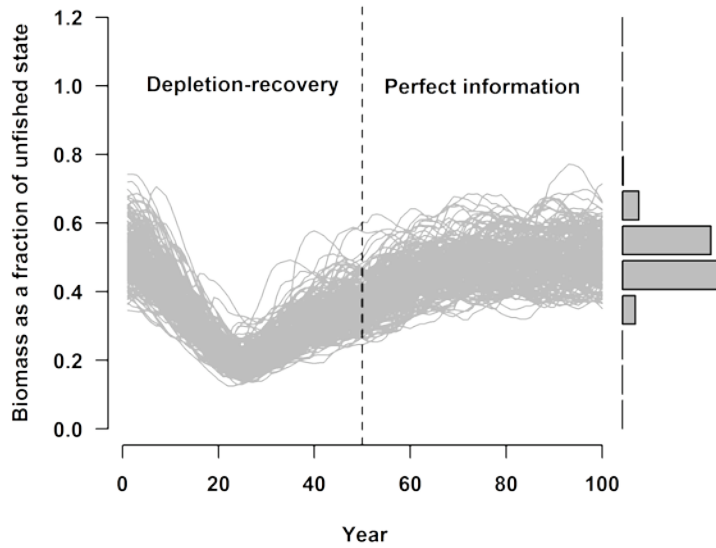
Figure 4.7. Simulated perfect information about target fishing effort following a 50-year period of biomass depletion and recovery. Histogram shows distribution of terminal biomass as fractions of unfished state for 200 simulation runs.
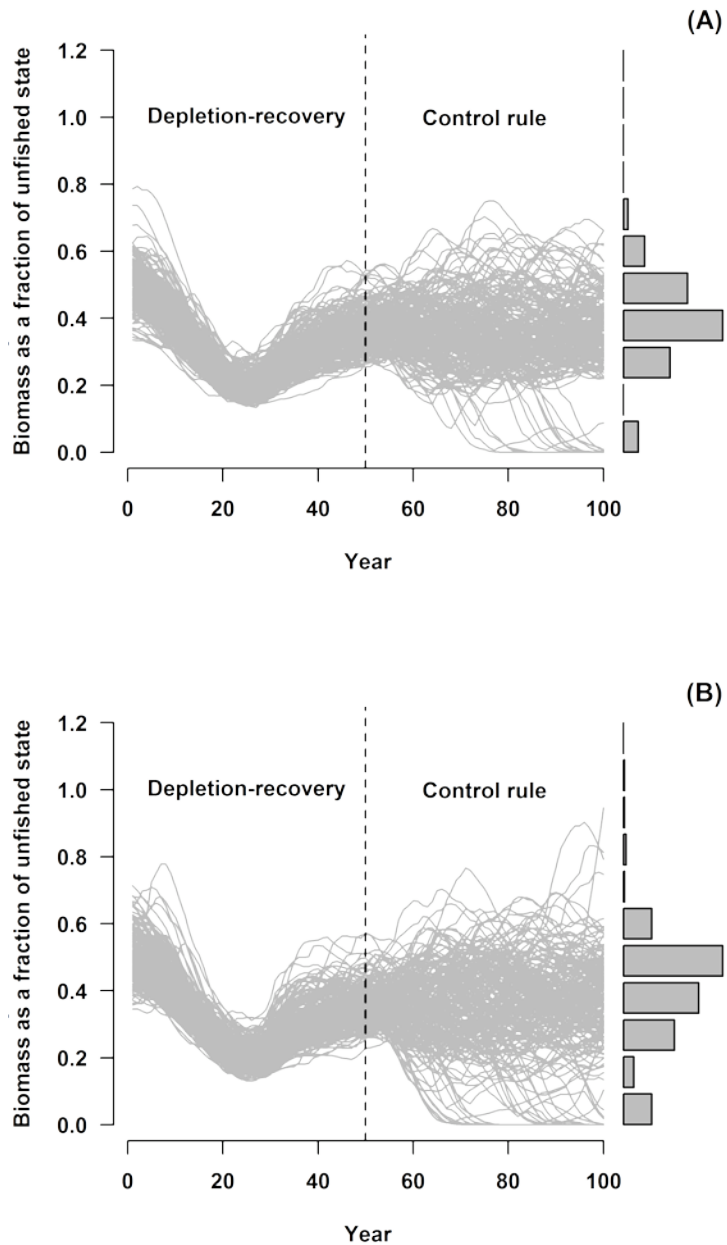
Figure 4.8. Simulated MSY control rule informed by fitting routine with survey target CVs of 0.2 (A) and 0.5 (B). Histograms show distribution of terminal biomass as fractions of unfished state for 200 simulation runs.
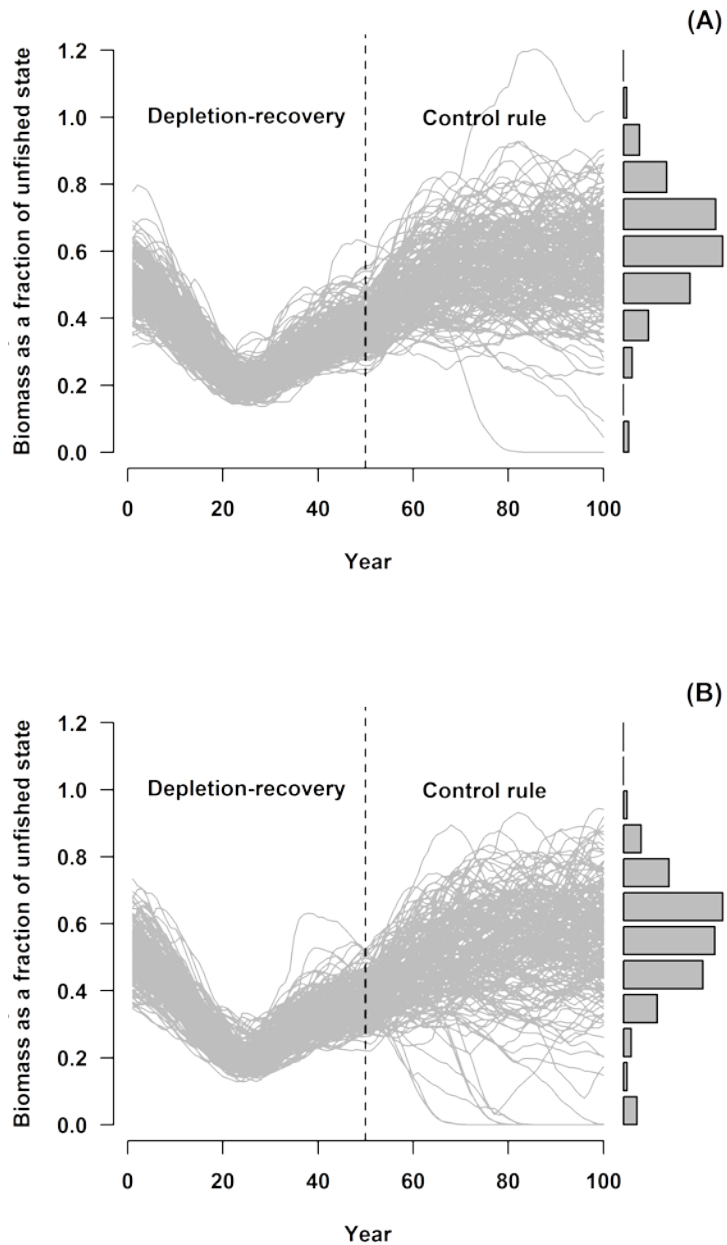
Figure 4.9. Simulated precautionary control rule informed by fitting routine with survey target CVs of 0.2 (A) and 0.5 (B). Histograms show distribution of terminal biomass as fractions of unfished state for 200 simulation runs.
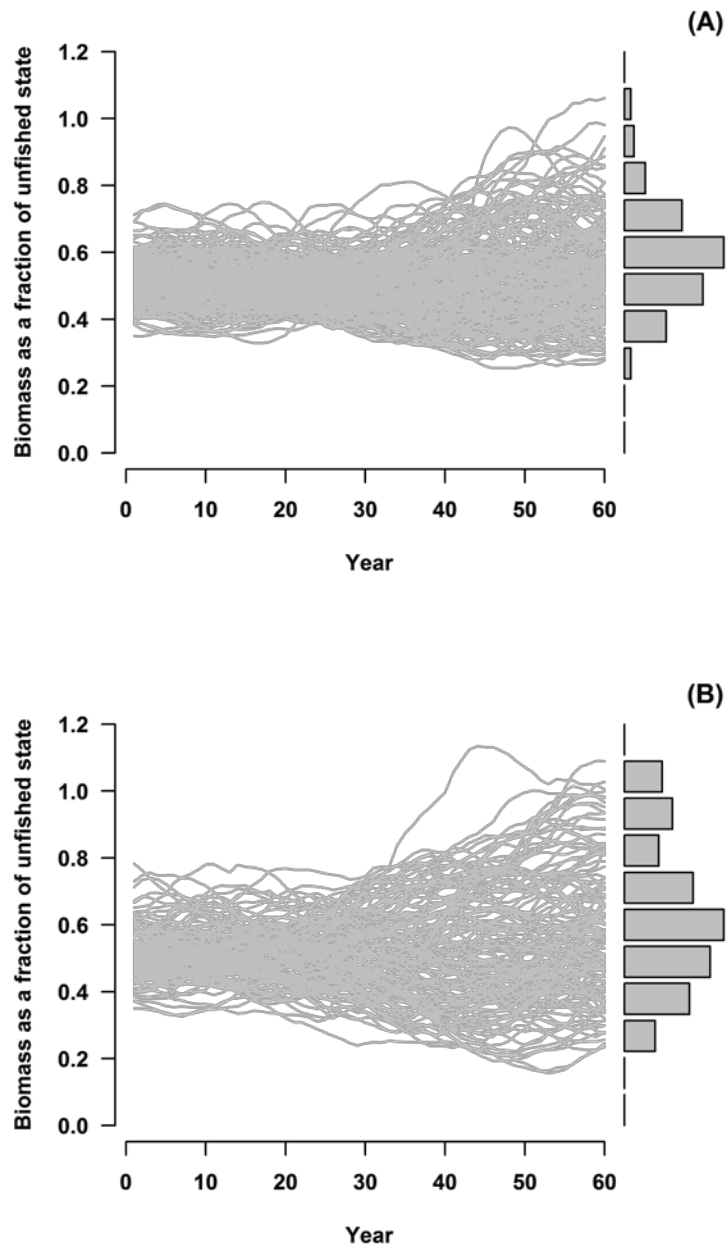
Figure 4.10. Simulated model-free control rule with survey target CVs of 0.2 (A) and 0.5 (B). Histograms show distribution of terminal biomass as fractions of unfished state for 200 simulation runs.

CHAPTER 5: MARK-RECOVERY FOR SPATIAL ASSESSMENT OF FISHERIES MANAGED USING MARINE RESERVES

Summary

Marine reserves are becoming widely implemented along with conventional fisheries controls as integrated approaches to fisheries management. However, spatial heterogeneity in the distribution of fishing effort, relative to the distribution of a resource that is partially protected by a marine reserve, necessitates spatially explicit design considerations for monitoring and population assessment. Simulation modeling was used to evaluate whether a mark-recovery design could be used to accurately estimate fishing mortality rates for a fishery managed in conjunction with a marine reserve. A spatially explicit individual-based simulation framework was developed with environmental characteristics of Glover's Reef Marine Reserve, Belize and with biological characteristics of a fished population of Caribbean spiny lobster (*Panulirus argus)*. Simulations revealed that mark-recovery sampling has the potential to provide accurate estimates of fishing mortality that are robust to uncertainty about resource transfer rates between a marine reserve and a fished area. This study highlighted the need for critical evaluation of information gathering priorities for integrating marine reserves with other fishery regulations. Where marine reserves are used, spatially explicit population assessments will be needed to support management actions. Although spatially explicit approaches to population assessment exist with extensive data requirements, this research contributes to the development of approaches that require more moderate data inputs.

Background

Marine reserves are areas of the ocean that are protected from harvesting and other destructive human activities (Lubchenco et al. 2003). Marine reserves have become increasingly popular as a means to achieve fisheries and conservation goals, but globally their implementation has produced variable responses in biomass, organism size, species richness within reserve boundaries (Côté et al. 2001, Molloy et al. 2009, Lester et al. 2009). Variable responses by fish populations are attributed to reserve size and shape, dispersal of larval fish and movement of adults, and the manner in which surrounding fisheries are controlled (Botsford et al. 2003, Halpern 2003, Meester et al. 2004). Consequently, increased research is needed to couple conventional fisheries controls, such as catch regulation, with marine reserve design as integrated approaches for fisheries management (Hilborn et al. 2006, White et al. 2010).

Integrated spatial strategies for fisheries management require spatially explicit monitoring to evaluate whether management goals are being achieved (Field et al. 2006). Further, monitoring designs should be linked with fishery population assessments, which determine the biological status of fish populations. Subsequent to the placement of a marine reserve, prohibition of fishing from within the reserve will result in either reduction of total fishing effort or re-allocation of fishing effort to surrounding areas. Since part of the fish population may no longer be monitored (via fishery statistics), modified or alternative designs including fishery-independent sampling are likely to be necessary. For some fisheries, monitoring abundance trends within reserves and transfer rates between reserves and surrounding fished areas may be feasible (Zeller & Russ 1998, Punt et al. 2000, Farmer & Ault 2011, Karnauskas, Huntington, et al. 2011). This may be

the case when the economic value of the fishery enables additional investment in fishery-independent monitoring; however, for fisheries that are of low economic value, implementing spatially explicit monitoring programs may be less economically feasible (Jennings 2001, Halpern et al. 2006).

When fisheries-dependent data are used in population assessment, following marine reserve placement, estimation of total fish population abundance and fishing mortality rate may become less accurate (Ton 2013). These inaccuracies can arise because most conventional population assessments assume that all areas inhabited by the fish population are subject to fishing and therefore fishery statistics will adequately characterize the entire fish population. This assumption is violated whenever part of a fish population is not fished, as is the case for the use of marine reserves (Beverton & Holt 1957, Punt & Methot 2004). Spatially explicit population assessment, which can be used to account for spatial heterogeneity in the distribution of fishing effort, can be sensitive to fish movement (Punt & Methot 2004). However, larval fish dispersal and rates of adult fish movement between marine reserves and fished areas are typically unknown and are frequently identified as key management uncertainties (Guénette et al. 1998, Meester et al. 2001, Sale et al. 2005). Although decision-making in the face of uncertainty has been addressed for several aspects of marine reserve design, few studies have considered how to address movement uncertainty in spatially explicit population assessment (Gerber et al. 2005, 2007, Halpern et al. 2006). Monitoring designs and assessment procedures are therefore needed that can guide fisheries decision-making under uncertainty about fish movement.

The approach taken here to addressing key uncertainties in fisheries management was to identify management strategies that are robust to these uncertainties; that is, an approach to monitoring, assessment, and decision-making was sought that could lead to achievement of management goals without first requiring substantial reduction of key uncertainties (Sainsbury et al. 2000, Peterman 2004). Simulation modeling was used to evaluate whether a mark-recovery design for monitoring and assessment could produce accurate estimates of fishing mortality rates under uncertainty about adult fish transfer rates between a marine reserve and a fished area. Mark-recovery sampling (or tagging) has been previously useful in providing information for population assessment (Youngs & Robson 1975, Hoenig, Barrowman, Hearn, et al. 1998, Martell & Walters 2002). Here, the expectation was that marking individual fish within a marine reserve and in a fished area, with subsequent recovery by the fishery, could provide accurate estimates of fishing mortality rates. The idea was that since individuals carry markings (tags) with them when they move, accurate estimates of fishing mortality could be obtained without reliable knowledge of transfer rates between the reserve and the fished area.

The use of mark-recovery sampling for spatially explicit assessment of fishing mortality rates was developed using a spatially explicit individual-based simulation framework with spatial dimensions and environmental characteristics of Glover's Reef Marine Reserve, Belize and with biological characteristics of a fished population of Caribbean spiny lobster (*Panulirus argus)*. At Glover's Reef, a no-take marine reserve covers approximately 20% of the coral atoll and spiny lobster is the most economically important fishery resource (Gongora 2010, Belize Fisheries Department 2013). Like many spiny lobster fisheries, catches at Glover's Reef tend to consist of newly recruited

two and three year-old individuals, which are rapidly depleted through the fishing season (Medley & Ninnes 1997, Cruz et al. 2001, Gongora 2010). The simulation framework consisted of a suite of plausible scenarios about the spatial dynamics of spiny lobster at Glover's Reef. Spatial dynamics scenarios were simulated along with marking of spiny lobster and subsequent recovery by a fishery operating in an area outside of the marine reserve. Simulated mark-recovery data were then used to evaluate whether accurate estimates of fishing mortality rates could be obtained without information about movement being available to the estimation procedure. The simulations were not intended to directly support management decisions at Glover's Reef; rather, characteristics of Glover's Reef coral atoll and spiny lobster spatial dynamics were utilized as a representation of places where marine reserves are used to manage fisheries targeting reef-associated fishes and invertebrates (e.g. Zeller & Russ 1998, Acosta 1999, McClanahan & Mangi 2000, Galal et al. 2002, Russ et al. 2003, Ault et al. 2013).

Methods

Spatially explicit simulation framework

     Purpose - The simulation framework supported an investigation of how the spatial distribution and movement patterns of spiny lobster can influence the effectiveness of mark-recovery sampling for estimating fishing mortality rates. Spatially explicit IBMs can be used to describe the movement patterns of fishes relative to jurisdictional and management boundaries, from which patterns of connectivity, spillover, and dispersal among areas can be quantified (Huse & Giske 1998, Railsback et al. 1999, Huse 2001, Werner et al. 2001, Nathan et al. 2008). Since individual-based

models (IBMs) simulate the independent actions of many individuals, their use is intuitive for mark-recovery sampling where individuals carrying marks move across landscapes to be later recaptured in different locations. In the following sections, the simulation framework is summarized according to a protocol for communicating the development of IBMs that is known as Overview, Design concepts, and Details, or ODD (Grimm et al. 2006). Additional details about simulation properties are provided in Appendix D.

State variables and scales – The simulation framework comprised three primary components: individual spiny lobster, the coral reef environment, and management boundaries and the fishery. All spiny lobster were considered to be adult sized and fully recruited to the fishery. For the purpose of conceptual investigation of the proposed mark-recovery procedure, spiny lobster inhabiting the simulated environment were considered to be a single biological population. In reality, population structure is unknown, owing to uncertainty about the relative importance of localized recruitment versus long-distance dispersal of larval spiny lobster (Truelove et al., Ehrhardt 2005). Nevertheless, fishery management concerns for spiny persist at local, national, and international scales (FAO 2001, Gongora 2010, Babcock et al. 2013). Simulated individuals were characterized by age, location, and whether they were carrying a unique mark assigned during mark-recovery sampling. Movement of adult spiny lobster had two forms: dispersive and migratory. Dispersive movement consisted of relocations lacking strong directionality. Migratory movement consisted of directed relocations between shallow water and deep water habitats that occurred seasonally (Herrnkind 1980, Childress & Jury 2006). In general, lobster species also display homing-territorial

movements that pertain to daily activity patterns (Childress & Jury 2006). Daily activities were not included because they were not considered to be essential for achieving the stated purpose of the model.

The coral reef environment was simulated based on spatial dimensions and substrate characteristics of Glover's Reef Marine Reserve, Belize. Glover's Reef is a coral atoll located 45 km east of the coast of Belize (lat 16.82ºN, long 87.78ºW; Fig 5.1). The isolated lagoon is enclosed by emergent reef crest and the seaward sloping forereef descends 30º to 45º downward from the surface where it connects to the vertical wall reef, which continues to depths of 400 m to 2,000 m (Acosta 2002, Acosta & Robertson 2003, Karnauskas, Huntington, et al. 2011). The shallow benthic environment consists of dense patch reefs (>70% cover of living or dead corals) and diffuse patch reefs (<30% cover) dominated by *Montastrea annularis*, *M. cavernosa,* and *Siderastrea sidereal*, and surrounded by sand, seagrass, and macroalgae (Mumby & Harborne 1999a, Acosta & Robertson 2003, Huntington et al. 2011). Seaward of the reef crest, the benthic environment consists of forereef formations dominated by *Agaricia agaricites* and *A. tenuiforia* spur-and-groove formations (<5 m spur height) on the west slope and *M. annularis*, *Dendrogyra cylindrus*, and *Diploria spp*. on the east slope (Stoddart 1962, Mumby & Harborne 1999a, Acosta & Robertson 2003).

The simulated coral reef environment consisted of two parts: shallow reef habitat and deep wall reef habitat. Shallow reef habitats were represented using a grid of rectangular cells with dimensions of 25 m x 25 m. This grid was created from a more detailed GIS layer of Glover's Reef benthic geomorphology and benthic flora and fauna (Mumby et al. 1995, Mumby & Harborne 1999a, b). Shallow reef habitats consisted of all

coral reefs within the lagoon and fore reefs of the atoll (Acosta 1999, 2002, Acosta & Robertson 2003). The resulting grid of shallow reef habitat reflected the actual distribution of reef habitat at Glover's Reef and contained 63,426 cells (each grid cell 25 m resolution; area of 625 m^2; total area 3,964 ha; Fig 5.1). The deep wall reef habitat functioned as a natural refuge from fishing because its depths exceed those that are accessible by free-diving lobster fishers. Deep wall reef habitat was included in the simulations because of its potential importance in addressing emigration of spiny lobster as a source of bias in fishing mortality estimation. The deep wall reef was not represented in a spatially explicit manner; instead, individuals on the deep wall reef were separately aggregated from those in shallow habitats.

Commercial fishing at Glover's Reef occurs in shallow reef habitat of the general use zone and is excluded from the neighboring area known as the conservation zone (Fig 5.1). A geo-referenced GIS layer of the management zones at Glover's Reef was provided by the Wildlife Conservation Society, which enabled management boundaries to be accurately portrayed in the simulations. Each grid cell of the shallow reef habitat was designated as being located either in the general use zone or in the conservation zone. Within zones, 79.8% (3,164 ha) of shallow reef habitat was located within the general use zone and 20.2% (800 ha) was located within the conservation zone. Overlaying the shallow reef habitat grid was a 1 km by 1 km rectangular grid that denoted the distribution of fishing grounds, which was used to distribute fishing effort.

Process overview and scheduling – Simulations were carried out using a weekly time step and each simulation consisted of a 35 week fishing season. During each weekly time step, model processes occurred in the following order: mortality, dispersive

movement, migratory movement, and addition of new recruits. With the exception of recruitment, weekly processes were carried out through synchronous updating of state variables. The simulations were developed using the Java programming language and the multi-individual simulation libraries MASON and GeoMASON (Luke et al. 2005, Sullivan et al. 2013).

Design concepts – Population dynamics emerged from the state variables of individuals; however, individual states were imposed though probability-based rules that produced stochastic outcomes. Fitness-seeking behaviors of individuals that are often the focus of individual-based ecological models were not explicitly included. Challenges associated with specifying fitness-related rules are often immense, particularly for movement behaviors (Tyler & Rose 1994, Railsback et al. 1999, Huse 2001, Grimm & Railsback 2005). These challenge are no less immense for modeling lobster movement, as numerous ecological and physiological factors affect movement behavior and interpreting behavior from empirical movement patterns is limited by a lack of information about individual states (e.g. starvation, predation risk, reproductive state; Butler 2005, Childress & Jury 2006).

Initialization – Each simulation was initialized with a random seed. Prior to simulation analyses, model processes were initially run for 25 consecutive years to generate a spiny lobster population with desired exploitation characteristics.

Input – Model inputs were: (1) a geo-referenced grid of shallow reef habitats, (2) a geo-referenced grid of management boundaries and fishing grounds, (3) a temporal schedule of weekly fishing effort, (4) a spatial strategy for fishing effort distribution, (5) a target annual fishing mortality rate, and (6) natural mortality rate.

Submodels – Median annual recruitment to the fishery was specified as 70,000 individuals, which was consistent with actual estimates for Glover's Reef reported by Babcock et al. (2013). Lognormal inter-annual recruitment standard deviation of 0.6 was specified to enable simulation of a wide range of population sizes. Peak spawning and subsequent recruitment to the fishery is thought to occur throughout the Caribbean in spring, often corresponding to fishery closure, and in some locations a secondary peak occurs during autumn (Villegas et al. 1982, Chubb 1994, FAO 2001, Cruz & Bertelsen 2008). Therefore, of the total recruits added annually, 70% were added during a 10-week period in spring prior to fishery opening, and 30% were added during a 10-week period in autumn, which was assumed to reasonably reflect the temporal pattern of spiny lobster recruitment in the broader Caribbean region. New recruits were distributed randomly among shallow reef habitats, with a small fraction (0.03%) recruiting directly to the deep wall reef to reflect the assumption that some individuals of recruitment age could have already moved to the deep wall reef. Individuals were subject to a weekly mortality probability that was based on an annual instantaneous natural mortality rate, $M = 0.34$ year^{-1} (Gongora 2010). Fishing mortality rate, F, varied weekly with fishing effort and with an individual's location. Weekly survival probability was calculated as $\exp(-M - F)$, and an individual was removed if a random draw from a uniform distribution between zero and one was greater than its survival probability. Individuals removed from the population were added to the catch if a second random draw between zero and one was less than $F/(F + M)$.

Individuals were subject to dispersive movement among shallow reef habitats and migratory movement to/from the deep wall reef. Spiny lobster dispersed among shallow

reef habitats according to probabilistic departure and destination rules. If an individual's dispersal probability was greater than a random number drawn from a uniform distribution between zero and one, the individual departed its current location. Departure probability reflected available empirical patterns, but alternative dispersal probabilities were considered in the simulation analysis (Appendix D). For departing individuals, destination shallow reef grid cells were selected probabilistically from a set of alternatives. Each destination cell from the set of alternatives was considered to have equal habitat quality, but was assigned a weighting that was inversely proportional to travel distance (i.e. weighting $\propto$ 1/distance). Inverse distance weighting is a common approach to simulating animal movement, which implies that neighboring locations are more likely to be selected than distant locations because of travel costs or repeated use of nearby shelters (Herrnkind & Redig 1975, Herrnkind et al. 1975, Mitchell & Powell 2004, Bertelsen & Hornbeck 2009, Van Moorter et al. 2009). The set of alternative destination habitats was also constrained to a maximum weekly dispersal distance of 750 m, which reflected empirical estimates of spiny lobster movement (Gregory & Labisky 1986, Davis & Dodrill 1989, Acosta 2002, Bertelsen & Hornbeck 2009). Selection of a destination habitat was determined by first rescaling the set of destination choices to sum to one, and then generating the cumulative density function of the destination choice set. Then, by drawing a random value from a uniform distribution between zero and one, a destination location was identified as the destination choice that contained the random value within its corresponding contiguous cumulative density interval (Law 2006). Individuals also migrated to the deep wall reef in some of the spatial dynamics scenarios. In these scenarios, unique migration rules were specified for the movement to deep water.

The spiny lobster fishery at Glover's Reef operates by free-diving from June 15 to February 14 of the following year, with a seasonal closure during the intervening weeks. Fishing effort varies weekly, with a peak at the beginning of the season followed by a subsequent decline (Fig. 5.2; Babcock et al. 2012). These fishery characteristics were incorporated into the simulations as a representation of current fishery practices. For simplicity, all shallow reef habitats were assumed to be accessible by free-diving. This assumption was made because no suitable high resolution bathymetry layer was available to determine habitat depth and because the GIS layer that was used to generate the shallow reef habitat grid was developed from remotely sensed imagery that, on average, penetrates water depth to 25 m (Mumby & Harborne 1999b). Two approaches were specified for distributing fishing effort spatially among fishing grounds at the beginning of each week. The first approach distributed fishing effort uniformly among all fishing grounds, thus making all spiny lobster in the general use zone equally vulnerable to capture. The second approach distributed fishing effort in proportion to spiny lobster abundance, reflecting the expectation that fishers were unlikely to be uniformly distributed (Caddy 1975, Walters & Bonfil 1999, Walters et al. 1999). The second approach resulted in fishing grounds with higher abundance experiencing proportionally higher fishing mortality rates. Algorithms for distributing fishing effort among shallow reef habitats are available in Appendix D. The actual spatial distribution of fishing effort at Glover's Reef is unknown, but it is expected that fishers are not uniformly distributed because fishing occurs via larger sailing vessels that transport crews to the reef, who then fish surrounding areas in smaller boats.

Spatial dynamics scenarios

Spatial dynamics scenarios reflected uncertainty in the movement patterns of spiny lobster, which were expected to have effects on patterns of yield and tag recovery. Scenarios were specified to investigate the effects of dispersal rate and migration patterns on estimation accuracy of fishing mortality rates (Table 5.1). Alternative scenarios varied the probability of dispersive movement among shallow reef habitats. Scenarios also varied the magnitude of seasonal migrations between the deep wall reef and shallow reef habitats. Scenarios one through three were used to investigate general spatial considerations related to mark-recovery-based fishing mortality estimation when fishing occurred in areas surrounding a no-take reserve. In these scenarios, no migrating occurred, and thus, spiny lobster inhabited only two-areas: the fished area (general use zone) and the non-fished area (conservation zone). Scenario one was named the No Move scenario. Scenarios two and three differed with respect to degree of dispersive movement between shallow reef grid cells and were named the Reference Dispersal scenario and the Increased Dispersal scenario, respectively. The Reference Dispersal scenario was parameterized to reflect observed movement rates reported by Acosta (1999) and Acosta (2002). In the Increased Dispersal scenario, dispersal probability greatly exceeded observed movement rates.

Each of the remaining three scenarios modified the frequency and timing of movement to and from the deep wall reef. In these scenarios, a small fraction (0.03%) of newly recruiting individuals were recruited directly to the deep reef to reflect the empirical observation that some individuals of recruitment age are found on the deep wall reef (Acosta & Robertson 2003). Scenario four was named the Deep Refuge – Reference

Dispersal scenario as spiny lobster migrated from shallow reef habitats to the deep wall reef but were not permitted to return. In this scenario, the migration probability of individuals was parameterized such that approximately 5% of the simulated population inhabited the deep wall reef, which was based on an empirical comparison of spiny lobster density between shallow reef and deep reef habitats (Appendix D; Acosta & Robertson 2003). Scenario five was named the Mass Migration – Reference Dispersal scenario reflecting an autumn return to shallow reef habitats of those lobsters that had previously migrated to the deep wall reef. Specifying a return of 50% of deep-reef individuals to shallow reef habitats over a 10-week period in autumn was arbitrary, but reflected the idea that a mass return would introduce additional exploitable abundance to the fishery towards the end of the fishing season. This simulated mass return of individuals to shallow reef habitats reflected uncertainty about causes of observed relative abundance trends occurring through the fishing season (Fig. 5.2). At Glover's Reef, observed relative abundance declines steeply during the first half of the fishing season, followed by an increasing relative abundance trend in the autumn period of the fishing season. This relative abundance increase could reflect a secondary autumn recruitment peak, movement of invulnerable adult spiny lobster into fished areas, or both. Mass migrations are known to occur in autumn in the Cuban spiny lobster fishery (Baisre & Cruz 1994, Cruz & Adriano 2001, Childress & Jury 2006). Scenario six, the Temporary Refuge – Reference Dispersal scenario, treated the deep wall reef as only a temporary refuge from fishing with 80% of individuals returning to shallow reef habitats during a 10-week autumn period.

Mark-recovery simulation

Mark-recovery simulation consisted of marking of spiny lobster prior to fishing, recovery by the fishery, and the use of a statistical model to estimate fishing mortality rates. Estimated fishing mortality rates were compared to true values that were simulated under different conditions (Fig 5.3). The conditions that differed between simulations were: (a) the magnitude of the annual fishing mortality rate, (b) the fraction of the population tagged, (c) the spatial dynamics scenario, and, (d) the spatial distribution of fishing effort. Spatial dynamics scenario two (Reference Dispersal scenario) was used to simulate the combined effects of annual fishing mortality rate and the fraction of the population tagged on fishing mortality estimation. Model tuning was carried out to identify effort levels that would expose individuals in the general use zone to fishing mortality equivalent to the natural mortality rate (low mortality; 0.34 yr^{-1}) and to approximately 1.5 yr^{-1} (high mortality). The low fishing mortality rate was chosen to represent a precautionary value and the high level was chosen to be consistent with actual estimates of fishing mortality for spiny lobster in Belize (Gongora 2010, Babcock et al. 2012). The fraction of the population tagged ranged from 0.1% to 10%. Fishing effort was distributed uniformly across the general use zone or in proportion to spiny lobster abundance. For each analysis, 100 simulated datasets were generated for each combination of factors considered. After initialization, datasets were generated that consisted of 35-week fishing seasons.

The algorithm for marking spiny lobster was implemented as follows. First, a sampling grid of 100 m by 100 m rectangular cells was used to aggregate shallow reef habitats into tagging sites. Plausible tagging sites were those that contained reef habitat,

which resulted in 1,600 and 6,223 available tagging sites within the conservation zone and general use zone, respectively. Second, the fraction of tagging sites within each zone that were visited was set to the specified fraction of the population to be tagged. Finally, all individuals within each selected site were marked with unique identifiers. This algorithm resulted in: (1) the fraction of the population tagged reflecting the intended fraction to be tagged; (2) total tags being distributed in proportion to spiny lobster abundance in the general use zone and in the conservation zone; and (3) marked individuals being aggregated within tagging sites. Marking aggregations of individuals at randomly selected sites reflected a realistic sampling constraint of many mark-recovery designs (Hoenig, Barrowman, Pollock, et al. 1998, Smith et al. 2009). Marking was carried out the week prior to the opening of the fishery and tags were assumed to be retained through the fishing season. Post-release survival, tag retention rate, and tag reporting rate were all specified to be equal to one. In scenarios that included migration, no tags were distributed to individuals inhabiting the deep wall reef.

Estimation of tag recovery rates (ρ_t) was based on c_t cumulative returns of tagged spiny lobster through week t, from C initially tagged individuals:

$$c_t \sim Binomial\left(C, \rho_t\right). \tag{5.1}$$

Tag recovery rate was modeled as

$$\rho_t = \phi \lambda \mu_t, \tag{5.2}$$

where ϕ was the probability of surviving the tagging process, μ_t was the harvest rate, and λ was the tag reporting rate (Hoenig, Barrowman, Hearn, et al. 1998, Pine et al. 2003). Harvest rate was:

$$\mu_t = \frac{F_t}{\left(F_t + M\Delta t / 52\right)}\left(1 - \exp\left(-F_t - M\Delta t / 52\right)\right) \qquad (5.3)$$

where F_t denoted fishing mortality rate through week t, M was the annual natural

mortality rate, and Δt was the number of weeks since individuals were marked. For each

simulation, j, bias in fishing mortality estimates was calculated as

$$\% \text{ bias}_{t,j} = \frac{\left(F_{t,j} - F^*_{t,j}\right)}{F^*_{t,j}}100 \qquad (5.4)$$

where $F^*_{t,j}$ was the true fishing mortality rate, which was calculated using aggregate

catch and total abundance from the general use zone and conservation zone. Precision

was expressed as a coefficient of variation (CV):

$$CV_{t,j} = \frac{\sigma_{t,j}}{F_{t,j}} \qquad (5.5)$$

where $\sigma_{t,j}$ was the estimated standard error of the mean fishing mortality estimate.

The software OpenBUGS was used to estimate fishing mortality rates from

simulated mark-recovery data (Lunn et al. 2000). Weekly fishing mortalities were

assigned diffuse priors ($F_t \sim \text{Uniform}(0,2)$). In model fitting, ϕ, λ, and M were

specified as known constants reflecting true values. By specifying model parameters

(other than fishing mortality) as known constants, model outcomes reflected bias and

imprecision in spatial aspects of the mark-recovery design and not survival and reporting

processes. Convergence of the Markov chain Monte Carlo (MCMC) algorithm on its

target distribution was checked against Gelman-Rubin convergence criteria (Gelman et

al. 2004) and was usually reached by 1,000 iterations and a more conservative 2,000

iterations was used as a burn-in period. Posterior samples were retained from 5,000

subsequent iterations from two chains and posterior means of parameters were calculated

from the resulting 10,000 saved iterations.

Results

Spatially explicit simulation framework

To better understand the population-level distribution of spiny lobster, a summary

of the simulation framework properties is provided here, with additional details reported

in Appendix D. Simulations were carried out using the Deep Refuge – Reference

Dispersal scenario and the high annual fishing mortality rate (Table 5.1). Based on 50

replicate simulations, at the beginning of the fishing season (week 1), the general use

zone contained a median of 60% of the spiny lobster. Under the high exploitation rate

used to generate these results, abundance in the general use zone was rapidly depleted,

resulting in the conservation zone containing a higher fraction of spiny lobster by the

mid-point of the fishing season (week 18: median 57%; week 35: median 53%).

Model tuning to achieve low and high fishing mortality rates in the general use

zone of 0.34 yr^{-1} and 1.5 yr^{-1}, respectively, was sensitive to spiny lobster dispersive

movement and the spatial distribution of fishing effort. When effort was distributed

equally among all fishing grounds, the high level of fishing mortality resulted in atoll-

wide rates of 0.58 yr^{-1} (standard error ±0.11 yr^{-1}), 0.70% (±0.07 yr^{-1}), 0.77% (±0.08 yr^{-1}), for the Decreased Dispersal, Reference Dispersal, and Increased Dispersal scenarios,

respectively. When effort was distributed in proportion to spiny lobster abundance, the

high level of fishing mortality resulted in atoll-wide rates of 0.72 yr^{-1} (±0.16 yr^{-1}), 0.90%

(± 0.18 yr^{-1}), 1.03% (± 0.18 yr^{-1}), for the Decreased Dispersal, Reference Dispersal, and Increased Dispersal scenarios, respectively. Note that as spiny lobster movement increased, a higher fraction of the population became vulnerable to capture (via movement into the general use zone), which resulted in higher atoll-wide fishing mortality rates.

Simulations were also carried out to approximate the contribution of spiny lobster in the conservation zone to the catch, via movement into general use zone. In these simulations, the high annual fishing mortality rate was specified and fishing effort was distributed in proportion to spiny lobster abundance. The Reference Dispersal scenario resulted in 6%, on average of the abundance within the conservation zone at the beginning of the season becoming captured by the fishery throughout the season (range 1% - 12%). By increasing departure probability in the Increased Dispersal scenario, 13%, on average, of the abundance within conservation zone at the beginning of the season was subsequently captured by the fishery (range 2% - 26%).

Mark-recovery simulation

The mark-recovery assessment procedure used in this study assumes that all tagged and untagged individuals have equal probability of capture. This assumption implies that (1) tagged individuals are distributed in proportion to abundance over the population distribution, and (2) tagged individuals are caught at the same rate as untagged individuals. Both of these assumptions were met in the simulations, but because fishing was constrained to only a fraction of the population distribution, the atoll-wide fishing mortality rate could be obtained. Individuals tagged in the conservation zone would not be caught by the fishery, unless movement to the general use zone occurred, and thus,

this approach utilized the spatial distribution of fishing effort to achieve estimation of atoll-wide fishing mortality. Bias and precision of fishing mortality estimates were strongly influenced by the fraction of the population tagged. Tagging extremely low fractions of the population (0.1%) considerably increased the chances of obtaining biased fishing mortality estimates (Fig 5.4A). Marking 1% or 2% of the population considerably reduced the potential for biased estimates. Fishing mortality precision was also poor when only 0.1% of the population was tagged, but coefficient of variation estimates were generally <0.1 when at least 1% of population was tagged (Fig 5.4B). These patterns of bias and precision related to percentages of the population tagged were consistent at both low and high levels of annual fishing mortality.

Having investigated the effects of the fraction of the population tagged on fishing mortality estimation, the remainder of the analysis was carried out by tagging 1% of the population. For simplicity, simulations were initially run with fishing effort distributed uniformly throughout the general use zone. On average, fishing mortality estimates were relatively unbiased by the degree of dispersive movement by spiny lobster; that is, spatial dynamics scenarios 1 through 3 produced similarly unbiased results (Fig 5.5). Annual fishing mortality estimates, calculated after week 35 of simulated fishing seasons, had average biases of 0.71% (standard error $\pm15.4\%$), 0.70% ($\pm13.4\%$), and 3.1% ($\pm14.6\%$) for scenarios 1, 2, and 3, respectively. In scenarios 4 through 6, migration patterns did not appear to introduce substantial bias in fishing mortality estimation (Fig 5.5). However, a lack of bias caused by migration should be interpreted in context of the fraction of individuals protected from fishing in the deep reef, as a result to the assumed shallow-to-deep migration rate. Under conditions of the Deep Refuge – Reference Dispersal scenario

(scenario 4), approximately 5% of atoll-wide abundance inhabited the deep reef area (Appendix B). Such small numbers of emigrants explain the inconsequential effect of migration on fishing mortality estimation in these simulations.

Within simulated fishing seasons, encouraging results were also obtained. Given that at least 1% of the population was tagged, fishing mortality estimation was reasonably unbiased and precise regardless of whether estimates were made at the beginning of the season (week 4), the middle of the season (week 17), or at the end of the season (week 35; Fig. 5.5). This is a relevant finding because as the season progresses the total number of tag returns increases. It was initially unclear whether there would be enough tag returns near the beginning of the season to estimate fishing mortality, but this appears to be plausible at the levels of fishing mortality and fraction of the population tagged that were used in the simulations. This finding is also relevant because fishing mortality estimates were not noticeably influenced by a secondary recruitment pulse that occurred between weeks 20 and 29 of the fishing season (Fig. 5.5). The results in Fig 5.4 and 5.5 pertained to the high annual fishing mortality rate (i.e. approximate general use zone value of 1.5 yr^{-1}). Similar results were found when the annual fishing mortality rate was specified as low (i.e. approximate general use zone value of 0.34 yr^{-1}).

The analysis revealed a potential bias in fishing mortality estimation when fishing effort was distributed in proportion to abundance in the general use zone. When effort was distributed proportional to abundance, some areas within the general use zone experience higher fishing mortality than others. In these simulation runs, an underestimation of "true" fishing mortality occurred primarily towards the end of season. While this bias was generally small (mean: -3.9%; centered 95% of simulations: -31.4%

to 40.6%), annual fishing mortality (week 35) was systematically underestimated. Tagging a practically unreasonable 25% of the population (~15,000 individuals on average) did not eliminate this bias (mean: -6.2%; centered 95% of simulations: -12.0% to 1.3%). This result revealed a potential difficulty in calculating fishing mortality from mark-recovery data, where tagged individuals were subject to different localized degrees of fishing mortality. This bias appears to arise because fishing mortality estimated from mark-recovery was subject to the effects of highly aggregated fishing effort, whereas "true" fishing mortality was calculated based on simply aggregating catches from all fishing grounds and abundance across all zones.

Discussion

Simulation of mark-recovery sampling resulted in reliable estimates of fishing mortality rates under a variety of circumstances. Fishing mortality rates were well approximated with 1% of the population tagged, which corresponded to 500-1000 tags for the population size range used in the simulations. Reasonable precision (CVs commonly <0.1) of fishing mortality estimates obtained from deploying several hundred tags were consistent with previous simulation studies (Frusher et al. 2001, Martell & Walters 2002). However, fishing mortality estimates reported here were likely to be overly precise in comparison with any actual mark-recovery procedure because several parameters were fixed at their true values, rather than estimated with uncertainty from auxiliary data. Acosta (1999) demonstrated that spiny lobster in shallow water habitats at Glover's Reef could be tagged by divers using SCUBA or snorkel, although it remains unclear what sampling effort and cost would have to be expended to achieve appropriate

sample sizes. As a coarse estimate of the minimum number of hours it could take to mark 500-1000 individuals, a comparison to efficiency of the commercial fishery can be made. Babcock et al. (2013) estimated medians of 3.5 and 5.3 individuals captured per fisher hour at the beginning of the fishing seasons in 2011 and 2012, respectively. Using an average value of 4.4 would require a minimum of 113 fisher hours to tag 500 individuals. This is a minimum value because the sampling design necessitates traveling between sampling sites and because tagging and release takes longer than harvesting.

Under a range of dispersal scenarios between the conservation zone and the general use zone, fishing mortality estimation did not require specific knowledge of spiny lobster movement patterns. Movement scenarios were specified to reflect the current state of knowledge about spiny lobster dispersal and migration and several additional scenarios reflecting movement uncertainty. These scenarios resulted in between 0% (no lobster movement) to, on average, 13% (Increased Dispersal scenario) of individuals that were tagged in the conservation zone being later recaptured by the fishery in the general use zone. Thus, the robustness of the mark-recovery design to movement uncertainty was limited to the range of movement scenarios that were considered in the simulations. Nevertheless, the simulations illuminated the potential usefulness of mark-recovery for estimating fishing mortality without additional input of movement rates between fished and unfished areas. Direct monitoring of fishing mortality may also be useful for managing fisheries, like those capturing spiny lobster, which induce sharp population depletion through a single fishing season. Mark-recovery sampling could facilitate rapid in-season assessment or could provide complementary information for supporting other population assessment techniques (Walters & Martell 2004, Smith et al. 2009).

The accuracy of the mark-recovery-based fishing mortality estimates were in stark contrast to inaccuracies that can arise when catch and effort data from the fished area are used to estimate fishing mortality rates. Ton (2013) used simulated catch and effort data generated from the same simulation framework develop herein to demonstrate that population assessment based on data collected from the fished area can result in fishing mortality estimates that are positively biased, on average, between 95.4% to 155.5% depending on which spatial dynamics scenario was used. In addition, Ton (2013) found that the degree of fishing mortality bias is sensitive to degree of movement between fished and unfished areas. This sensitivity led Babcock et al. (2013) to consider the possibility of using biases reported by Ton (2013) to aid in constructing a range of plausible assessment outcomes based on an actual population assessment of the spiny lobster fishery at Glover's Reef.

When the complexities of migration and spatial heterogeneity in fishing effort were introduced into simulations, mark-recovery performance was reasonable, but required some careful interpretation. Migration can bias fishing mortality estimates resulting in "apparent survival" estimates that inadvertently incorporate emigration from the study area (Pine et al. 2003). This effect was minimal in the simulations because emigration was specified at a very low rate, which reflected the available empirical information (Acosta & Robertson 2003). Alternative capture-recapture designs can be implemented that enable emigration and survival rates to be separately estimated (Fabrizio et al. 1997, Punt et al. 2000, Hightower et al. 2001, Williams et al. 2002, Bacheler et al. 2009, Kéry & Schaub 2012). , When fishing effort was heterogeneously distributed (in proportion to spiny lobster abundance), mark-recovery-based fishing

mortality estimates differed slightly from true values that were calculated from known total catch and abundance. These differences likely reflected spatial variation in fishing mortality rate relative to the average rate calculated from aggregate catch and abundance data. In practice, fisheries used to recover tags may not be distributed in proportion to abundance; rather they may be even more highly aggregated, for example, in areas where the fishery has been traditionally active. Thus, actual tagging studies should be concerned with understanding the extent of the distribution of fishing effort and how it may affect estimation of fishing mortality rates.

Despite the apparent usefulness of mark-recovery sampling for fishing mortality estimation, several simplifications and assumptions were made in the simulations that would need to be addressed before applying this approach. Rates of tag retention, natural mortality, and tag reporting were assumed known, but will require estimation in actual mark-recovery designs. Empirical studies of tagging methods for lobster species suggest that tag retention can vary considerably. Since lobster growth occurs discretely in a series of molts, tag loss can occur at molting, and thus, quantifying tag retention rates will be essential for accurate fishing mortality estimation. In practice, retention rates >80% can be achieved over a single season, insertion protocols for plastic "spaghetti" tags that promote retention through successive molts have been developed, and alternative technologies like passive integrated transponders and genetic mark-recapture techniques are available (Davis 1978, Melville-Smith & Chubb 1997, Taberlet et al. 1999, Rowe & Haedrich 2001, O'Malley 2008, McMahan et al. 2012). Estimates of natural mortality may be improved through combined telemetry and mark-recovery methods (Hightower et al. 2001, Bacheler et al. 2009). To produce unbiased approximations, tag reporting rates

must also be known. Of particular concern at Glover's Reef remains the consideration that landings consist mainly of tails, and special care would be required to ensure fishers retain tags for reporting. Achieving accurate reporting rates often requires creative approaches to stakeholder involvement and education, which frequently include high-reward tags (Martell & Walters 2002, Smith et al. 2009).

There also remains an important policy consideration associated with fishing mortality estimation when fisheries are managed in conjunction with marine reserves. In places where marine reserves protect part of an exploited population from fishing, it is sometimes unclear whether the protected part of the population should remain a component of the total abundance from which acceptable harvest limitations are to be derived. While the simulated mark-recovery sampling moved away from abundance estimation, it maintained the assumption that fishing mortality estimation pertained to the combined population inhabiting the fished area and the unfished area. However, the question of whether abundance within a marine reserve should be included as part of the total population abundance when establishing harvest strategies remains an open policy question (Field et al. 2006). Including abundance inside of a reserve in the total abundance calculation will generally lead to the allowance of higher fishing mortality rates in the fished area (except under population rebuilding), which raises the question of whether such an approach is either precautionary or would lead to economically optimal outcomes (Field et al. 2006, Hilborn et al. 2006).

Although marine reserves are sometimes established as a means to reduce fishing mortality rates in fisheries that are not closely regulated, they do not eliminate the need to assess and regulate the surrounding fishery (Gerber et al. 2002, Hilborn et al. 2004). This

study demonstrated that mark-recovery sampling for fishing mortality estimation can be useful in addressing management complexities associated with fisheries that surround marine reserves. Integrating marine reserves with other regulations may be especially problematic in data poor situations where monitoring data are lacking. Monitoring may be impractical in developing countries that have limited capacity for such procedures (Worm et al. 2009, Mora et al. 2009), but where marine reserves may also be viewed as important fishery management tools. At Glover's Reef, management proceeds without time series of historical catches or abundance-at-age indices and with limited fishery-independent sampling of relative abundance (Babcock et al. 2013, Belize Fisheries Department 2013). Recently, increased entry to the fishery has led to calls for additional catch restrictions in the fished area. This situation is not unique to Glover's Reef, as fisheries for many invertebrates, and lobster in particular, have developed rapidly in recent years in many regions that include marine reserves (FAO 2001, Anderson et al. 2011). Thus, spatially explicit fishery analyses are needed to support management decision-making. Some fishery analyses already exist that require extensive data inputs about the spatial distribution of fish and fishing activities (Quinn & Deriso 1999, Punt & Methot 2004), but fewer approaches with moderate data requirements are readily available for integrating fisheries management with marine reserves (McGilliard et al. 2011, Babcock & MacCall 2011).

More broadly, this study highlights the need to critically consider the types of data that are being collected to support management decision-making. Managing spiny lobster fisheries is complicated by fisheries targeting newly recruited two and three year-old individuals, which has led to management tactics that rely on highly variable abundance

estimates of pre-exploitation sized lobster (Caputi & Brown 1986, Baisre & Cruz 1994, Phillips et al. 1994, Medley & Ninnes 1997, Cruz & Adriano 2001). Although the goal of harvest limits is generally to regulate fishing mortality, harvest limits are often derived from abundance estimates despite the fact that abundance is one of the most difficult fisheries management quantities to estimate reliably (Hilborn 2002, Walters & Martell 2004). Martell and Walters (2002) point out that direct assessment of fishing mortality shifts policy focus away from difficulties associated with accurate abundance estimation. Mark recovery sampling for direct estimation of fishing mortality would be a novel approach for spiny lobster fishery management and may be especially useful for managing fisheries in conjunction with nearby no-take marine reserves. Comparisons are needed between assessment approaches and the management actions they inform, including fishing mortality rate based methods and those that rely on abundance estimation for total allowable catch controls. Quota-based systems employed along with no-take reserves can be complementary tools for fisheries management (Little et al. 2011). Still, there remain a limited number of examples describing how marine reserves could be integrated with other fishery controls (Hilborn et al. 2004, 2006, White et al. 2010). Management strategy evaluation is a framework for simulating alternative approaches to data collection and management decision-making (Butterworth & Punt 1999, Sainsbury et al. 2000). Spatially explicit management strategy evaluation could prove valuable for comparing costs, informational value, and ability to achieve management objectives as spatial management strategies becoming increasingly complex.

Table 5.1. Spatial dynamics scenarios describing simulated spiny lobster movement at Glover's Reef, Belize.

Scenario	Movement to/from deep wall reef?	Dispersive movement rate
1. No movement	No	0.0
2. Reference Dispersal	No	0.3
3. Increased Dispersal	No	0.8
4. Deep Refuge – Reference Dispersal	Yes	0.3
5. Mass Migration – Reference Dispersal	Yes	0.3
6. Temporary Refuge – Reference Dispersal	Yes	0.3

.
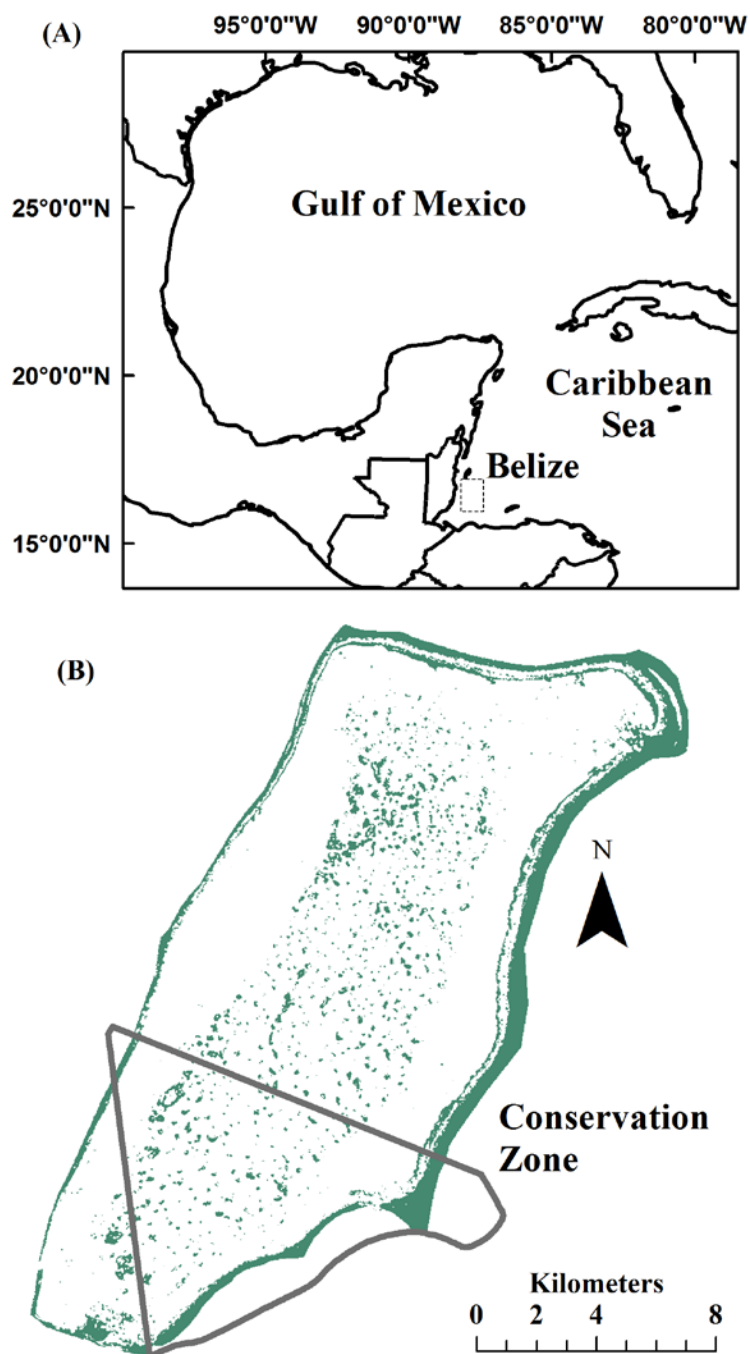
Figure 5.1. Location of Glover's Reef Atoll, Belize (dotted rectangle) within the western Caribbean (A), and distribution of shallow reef grid habitat (solid filled areas) within Glover's Reef Atoll with respect to the Conservation Zone (B).
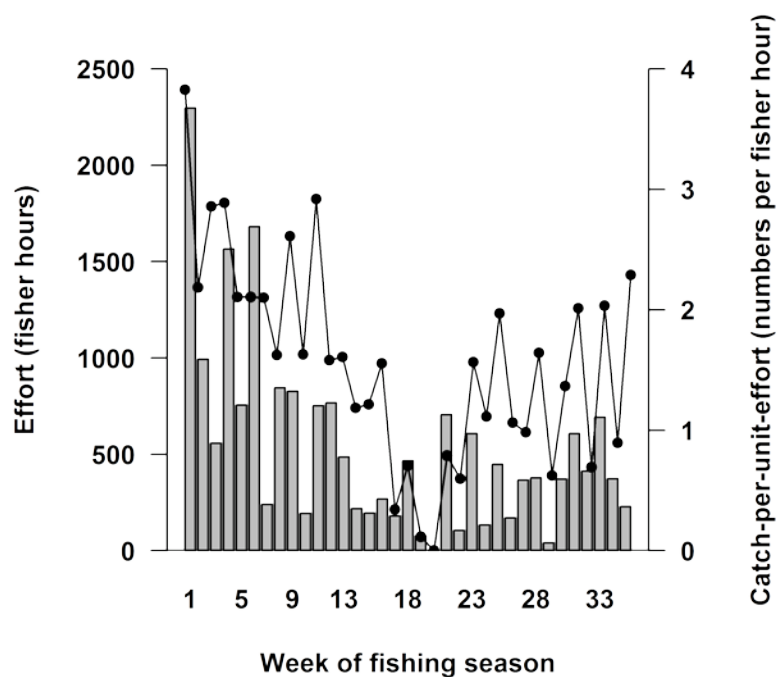
Figure 5.2. Reported effort (bars) and catch-per-unit-effort (points) for the spiny lobster fishing season at Glover's Reef Atoll. Fishing season operated from June 15th, 2011 to February 14th, 2012, totaling 35 weeks.
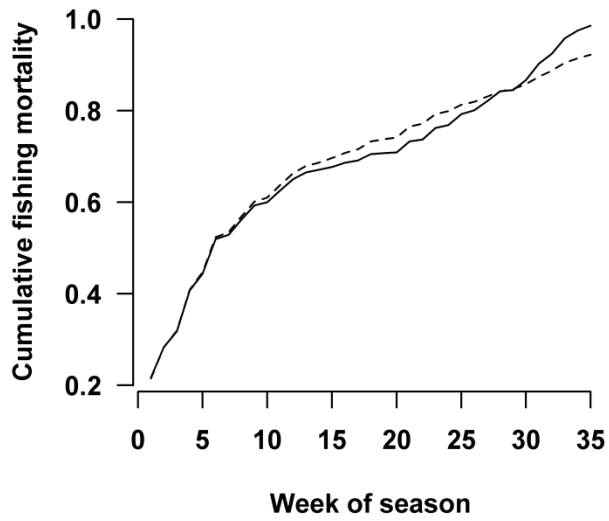
Figure 5.3. Example of simulated cumulative fishing mortality through a 35 week fishing season (solid line) and estimated cumulative fishing mortality using mark-recovery data (dashed line).
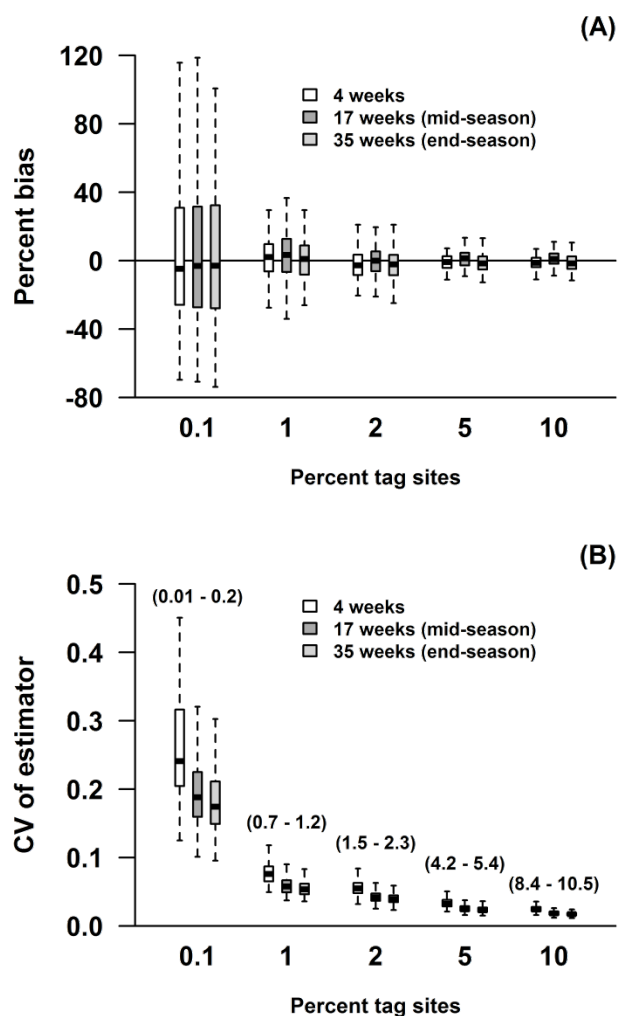
Figure 5.4. Bias (A) and coefficient of variation (CV; B) of estimated fishing mortality at four levels of tagging intensity. Values are reported at weeks 4, 17, and 35 of the 35-week fishing season under the conditions of: equal fishing effort distribution, high annual fishing mortality rate, and Reference Dispersal movement rate. Parentheses contain fractions of the population tagged at each level of percent tag sites visited.
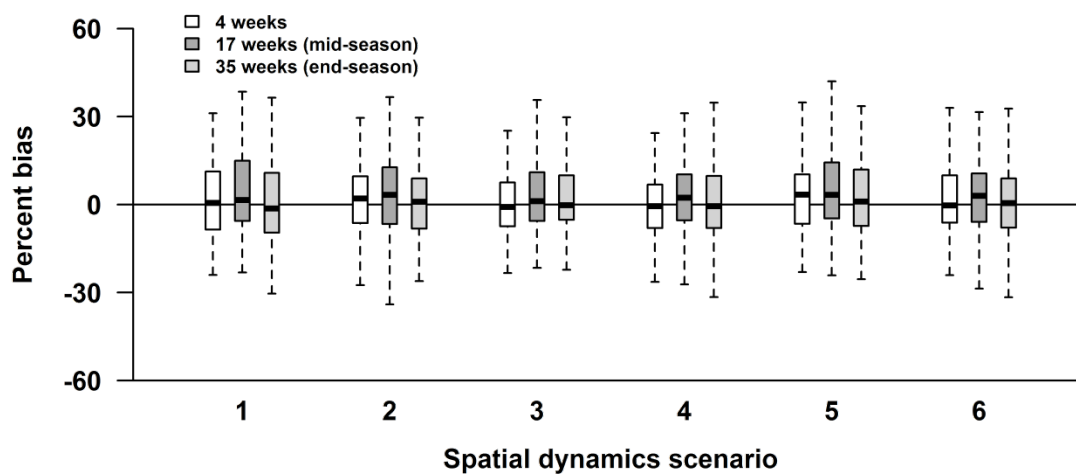
Figure 5.5. Bias of estimated fishing mortality for three migration variants of the spatial dynamics scenarios (scenarios described in Table 5.1). Values are reported at weeks 4, 17, and 35 of the 35-week fishing season under the conditions of: uniform fishing effort distribution, high annual fishing mortality rate, and 1% of tagging sites visited.

CHAPTER 6: SYNTHESIS AND CONCLUSIONS

Many fisheries face management challenges that arise because data limitations prevent population assessments from adequately informing decision-making. Spatially explicit IBMs were used to identify how data limitations related to the spatial distribution of fish and their fisheries contribute to management deficiencies in coral reef ecosystems. By emphasizing linkages between sampling, population assessment, and decision making, simulation analysis provided a means to link management concerns with choices about data gathering priorities and population assessment procedures (Walters & Martell 2004). This approach was valuable because it enabled the performance of management strategies to be evaluated regardless of whether existing monitoring designs are currently sufficient to support the various alternatives. Thus, simulation modeling illuminated potential pathways to move beyond information constraints and towards improved fisheries management.

Connecting data collection to population assessment and to harvest control rules

In the simulation framework representative of black grouper, management strategy evaluation revealed that precautionary fishing mortality targets may be necessary to compensate for the imprecision of biomass surveys if sampling precision is low. Rather than focus on isolated components of management strategies, simulations were used to evaluate complete management strategies and to contrast the performance of model-free control rules with model-based control rules that each relied on information from survey biomass indices. This approach was important because the performance of management strategies requiring simple or low amounts of data input appears to be less

well understood than the performance of more complex management strategies (Butterworth & Punt 1999, Sainsbury et al. 2000, Punt et al. 2008).

In the simulation modeling representative of spiny lobster, the analysis addressed a management concern of whether spatially explicit sampling could be implemented to manage a fishery in conjunction with the use of a marine reserve. At Glover's Reef Marine Reserve, Belize, fishery management relies on a marine reserve in addition to existing fishery controls, but management proceeds largely without detailed spatial information about its fishery resources (Belize Fisheries Department 2013). Management of the spiny lobster fishery at Glover's Reef exemplifies a general challenge in fisheries management where decision-making complexity can outpace the availability of supporting information (Campbell & Dowling 2005, Bernard et al. 2013). Spatially explicit population assessment procedures are needed for many fisheries where data limitations currently prevent such assessments, particularly in the context of integrating marine reserves with surrounding fisheries controls (McGilliard et al. 2011, Babcock & MacCall 2011, Pincin & Wilberg 2012). Here, simulations demonstrated the use of a spatially explicit monitoring design and assessment procedure that required moderately intensive data inputs. Assessment procedures are also needed that can provide estimates of population status that are robust to fish movement uncertainty. Demonstrating a sampling and assessment procedure that was robust to movement uncertainty was novel in that it directly addressed the issue of fish movement uncertainty. Fish movement uncertainty is frequently noted as being a key limitation associated with integrating marine reserves with other fishery controls (Field et al. 2006, Hilborn et al. 2006, White et al. 2010, Babcock & MacCall 2011). But despite widespread acknowledgement of this

uncertainty, (Jennings 2001, Gerber et al. 2003, Sale et al. 2005), fish movement has rarely been an explicit focus in evaluations of spatial options for fisheries management (Meester et al. 2001, Kellner et al. 2007).

Confronting data limitations through simulation modeling

In many IBMs, emphasis is placed on mechanistically describing the fitness-related behaviors of individuals with population-level properties emerging as model output (Grimm & Railsback 2005). Within population biology, IBMs have been useful for gauging population-level responses to novel conditions, such as environmental change or habitat degradation (Tyler & Rose 1994, Railsback et al. 1999, Huse 2001, Grimm & Railsback 2005). However, the challenges associated with specifying fitness-related behaviors are large, considering the numerous ecological and physiological factors affecting behavioral decisions and the complexity of empirical data required to support model specification. Given the applied focus of this dissertation on fisheries management, fitness-seeking behaviors were not the focus of model development; rather, biological characteristics were imposed model properties. The perspective was taken that efficiency in model building could be achieved by imposing key biological characteristics rather than focusing exclusively on underlying mechanistic causes of these characters (Walters & Martell 2004, Saul et al. 2012). Like development of fitness-driven IBMs, the approach taken here allowed model building to proceed from simple to complex in a pragmatic manner that emphasized balancing model realism with utility in problem solving (Grimm & Railsback 2005). Further, imposing biological characteristics allowed a variety of ecological scenarios to be generated and used in screening of management

strategy options, thus enabling provision of management advice across a range of conditions.

The application of IBMs to fisheries science should continue to be explored, particularly in the context of emphasizing biological characteristics that are otherwise difficult to incorporate in numerical simulations. For instance, spatially explicit IBMs have considerable potential for simulating spatial variation in fish abundance. Spatial IBMs have begun to consider movement algorithms that account for habitat-specific survival rates, ontogenetic habitat shifts, optimal foraging and behavioral energetics, spatially-variable physical environments, and home-range behavior (Railsback et al. 1999, Werner et al. 2001, Wildhaber & Lamberson 2004, Goodwin, Nestler, et al. 2006, Van Moorter et al. 2009, Saul et al. 2012). Model developments like these are important to enable spatially stratified monitoring designs for spatially-structured fish populations to be evaluated before they are implemented (Thorson et al. 2012). The strength of the individual-based approach to evaluating resource monitoring and assessment concerns is the flexibility that is provided by this approach in constructing reasonably realistic representations of fish spatial dynamics. This flexibility suggests that modeling is mainly limited by the availability of supporting empirical and experimental data (Grimm & Railsback 2005).

Moving beyond data limitations through emphasis on management trade-offs

Fisheries management continually faces decisions about information gathering priorities. Data limitations may be addressed by the development of low-data assessment procedures that rely on biological indicators or simple assessment procedures (Hilborn & Walters 1992, Ault et al. 1998, Froese 2004, Cope & Punt 2009, Martell & Froese 2012).

Alternatively, fisheries management may be improved strategically by obtaining additional data or by seeking alternative information sources (Walters & Martell 2004). Of course, management strategies can be designed to concurrently seek improved monitoring while also coping with existing data-limitations. For example, improved monitoring may be motivated by the viewpoint that management concerns should guide data collection priorities, while simultaneously recognizing that a lack of historical data will continue to limit the types of assessment procedures that can be used to inform management decisions (Walters & Martell 2004).

In practice, management strategies to address spatial complexities can be designed effectively by focusing on trade-offs between management objectives and data availability. Where existing fisheries management policies specify objectives, there may be a trade-off between which management strategies are preferred, given the objectives, and which objectives are achievable, given the available data. For instance, the United States Magnusson-Stevens Fisheries Conservation and Management Act establishes national standards to prevent overfishing while achieving optimal yield (NOAA 2007). Legislation is operationalized through technical guidelines, which define optimal yield and other management reference points, often in relation to maximum sustainable yield (Restrepo & Powers 1999, Hilborn & Stokes 2010). Consequently, development of assessment procedures of warm-temperate and tropical fishes within the U.S. Atlantic has been driven by operational constraints (Porch et al. 2006). However, many grouper-snapper species within this region lack detailed catch histories and spatially explicit biological data. Many of these species are vulnerable to becoming overfished because of their life history characteristics (Coleman et al. 2000, Ault, Bohnsack, et al. 2005, Ault,

Smith, et al. 2005). Development of monitoring programs, assessment procedures, and harvest control rules are needed to remedy a variety of data limitations for many grouper-snapper species to enable allowable biological catches to be specified and to ensure long-term fishery sustainability (Ault, Bohnsack, et al. 2005, NOAA 2007, Ault et al. 2013).

There remains a need for continued evaluation of trade-offs between management strategies that differ in terms of types of data inputs and types of assessment procedures that are applied to those data. There are numerous approaches for population status determination that were not explored in this research that could complement spatial sampling designs; including, simple quantitative indicators, length-based metrics (Beverton & Holt 1957, Ault et al. 1998, Froese 2004, Cope & Punt 2009), and age-structured population assessment models (Quinn & Deriso 1999, Methot & Wetzel 2013). Importantly, monitoring and assessment are interconnected components that affect management actions. Clearly then, coupling monitoring, assessment, and harvest control rules is a desirable approach for advancing understanding of fisheries management strategies. Simulation-based comparisons between management strategies that differ in data inputs could help to resolve information-gathering priorities in terms of ability to achieve management objectives relative to the costs of doing so. Formulating contrasts between a diverse suite of fishery management strategies is where simulation modeling will continue to be helpful (Magnusson & Hilborn 2007, Deroba & Bence 2008). Further, spatially explicit simulation modeling will enable evaluation of the effects of spatial heterogeneity in fish distribution on the design and performance of fisheries management strategies (Pelletier & Mahévas 2005).

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APPENDIX A: ARTIFICIAL LANDSCAPE GENERATION FOR BLACK GROUPER SIMULATIONS

Background

To create contiguous artificial landscapes in the black grouper simulation framework, a three-part algorithm was implemented. This algorithm produced fractional Brownian surfaces that achieved a minimal degree of consistency with spatial properties of the Florida Keys reef tract. Two-dimensional fractional Brownian surfaces are landscapes that have a degree of spatial autocorrelation in their specified values (Peitgen & Saupe 1988, Keitt 2000, Stein 2002). These simulated landscapes exist within a broad class of neutral landscape models employed in landscape ecology and can be used to capture the spatial properties of actual landscapes (With & King 1997, Keitt 2000, Li et al. 2004). In the first part of the landscape algorithm, a rectangular lattice of habitat values was simulated to have spatial autocorrelation consistent with an observed environmental feature of interest. Maximum vertical relief (m) was used as representative environmental feature of the simulated reef tract. Maximum vertical relief describes the height of the tallest benthic structure, including hard structures (e.g. coral and rocky outcrops) and soft structures (e.g. octocorals, sponges, and macroalgae) (Brandt et al. 2009). In the second part of the landscape algorithm, an irregularly shaped pattern of grid cells was extracted from the rectangular grid that reflected the geographic distribution of the Florida Keys reef tract. In the third part of the landscape algorithm, the simulated values of the irregular grid were rescaled to reflect the statistical properties of the observed environmental feature. These statistical properties included the unique properties of disparate reef formation types, which are distributed spatially across the shallow water shelf of the reef tract (Table A1). The use of unique properties of each reef

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formation type (i.e. habitat stratum) enabled scaling of simulated grid cell values to more accurately reflect variation in substrate relief of the Florida Keys reef tract.

Methods

The implementation details of the landscape algorithm were as follows. A algorithm for simulating fractional Brownian surfaces described by Stein (2002) was used to produce the rectangular lattice of spatially auto-correlated grid cell values. Spatially auto-correlated grid cell values were simulated using the RandomFields package in the statistical computing software R (R Development Core Team 2012, Schlather et al. 2013). Spatial autocorrelation was controlled by a single parameter, $\kappa \in [0, 2)$, with larger values producing smoother landscapes (Stein 2002). The rectangular lattice had dimensions 1024 by 1024 grid cells, each representing a 200 m by 200 m grid cell. This spatial scale was consistent with the minimum mapping unit of a geo-referenced data layer that forms the stratification scheme and spatial sampling extent of a large-scale diver visual survey of the Florida reef tract, from which maximum vertical relief data were obtained for comparison with simulated landscapes (Brandt et al. 2009, Smith et al. 2011). An initial comparison between simulated landscapes and empirical data suggested that fractional Brownian surfaces produced localized (<10 km^2) patterns of spatial autocorrelation that were greater than empirical estimates, even when very small values for the autocorrelation parameter were used. Accordingly, random variation from a standard normal distribution was introduced to reduce spatial autocorrelation (Fig. A1; Travis & Dytham 2004). Cell utility was calculated as a weighted average of spatially auto-correlated variation and localized random variation,

where weights for each type of variation were set to 0.5. The rectangular lattice consisted of normalized values, which allowed for straightforward scaling to the representative environmental feature.

Next, a geo referenced data layer defining the spatial boundaries of the Florida Keys reef tract was used to extract the corresponding grid cells from the rectangular lattice, creating a new irregularly shaped grid. The shape of the extracted irregular grid reflected the narrow cross-shelf distribution of Florida Keys reef tract that extends along the coastline for a distance of approximately 250 km between Key West and Miami, Florida. Each extracted grid cell was also assigned a reef formation type, which was available from the geo referenced reef tract data layer.

Then, cell values of the irregular grid were re-scaled to reflect statistical properties of observed maximum vertical within reef formation types. First, observed values of the environmental feature were log-transformed to achieve approximate normality. Second, means and standard deviations of the log-transformed observations were estimated separately for each cross-shelf reef formation type (Table A1). Third, normalized grid values located within each reef habitat class were scaled to reflect observed log-transformed distributions. Finally, grid values were back-transformed to their original units producing a simulated reef tract (Fig. A1).

Results and Discussion

Simulated artificial landscapes were subjected to two analyses to ensure that grid values had desired statistical properties. Consistency in degree of spatial autocorrelation was evaluated using Moran's *I* statistic (Legendre & Legendre 1998). Isotropic spatial

autocorrelation was similar between survey data and artificial landscapes of maximum

vertical relief when the artificial landscape was produced with low spatial autocorrelation

($\kappa = 0.05$) and localized random variation (Fig. A2). Further, an empirical test was made

of whether means and variances in simulated cross-shelf strata reflected observed values.

One-hundred artificial landscapes representing maximum vertical relief were simulated,

and for each, differences between simulated and observed means and variances in each

stratum were calculated. The centered 95% interval of each of these differences

overlapped zero, thus simulated landscapes were deemed to have reasonably reproduced

the observed statistical characteristics.

Table A1. Reef formation types used as cross-shelf strata in fish distribution and in the simulated stratified random surveys. Grid cells is the total number of 200 m by 200 m Grid cells in the simulated and actual Florida Keys coral reef tract. Statistical properties of observed maximum vertical relief (m) in their original data scale, which were used as a representative environmental feature of the reef tract in simulated landscapes. SD is standard deviation of the sample, and n is the number of grid cells actually visited at random by divers, with replacement (see Smith et al. 2011).

| Habitat class	Rugosity	Grid cells	Observed Maximum vertical relief (m)				
			n	Min	Mean	Max	SD
i. Inshore patch reef	Low-med	417	99	0.10	1.16	3.12	0.70
ii. Mid-channel patch reef	Low-med	3103	390	0.12	1.37	4.27	0.77
iii. Offshore patch reef	Low-med	1814	228	0.10	1.08	4.00	0.64
iv. Offshore patch reef	High	98	45	0.90	2.41	3.97	0.83
v. Outer fore reef	Low-med	6330	1184	0.10	0.79	3.20	0.44
vi. Outer fore reef	Low-med	1609	275	0.14	1.40	3.70	0.51
vii. Outer fore reef	High	259	279	0.32	2.19	4.42	0.73
viii. Total		13630	2500				
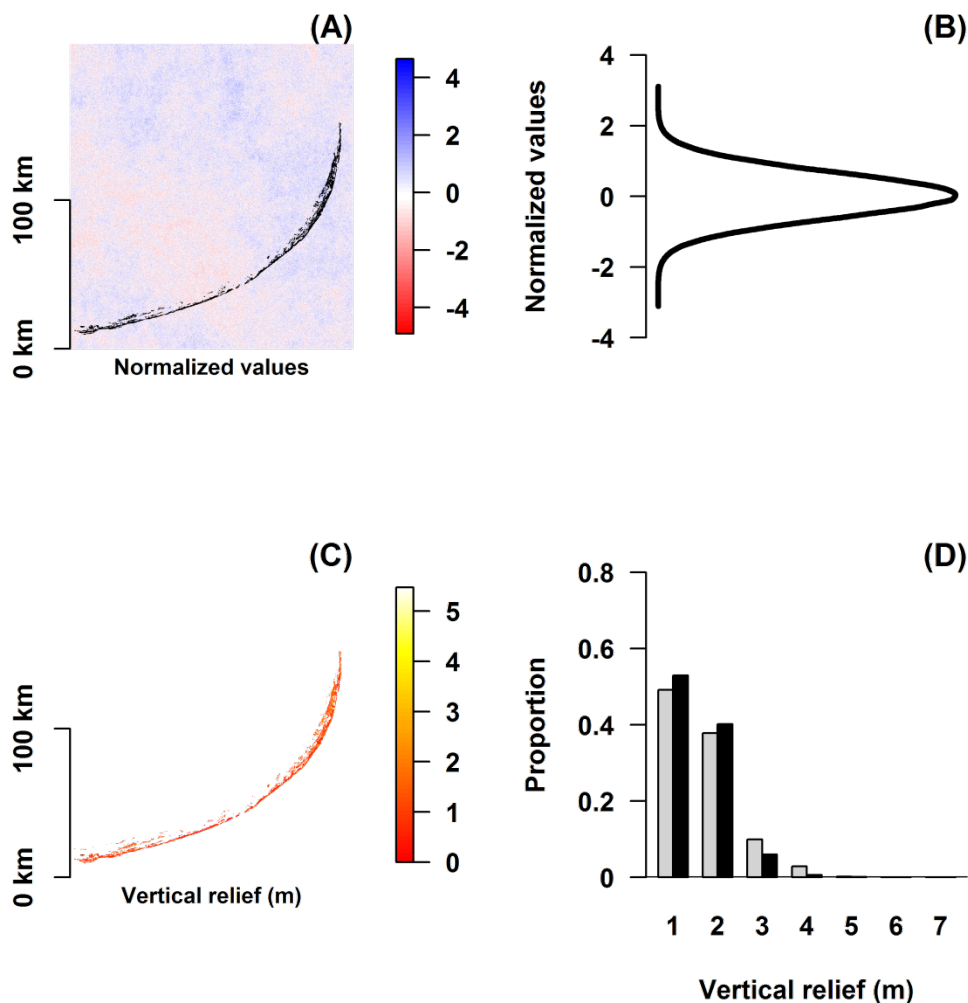
Figure A1. Artificial reef tract generated through the use of two-dimensional fractional Brownian surfaces. Panels are simulated fractional Brownian surfaces with black points representing the irregular grid of pixels representing the reef tract (A), histogram of normalized grid values (B), irregular grid scaled to original units (C), and histogram comparing observed (black bars) and simulated (grey bars) distributions of maximum vertical relief (D).
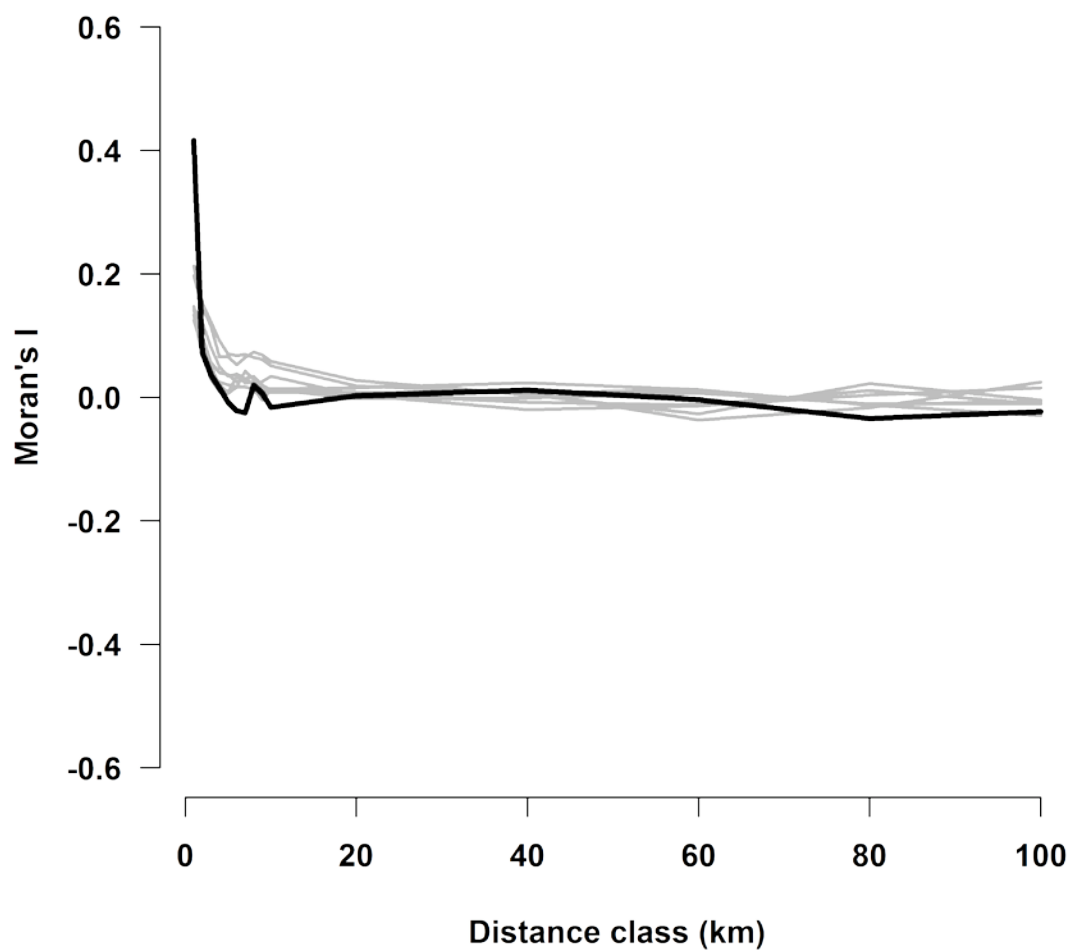
Figure A2. Isotropic spatial autocorrelation measured by Moran's *I* statistic for ten replicate artificial landscapes representing maximum vertical relief of the Florida Keys reef tract. Observed (black line) and simulated (grey lines) spatial autocorrelation.

APPENDIX B: QUANTIFYING INDIVIDUAL GROWTH VARIATION IN BLACK GROUPER

Background

Fisheries management has traditionally been informed by models that incorporate descriptions of somatic growth (Beverton & Holt 1957, Quinn & Deriso 1999). In many instances, models of growth describe the mean size-at-age of individuals in a population, despite widespread recognition that variation among individuals is inherent to fish populations. While the relative contributions of intrinsic and extrinsic factors to growth variation may be difficult to determine, statistical procedures are well developed for describing how growth trajectories vary among individuals (Sainsbury 1980, Pilling et al. 2002, Eveson et al. 2007, Zhang et al. 2009). Quantifying empirical patterns of black grouper growth variation enabled subsequent simulation of individuals that differed in their growth trajectories. Incorporating individual growth variation in individual-based modeling has been previously useful on the grounds of describing biological characteristics that are otherwise difficult to incorporate in numerical simulations, like individual variation in size and growth rate (Hart 2001, Bunnell & Miller 2005, Russo et al. 2009).

Methods

Patterns of growth variation in length-at-age were quantified by imposing a hierarchical structure on individual growth parameter estimates (Sainsbury 1980, Zhang et al. 2009). For a given growth parameter, like asymptotic length for instance, individual parameter estimates were constrained to arise from an underlying statistical distribution,

with the mean of this distribution corresponding to the mean value for the population. Individual variation was assumed to be linked to population mean through similar exposure to biological and environmental factors (Zhang et al. 2009). Such a hierarchical structure is beneficial, for instance, when length-at-age data consist of a single observation of length and age for each fish; thus, little information about a fish's growth trajectory will be contained in each observation. The hierarchical structure helped to address this data limitation because individual parameter estimates are considered to be related to one another and borrow strength from their assumed similarity (Gelman et al. 2004, Zhang et al. 2009, Kéry & Schaub 2012). It is the magnitude of this (dis)similarity, measured as the standard deviation of the common statistical distribution, which represents variation among individuals. The magnitude of growth dissimilarity among individuals produces characteristic population-level patterns of variation in length-at-age (Eveson et al. 2007). These population-level patterns of growth variation depend on the degree to which individuals differ with respect to Brody growth coefficient or asymptotic length, or both.

A collection of 2,141 black grouper (*Mycteroperca bonaci*) length-otolith pairings, utilized in the 2010 assessment of Gulf of Mexico and south Atlantic stocks were used in this analysis (Crabtree and Bullock 1998; SEDAR 2010a). Sectioned otoliths were aged by personnel from the Florida Fish and Wildlife Research Institute (O'Hop and Beaver 2009; SEDAR 2010a). Black grouper total lengths ranged from 26 mm (age 0 years) to 1518 mm (age 25 years), and the maximum observed age in the dataset was 33 years. Ten percent of the samples were aged to be older than 14 years. Fishery-dependent and fishery-independent sources contributed 70% and 30% of the

samples, respectively. Of the fishery-dependent samples, 96% were obtained from commercial gears.

The commonly used von Bertalanffy growth function (von Bertalanffy 1938) was extended to describe patterns of individual growth variation:

$$\hat{L}_i = L_{\infty,i}\left(1 - \exp\left[-K_i\left(t_i - t_0\right)\right]\right) + \varepsilon_i \tag{B.1}$$

where $\hat{L}_i$ is the estimated length at age t_i, $L_{\infty,i}$ is the asymptotic length, and K_i is the Brody growth coefficient, for individual i. The theoretical age at which length equals zero is denoted t_0, and ε_i is the residual error term. Hierarchical growth models for black grouper were constructed that allowed K and L_∞ to vary among individuals. The hierarchical model structure enabled variation in growth trajectories among individuals to be quantified in terms von Bertalanffy growth parameters.

Since the focus was on quantifying individual variation in growth, three models were compared that allowed either both K and L_∞ to vary among individuals (model A), or L_∞ only (model B), or K only (model C). Models of the types formulated in A, B, and C are referred to in the literature as nonlinear random effects models or as nonlinear mixed effects models. A fourth model, D, was constructed to describe only the mean growth of individuals.

In model A, both K and L_∞ were modeled as random effects

$$\text{Model } A: \ \hat{L}_i = L_{\infty,i}\left(1 - \exp\left[-K_i\left(t_i - t_0\right)\right]\right) + \varepsilon_i$$
$$L_{\infty,i} \sim N\left(\mu_\infty, \sigma_\infty^2\right), \ K_i \sim \Gamma\left(s_K, r_K\right)$$

where the estimated length, $\hat{L}_i$ and where $N\left(\mu_\infty, \sigma_\infty^2\right)$ denotes a normal distribution

describing the population distribution of $L_{\infty,i}$ with μ_∞ and σ_∞^2 indicating the population

mean asymptotic length and among-individual variance, respectively. The population

distribution of K_i was denoted by a gamma distribution, $\Gamma\left(s_K, r_K\right)$ with s_K and r_K

indicating shape and rate parameters, respectively. It is generally not clear how $L_{\infty,i}$ and

K_i should vary among individuals, but it is commonly assumed that $L_{\infty,i}$ and K_i follow

normal and gamma distributions, respectively (Sainsbury 1980, Eveson et al. 2007). A

gamma distribution was assumed for K_i due to its flexibility and its restriction to positive

real values. The mean and variance for the gamma distribution are s/r and s/r^2,

respectively (sub-scripts omitted). In practice, prior distributions can be placed on the

mean and variance of the gamma distribution and translated into shape and rate

parameters, allowing for a more straightforward interpretation of model outcomes.

Individual variation in the growth rate coefficient was parameterized according to the

hyperparameters μ_K and σ_K^2, which are the population mean Brody growth coefficient

and among-individual variance, respectively.

In model B, L_∞ was modeled as a random effect and k as a fixed effect

$$\text{Model } B: \ \hat{L}_i = L_{\infty,i}\left(1 - \exp\left[-K\left(t_i - t_0\right)\right]\right) + \varepsilon_i$$
$$L_{\infty,i} \sim N\left(\mu_\infty, \sigma_\infty^2\right), \ \mathrm{K}_i = \mu_K$$

Consistent with model A, individual variation in asymptotic length was assumed to

follow a normal distribution that was parameterized according to μ_∞ and σ_∞^2. Conversely

to model A, the growth rate coefficient for all individuals was fixed to the mean

population, μ_K.

In model C, K was modeled as a random effect and L_∞ as a fixed effect

$$\text{Model } C: \ \hat{L}_i = L_\infty \left(1 - \exp\left[-K_i\left(t_i - t_0\right)\right]\right) + \varepsilon_i$$
$$L_{\infty,i} = \mu_\infty, \ K_i \sim \Gamma\left(s_K, r_K\right)$$

Thus, variation in the growth rate coefficient among individuals was assumed to follow a

gamma distribution (as in model A), and parameterized according to μ_K and σ_K^2.

Asymptotic length for all individuals was fixed to the population mean, μ_∞.

In model D, both k and L_∞ were modeled as fixed effects, which describe the

mean growth curve of individuals in the population

$$\text{Model } D: \ \hat{L}_i = L_\infty \left(1 - \exp\left[-K\left(t_i - t_0\right)\right]\right) + \varepsilon_i$$
$$L_{\infty,i} = \mu_\infty, \ K_i = \mu_K$$

A Bayesian approach was used to fit life history functions using the software

OpenBUGS (Lunn et al. 2009). Growth model parameters were assigned diffuse priors:

$\mu_\infty \sim N\left(1000, 1 \times 10^6\right)$, a normal distribution with mean 1000 mm and standard deviation

1000; $\sqrt{\sigma_\infty^2} \sim U\left(0, 1000\right)$, a uniform distribution assigned to the standard deviation and

ranging between 0 and 1000; $\mu_K \sim \Gamma\left(0.01, 0.01\right)$; $\sqrt{\sigma_K^2} \sim U\left(0, 0.1\right)$; and, $t_0 \sim U\left(-10, 0\right)$.

Parameters were evaluated to determine whether the Markov chain Monte Carlo

(MCMC) algorithms converged on its target distribution. Convergence was checked

against Geweke and Gelman-Rubin convergence criteria (Geweke 1992, Congdon 2003,

Gelman et al. 2004). After discarding an initial burn-in period of 500,000 iterations,

diagnostic tests indicated convergence and approximations of posterior distributions were based upon a subsequent 500,000 iterations from two parallel chains, for a total of $1,000,000$ simulated draws.

The residual error structure of each of the von Bertalanffy functions was assumed to follow a truncated normal distribution. The truncated normal distribution was used because it is useful in accounting for truncated length-at-age observations that arise from fishery-dependent sources that are subject to minimum size restrictions (Diaz et al. 2004, SEDAR 2006, 2010a, b). The probability density function for the truncated normal distribution is:

$$f(L_i) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left\{-\frac{1}{2\sigma^2}(L_i - \hat{L}_i)^2\right\} \Big/ \left\{1 - \Phi((MIN_i - \hat{L}_i)/\sigma)\right\} \tag{B.2}$$

where $\hat{L}_i$ and σ are location and scale parameters, respectively, MIN_i is the minimum length limit assigned to observation i, and Φ denotes the cumulative density function of the standard normal distribution. Fishery-dependent samples were assigned minimum length limits in accordance with state and federal regulations at the time of collection (SEDAR 2010a). Fishery-independent samples were assigned a minimum harvest length value of zero (Diaz et al. 2004). The constant variance term, σ^2 was assigned a diffuse prior of the form $\sqrt{\sigma^2} \sim U(0,100)$.

To aid in model selection, the Deviance Information Criteria (DIC) was calculated (Spiegelhalter et al. 2002). In several previous studies, von Bertalanffy growth models have been compared using the DIC (Helser & Lai 2004, He & Bence 2007, Zhang et al. 2009). The DIC compares models according to a trade-off between model fit and complexity (Burnham & Anderson 2002, Spiegelhalter et al. 2002). The model having

the smallest DIC value is the best approximating model within the set (Spiegelhalter et al.
2002, Ntzoufras 2009). Models were ranked relative to the best model by calculating the
difference between the DIC score of a model and the DIC score of the best model.
Models with DIC differences < 2 indicated substantial competing support of being the
best-fitting model, values between 2 and 4 had some support, and values > 10 had
essentially no support (Burnham & Anderson 2002, Spiegelhalter et al. 2002).

Model adequacy was assessed by calculating a discrepancy measure $T(L, \mathbf{\theta})$ that
summarized goodness-of-fit between a model (where $\mathbf{\theta}$ is the parameter vector obtained
from a single MCMC iteration) and the observed data ($L = (L_1, ..., L_n)$) (Gelman et al.
2004, Gelman & Hill 2007, Ntzoufras 2009). Taking many random samples from the
posterior distribution $\mathbf{\theta}_j$, $j = 1, ..., K$, discrepancy between the model and the data was
calculated using the χ^2 discrepancy measure (Gelman et al. 2004, Ntzoufras 2009):

$$T(L, \mathbf{\theta}_j) = \sum_i \frac{\left(L_i - E\{L_i \mid \mathbf{\theta}_j\}\right)^2}{\operatorname{var}\{L_i \mid \mathbf{\theta}_j\}} \qquad (B.3)$$

For each of the random samples from the posterior distribution, a replicated dataset L^{rep}
was also simulated and used to calculate $T(L^{rep}, \mathbf{\theta}_j)$. Systematic differences between the
model and observed data were summarized through a scatterplot of the values $T(L, \mathbf{\theta}_j)$
and $T(L^{rep}, \mathbf{\theta}_j)$, and in terms of the Bayesian p-value. The graphical comparison revealed
whether the distributions of $T(L, \mathbf{\theta}_j)$ and $T(L^{rep}, \mathbf{\theta}_j)$ were symmetrical (Brooks et al.
2000, Gelman et al. 2004). The Bayesian p-value is defined as the proportion of times the

discrepancy measure for the simulated values $T\left(L^{rep}, \boldsymbol{\theta}_j\right)$ was greater than the discrepancy

measure of the observed data $T(L, \theta_j)$ (Ntzoufras 2009, Kéry 2010). A Bayesian p-value

near 0.5 indicated a good fit, while those close to zero or one indicated differences

between the model and the observed data (Gelman et al. 2004, Ntzoufras 2009). Residual

plots were also created to diagnose trends in residuals.

Results

      All growth models for black grouper converged on their target distributions and

samples from each chain were considered sufficient to approximate posterior

distributions. The population mean growth parameters (μ_∞, μ_K, t_0) were nearly identical

in each of the von Bertalanffy model formulations (Table B1). Model A (both K and L_∞

modeled as random effects) had the lowest DIC score. The remaining models had DIC

differences of >300, indicating essentially no support for any of these models as being the

best-fitting model (Table B1). The discrepancy plots, the Bayesian p-values, and residual

plots indicated that the selected hierarchical formulation (model A) fit the data well (Fig.

B1). The selected model of individual variation in K and L_∞ (model A) produced a

population mean asymptotic length of 1362 mm and an among-individual standard

deviation of 38 mm (Table B1). The 95% credible interval for individual asymptotic

length was 1282 – 1440 mm. The population mean growth rate coefficient was 0.138

year^{-1} and the 95% credible interval for individual variation in the growth rate coefficient

was 0.112 – 0.167 year^{-1} (Table B1). Observed and predicted 2.5 and 97.5 percentiles in

length-at-age were consistent across age classes, with the exception of the oldest age

classes for which only a small number of observations were available (Fig. B2).

Discussion

The fixed effects growth formulation (model *D*) was compared to results from Crabtree and Bullock (1998). Estimates of asymptotic length and the Brody growth coefficient differed somewhat from those previously reported by Crabtree and Bullock (1998). Estimates of asymptotic length and Brody growth coefficient reported by Crabtree and Bullock (1998) were 1306 mm and 0.169 year^{-1}, respectively. A number of factors appear to have attributed to these differences. Crabtree and Bullock's dataset consisted of approximately half of the samples utilized in this analysis and they assumed a log$_{10}$ transformation of data. As a comparison, the transformation used by Crabtree and Bullock (1998) produced point estimates of $L_\infty = 1339$ and $K = 0.14$ from the dataset used in this analysis. This analysis also assumed a truncated normal error structure, which differed from the regression analysis performed by Crabtree and Bullock (1998). O'Hop and Beaver (2009) compared fits of the von Bertalanffy function between Crabtree and Bullock's dataset and the larger dataset used in this study (that included Crabtree and Bullock's data). O'Hop and Beaver (2009) suggested that differences in parameter estimates were mainly attributable to differences in the composition of length-age pairings within each dataset (O'Hop & Beaver 2009). To a lesser extent, differences in estimates of asymptotic length and the growth rate coefficient were affected by re-examining and modifying ageing estimates made by Crabtree and Bullock (1998). An alternative ageing criterion was applied to Crabtree and Bullock's dataset in order to standardize their ageing estimates with newer samples in the dataset (O'Hop & Beaver 2009).

While the sources of individual growth variation are often unknown, deviations from mean size-at-age can be ascribed to genetic and environmental factors. In some cases, environmental and biological influences on intra-population and inter-population growth patterns have been identified (Francis 1994, Helser & Lai 2004, He & Bence 2007, Kimura 2008, Linde et al. 2011). Where environmental factors influence growth trajectories, the growth rate coefficient and asymptotic length appear to be related to food availability and temperature. The growth rate coefficient is expected to be positively influenced by temperature, owing to proportionality between k and metabolic cost (Beverton & Holt 1959, Pauly 1981). Conversely, asymptotic length is expected to be negatively influenced by temperature and positively influenced by food availability (Beverton & Holt 1959, Pauly 1979). Despite not necessarily knowing the extent to which intrinsic and extrinsic factors contribute to black grouper growth trajectories, patterns of growth variation can be quantified and incorporated fisheries analyses and simulation modeling.

Table B1. Estimated parameters means (standard errors in parentheses) and deviance information criteria (DIC) for von Bertalanffy growth model formulations for black grouper *Mycteroperca bonaci*.

Parameter	*Model A*	*Model B*	*Model C*	*Model D*	*Crabtree & Bullock 1998*
μ_{∞} (mm)	1362 (7)	1359 (8)	1363 (7)	1360 (8)	1306 (8)
σ_{∞}	38 (11)	30 (14)	-	-	-
μ_{k} (year^{-1})	0.138 (0.002)	0.137 (0.002)	0.138 (0.002)	0.137 (0.002)	0.169 (0.004)
σ_{k}	0.014 (0.002)	-	0.012 (0.002)	-	-
t_0 (year)	-0.87 (0.05)	-0.88 (0.06)	-0.87 (0.06)	-0.88 (0.06)	-0.77 (0.06)
σ	56.40	73.41	65.68	76.71	-
ΔDIC	0	380	330	460	-

Notes: ΔDIC is the difference between the DIC score of each model and the DIC score of the best model (i.e. the model with the lowest DIC score).
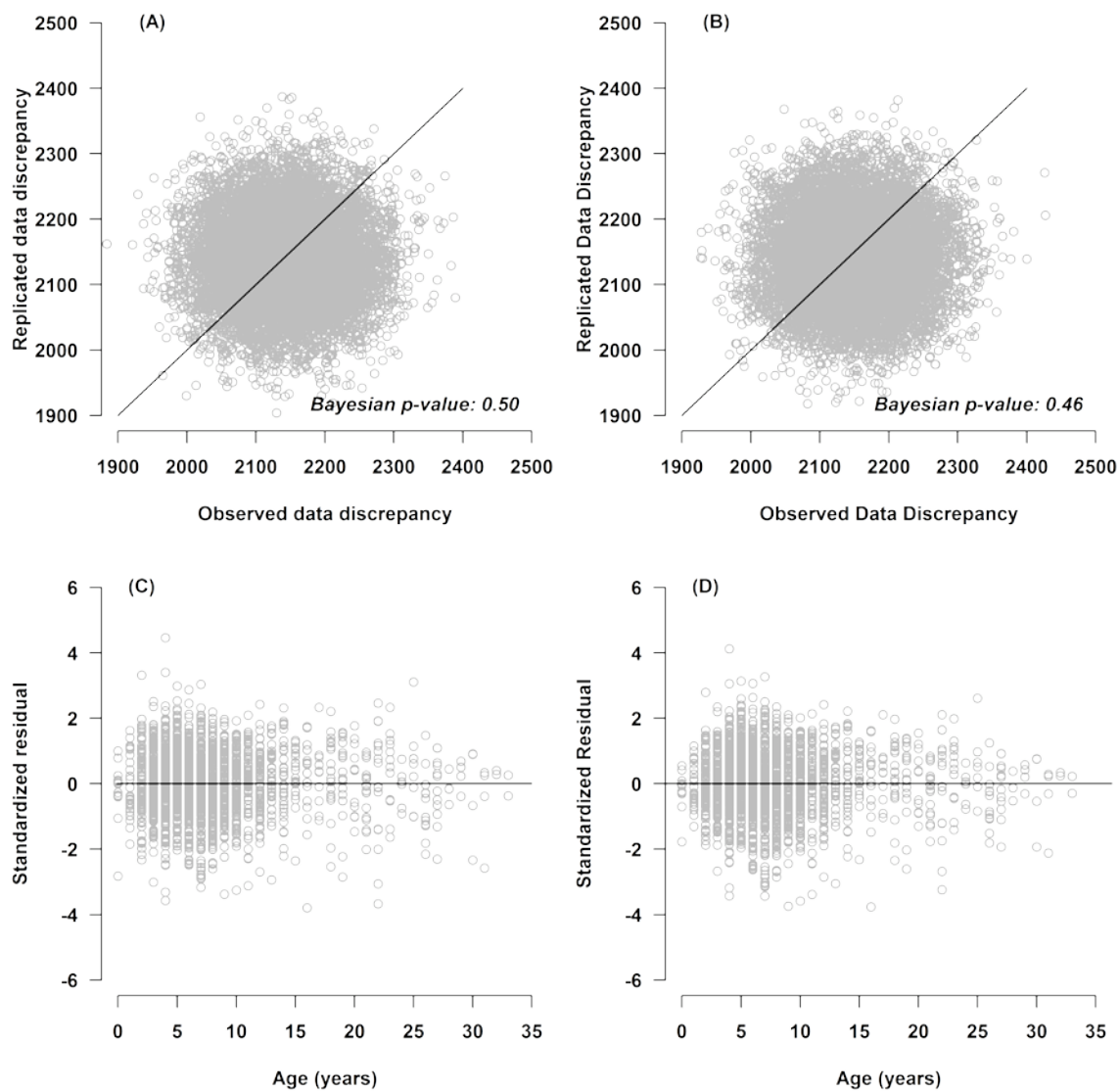
Figure B1. Goodness-of-fit plots for the von Bertalanffy model for black grouper Mycteroperca bonaci for model A (both k and L_∞ as random effects) and model D (fixed effects). Shown is model adequacy based on the χ^2 discrepancy measure and Bayesian p-value for random effects (A) and fixed effects (B) models. Standardized residuals plotted against age in years for random effects (C) and fixed effects (D) models.
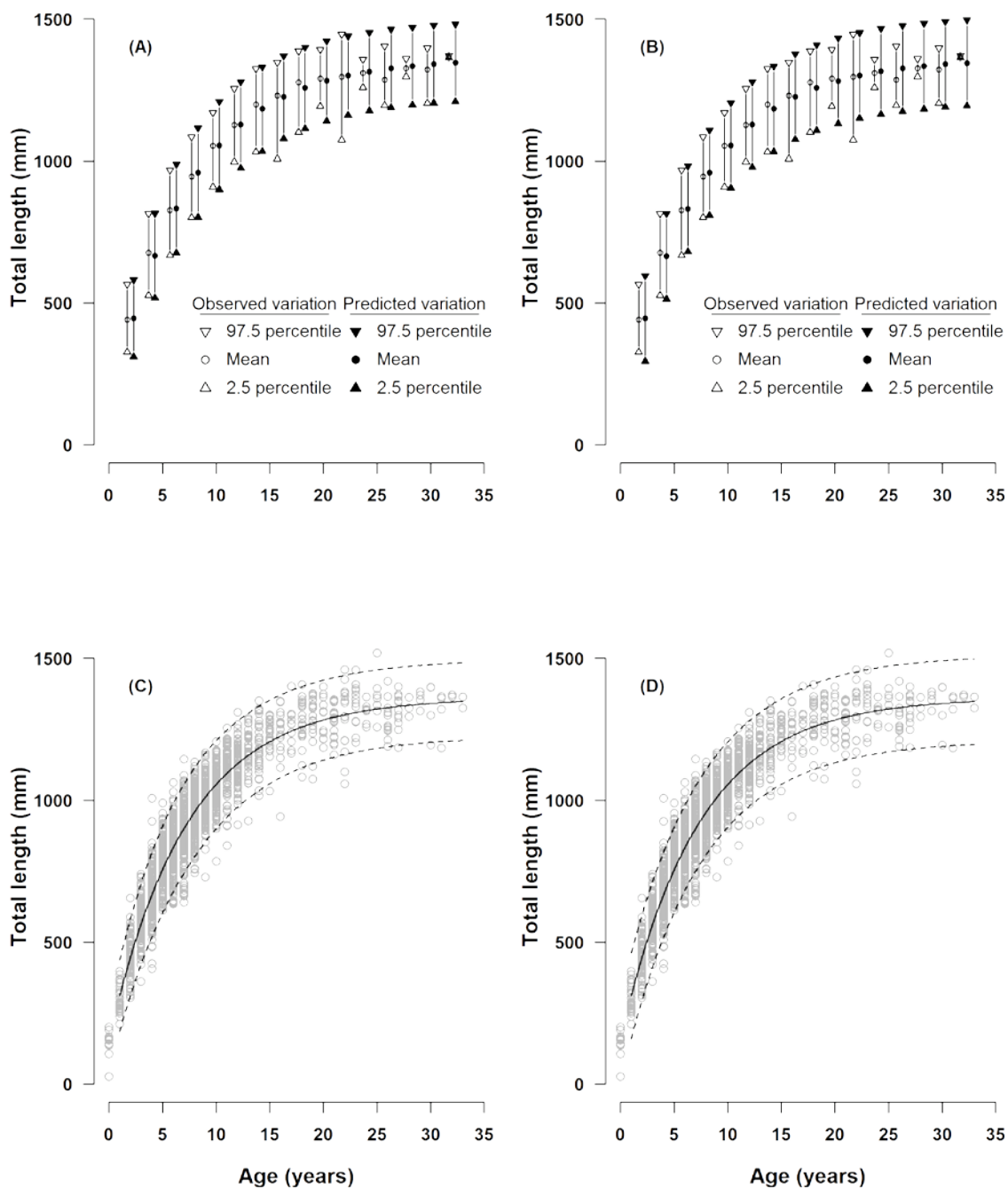
Figure B2. Observed and predicted patterns in length-at-age for black grouper *Mycteroperca bonaci* for growth model *A* (both *k* and L_∞ as random effects) and growth model *D* (fixed effects). Shown is the consistency between observed and predicted means and central 95% ranges in length-at-age at two-year age intervals for random effects (A) and fixed effects (B) models. Lower panels shows observed length-age pairings plotted against predicted mean length-at-age (solid line) and 95% credibility interval (dashed line) for random effects (C) and fixed effects (D) models.

APPENDIX C: PROPERTIES OF THE BLACK GROUPER SIMULATIONS

This appendix provides a comparison of the population-level properties produced by the individual-based simulation framework to properties produced by a traditional age-structured population model (Quinn & Deriso 1999, Haddon 2011). First, equilibrium age structure was simulated using the individual-based model and compared to the mean expectation from a traditional age-structured population model. Mean individual-based age-structure simulated from ten replicates under no fishing mortality and again under high fishing mortality (F=0.6) were consistent with expectations from an age-structured population model (Fig C1). Second, analysis of population dynamics was conducted by simulating per-recruit metrics using the individual-based model and comparing these metrics to those produced from the numerical per-recruit model described in chapter 2. For the per-recruit analysis, recruitment was fixed at a constant value (i.e. no stock-recruitment function). Individual-based patterns in yield-per-recruit and female spawning biomass-per-recruit were consistent with those expected from a traditional age-structured population model (Fig C2).
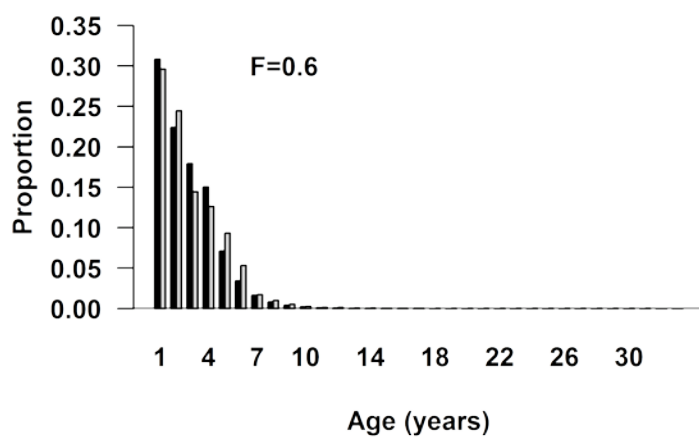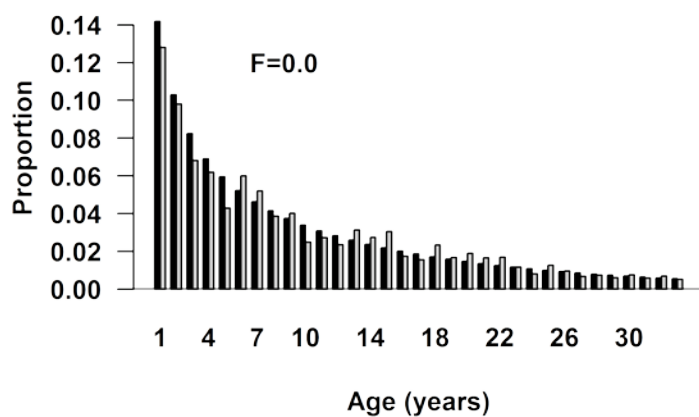
Figure C1. Equilibrium age structure produced by an aggregate-abundance model (black bars) and from the individual-based model (grey bars) for an unfished population (upper panel) and for a fished population (lower panel; *F=0.6*.
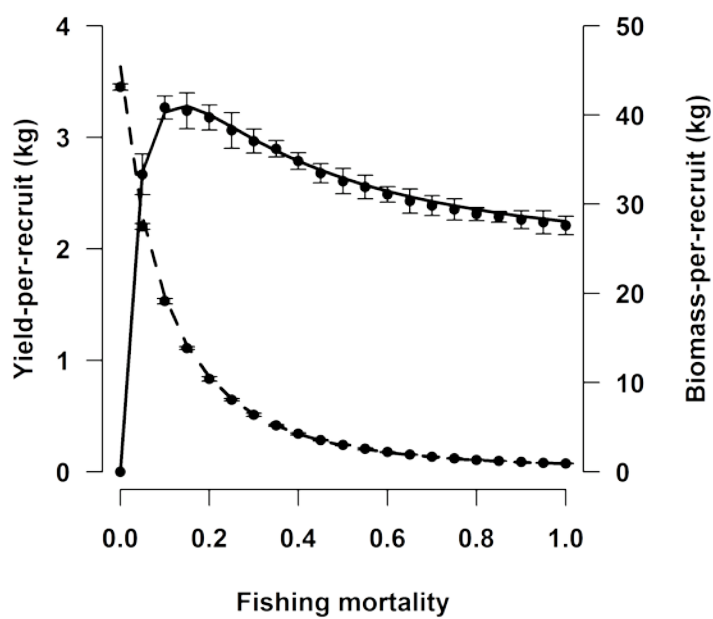
Figure C2. Per-recruit metrics calculated from aggregate-abundance model (lines) and individual-based model (points +/- two standard deviations). Solid line is yield-per-recruit (kg) and dashed line is female spawning biomass-per-recruit (kg).

APPENDIX D: PROPERTIES OF THE SPINY LOBSTER SIMULATIONS

This appendix provides details about the properties of the spatially explicit individual-based model (IBM) representative of Caribbean spiny lobster (*Panulirus argus)* at Glover's Reef Marine Reserve, Belize. Model properties are compared to empirical data about the ecology of spiny lobster and to a traditional age-structured model of cohort dynamics.

Temporal dynamics

The temporal dynamics of the IBM produced population-level properties that were equivalent to those produced by a traditional age-structured model that tracked mortality of cohort abundance using a weekly time step (Quinn & Deriso 1999, Haddon 2011). Yield in numbers were calculated using the Baranov catch equation (

$$Y^N = \frac{F}{M+F} N(1 - \exp(-(M+F)))$$), which is used in a similar manner in the IBM

calculations of total catch. Comparisons between the IBM and the age-structured simulation were made in terms of per-recruit metrics (Thompson & Bell 1934, Beverton & Holt 1957). Annual yield in numbers-per-recruit was consistent among representations as was simulated unfished age structure (Fig. D1).

Spatial dynamics

The spatial dynamics of spiny lobster were specified as two separate processes: dispersive movement among shallow reef habitats and migratory movement to/from the deep wall reef. Dispersive movement required specifying maximum weekly dispersal distance and a departure rate. Evidence suggests that spiny lobster move sporadically and

less than 350 m per day, with movement durations commonly lasting one to several days (Gregory & Labisky 1986, Davis & Dodrill 1989, Acosta 2002, Bertelsen & Hornbeck 2009). Maximum weekly dispersal distance was specified as 750 m to reflect empirical estimates and to reflect the patchy distribution of reef habitats, which ensured that all locations had at least one neighboring cell within the maximum search distance. Movement studies conducted by Acosta (1999) and Acosta (2002) enabled a general comparison of monthly movement distances of spiny lobster in the IBM with empirical patterns. Emigration rates of spiny lobster from isolated patch reefs (1000 m^2 average area) at Glover's Reef vary between 0.1 and 0.4 per 5- to 7-day observation periods (Acosta 1999). In addition, Acosta (2002) reported linear movement distances for up to 30 days. Noting that simulated dispersive movement was a function of movement parameters and the spatial mosaic of reef habitats, a weekly departure rate of 0.3 was reasonably consistent with empirical observations. A departure probability of 0.3 resulted in median monthly distance of 230.5 m, which was most consistent with the monthly mean movement distances reported by Acosta (2002) of 268.1 ($\pm$ 6.7 SE) for adult males and 232.2 ($\pm$ 8.3 SE) for adult females (Fig. D2). Departure probabilities of 0.1 and 0.5 performed more poorly; resulting in median monthly movement distances of 0 m and 395.3 m, respectively (Fig. D2).

Subsequent to dispersive movement, individuals migrated to and from the deep wall reef, depending of which spatial dynamics scenario was chosen. The probability of migrating to the deep reef migration reef was tuned to reflect an empirical estimate of the distribution of individuals between shallow reefs of the conservation zone and the deep fore reefs beyond the reach of the fishery. This contrast helped to determine the fractions

of the spiny lobster population that naturally inhabit shallow versus deep reef habitats in the absence of the effects of fishing on spiny lobster density. Acosta and Robertson (2003) found that densities of adult spiny lobster were, on average, 320.1 kg/ha in shallow reef habitats and 40.4 kg/ha within combined deep forereef and wall reef locations. Length frequency distributions from Acosta and Robertson (2003) were digitized, scaled to reflect the mean densities of adults ($\geq$ 75 mm length categories), and were fit to a logistic migration function using a nonlinear least squares routine (R Development Core Team 2012). Data from Acosta and Robertson (2003) suggested that the proportions of adult spiny lobster in shallow reefs and the deep reef were 12% and 88% respectively. Tuning the deep reef migration in the simulations to reflect these empirical patterns, mid-season (week 18) median proportions in the simulated conservation zone and deep wall reef were 8.5% and 85%, respectively. The specified weekly migration rate resulted in a median 5.3% of the total population (deep reef + conservation zone + general use zone) inhabiting the deep wall reef at the mid-point of the fishing season (Fig. D3).

The spatial properties of simulated spiny lobster distribution were summarized using the tuned deep reef migration rate, a shallow reef departure probability of 0.3, an annual fishing mortality rate of 1.5 yr^{-1}, and equal effort allocation among fishing grounds. This set of factor levels corresponded to the Deep Refuge – Reference Dispersal scenario. Fifty replicate simulations were carried out and the distribution of spiny lobster was reported as the percent of the total abundance inhabiting the conservation zone, the general use zone, and the deep wall reef. At the beginning of the fishing season (week 1), the general use zone contains the largest fraction of spiny lobster (median 60%; Fig. D3).

However, under the high exploitation rate used to generate these results, the abundance in the general use zone is rapidly depleted and the conservation zone then contains the largest fraction of spiny lobster by the mid-point of the fishing season (week 18: median 57%; week 35: 53%; Fig. D3). Between weeks 18 and 35 a slight, but noticeable, increase in the percent of abundance in the general use zone is evident (Fig. D3). This increase in percent of abundance reflects recruitment occurring in the latter half of the fishing season, distributed proportional to shallow reef habitat distribution, which results in an apparent disproportionate increase in new recruits to the general use zone.

Spiny lobster fishery

Weekly fishing effort was distributed among fishing grounds as follows:

$$f[t, A] = \frac{v[t, A]}{\sum_{j} v[t, j]} f_{\text{Total}}[t],$$

(D.1)

where f is fishing effort allocated to fishing ground, A, in week, t, from weekly total fishing effort, f_{Total}, and v is the value of each fishing ground. Alternative model specifications assumed that fishing ground was either equal among all fishing grounds or was proportional to spiny lobster abundance (Caddy 1975, Walters & Bonfil 1999, Walters et al. 1999). Fishing mortality within each fishing ground was calculated:

$$F[t, r] = qf[t, r].$$

(D.2)

Catchability, q, was assumed to be constant and was specified to reflect a target annual fishing mortality rate, F_{Annual}, achieved by the fishery under average fishing conditions:

$$\frac{F_{\text{Annual}}}{n_{\text{Weeks}}} = \frac{qf_{\text{Average}}}{n_{\text{Grounds}}}$$

(D.3)

where f_{Average} is weekly total effort, $n_{Grounds}$ is the number of fishing grounds containing >0 grid cells, and n_{Weeks} is the number of weeks in the fishing season.

Fishing effort was spatially distributed uniformly across all fishing grounds or in proportion to spiny lobster abundance. The former case produced the effect that all vulnerable spiny lobster were subject to the same fishing mortality rate, while the latter case produced the effect that fishers distributed themselves in proportion to the availability of the resource, which resulted in heterogeneous patterns of fishing mortality. Notably, the latter effort allocation scheme did not result in fishers aggregating along the edge of the conservation zone to harvest spiny lobster moving into the fished area (Fig. D4). Edge-effects are sometimes imposed in simulations of marine reserve design (Kellner et al. 2007). Because patch reefs near the edge of the conservation zone are rather sparsely distributed relative to the forereef or patch reefs further north in the Atoll, abundance within 1 km x 1 km fishing grounds near the edge of the conservation zone had relatively low abundance, thus, attracting low fishing effort (Fig. D4).

Discussion

Spatial simulation models can enable exploration of the effects of spatial heterogeneity in fish distribution in relation to spatial heterogeneity in the distribution of fishing effort (Pelletier & Mahévas 2005). Accordingly, spatial modeling can be used to investigate design considerations for marine reserves (Guénette et al. 1998, Gerber et al. 2003, Pelletier & Mahévas 2005) and strategies for managing surrounding fisheries (Hilborn et al. 2006, Babcock & MacCall 2011). The simulation model presented herein is one of the few spatially explicit models of adult stage spiny lobster dynamics, although

there are noteworthy simulations of sub-adult movement in response to habitat degradation and presence of congeners (Butler et al. 2005, Dolan & Butler 2006). By simplifying the simulation framework to include only adult spiny lobster, the complexity of specifying survival rates for juvenile spiny lobster was avoided as these rates are highly uncertain. Further, this simplification avoided having to describing ontogenetic shifts in movement behaviors between juvenile and adult life stages (Butler et al. 2005, Childress & Jury 2006, Dolan & Butler 2006). In specifying how spiny lobster moved between shallow reef habitats, individuals required knowledge of surrounding destination choices. Decisions based on knowledge of surrounding habitat were not intended to represent behaviorally-based decisions; rather, each surrounding destination cell represented a probabilistic end-point from which stochastic outcomes were generated.

In developing the simulation framework, several important aspects about spiny lobster ecology were highly uncertain and require further attention before a more complete picture of the fishery and its resource at Glover's Reef can be established. Migration to the deep reef was probably highly uncertain, and could vary by season, year, or in a density-dependent manner (Acosta & Robertson 2003). Consequently, the simulation model is not suitable for providing advice about the degree to which the deep wall reef may provide protection for the spawning population. In addition, the temporal patterns in recruitment and migration that were assumed in the spatial dynamics scenarios were uncertain. Although peak spiny lobster recruitment is thought to occur throughout the Caribbean in spring, followed by additional autumn recruitment, this pattern has not been confirmed at Glover's Reef (Villegas et al. 1982, Chubb 1994, FAO 2001, Acosta & Robertson 2003, Cruz & Bertelsen 2008). In addition, the model did not attempt to link

spawning biomass to recruitment in subsequent years owing to the vast uncertainty associated with the importance of localized recruitment versus long-distance larval dispersal in spiny lobster population regulation (Ehrhardt 2005). Finally, the spatial distribution of fishing effort was based on two commonly used algorithms, but information about the actual distribution of fishing effort at Glover's Reef remains unknown. Should additional information about fishery dynamics become available, there are several alternative approaches for spatially distributing fishing effort that could be considered (Gillis et al. 1993, Kellner et al. 2007).
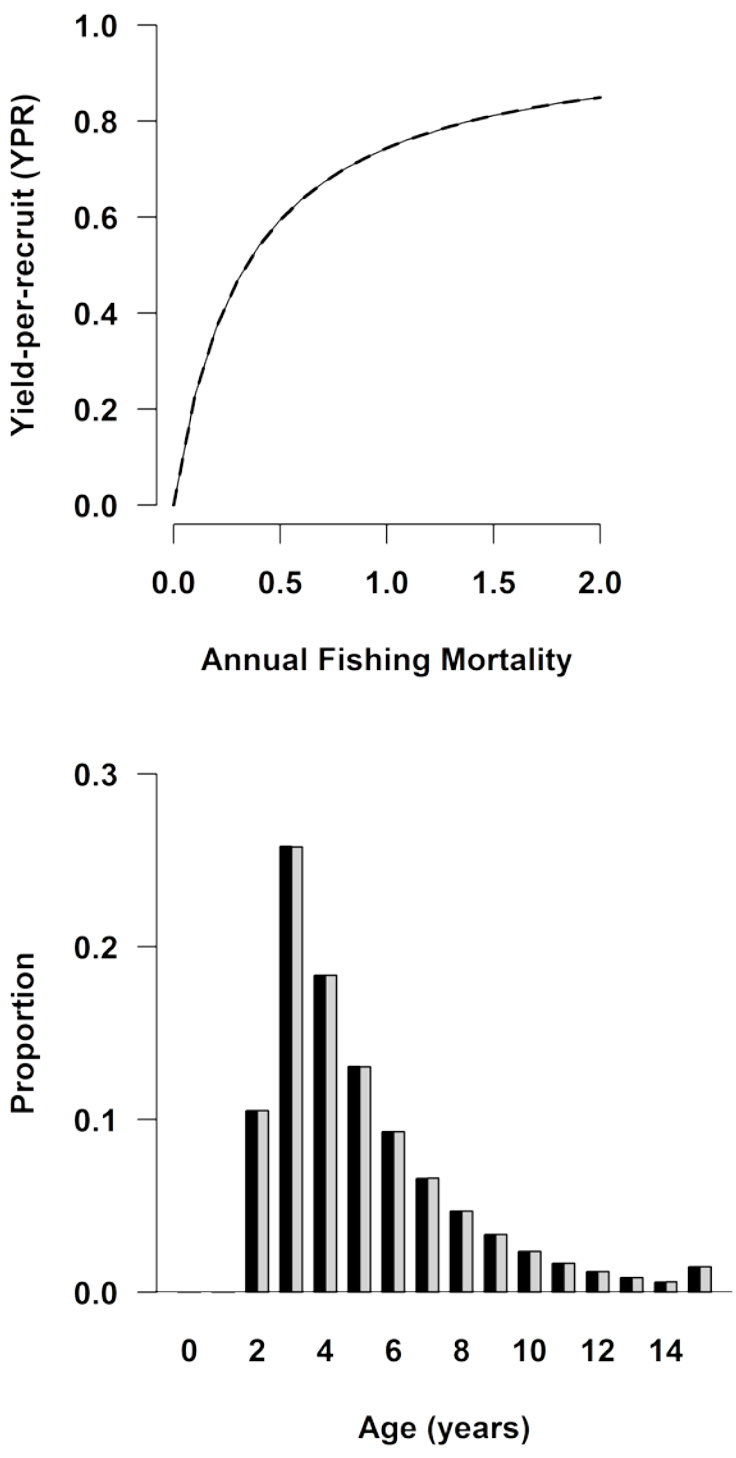
Figure D1. Yield-per-recruit in numbers (YPR) between the IBM and an age-structured simulation (A). Dashed lines are the IBM and solid lines are the age-structured simulation – difficulty distinguishing lines is due to the similarity in trends. Comparison of unfished population age structure between IBM (black bars) and a traditional age-structured simulation (grey bars) (B).
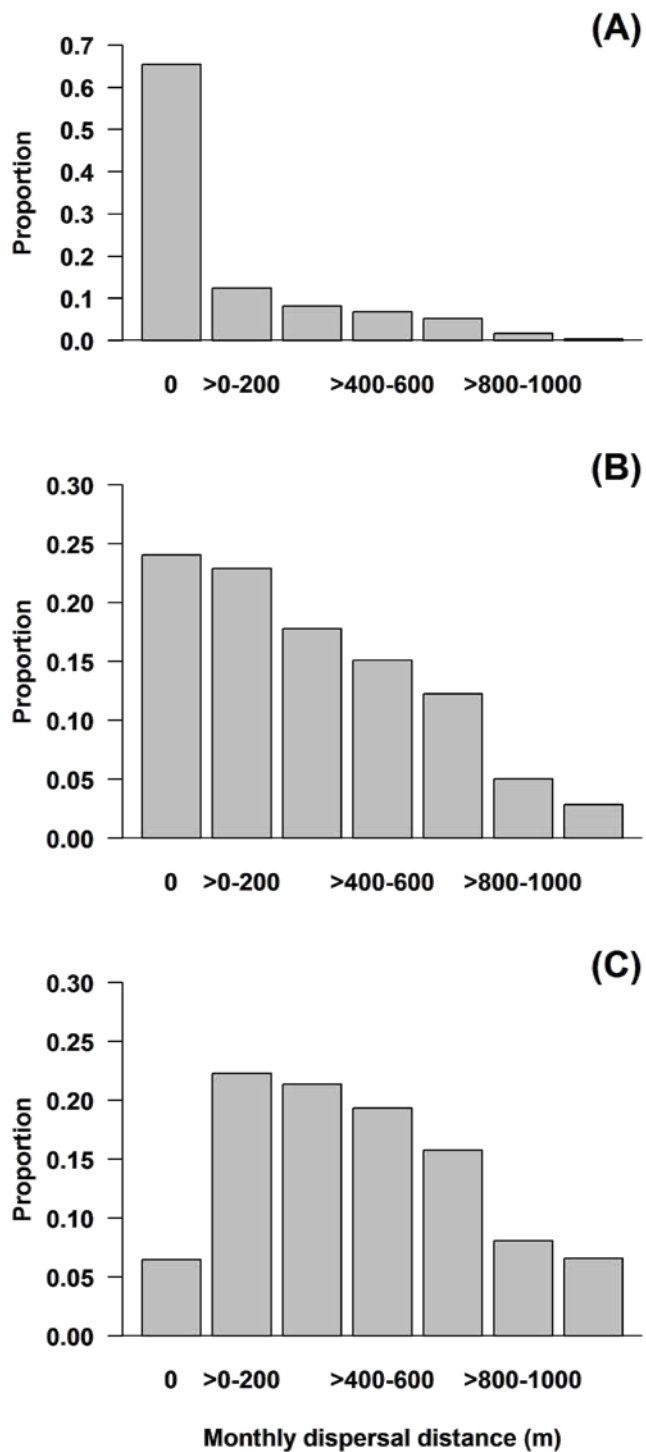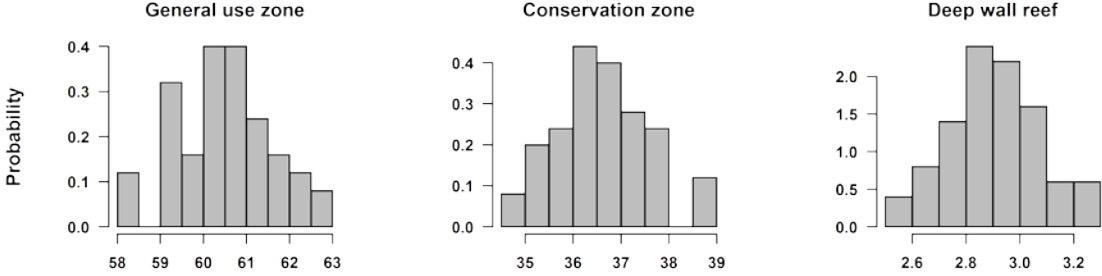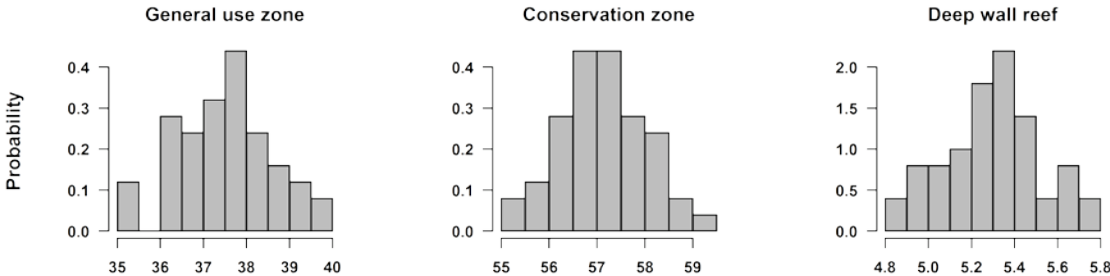
Figure D2. Simulated linear monthly movement distances for 100,000 spiny lobster, based on departure probabilities 0.1 (A), 0.3 (B), and 0.5 (C) between shallow reef grid cells.
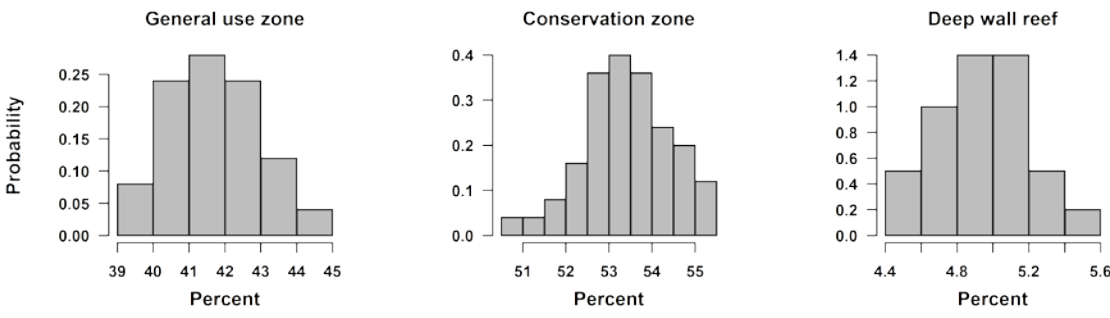
Figure D3. Abundance distribution of spiny lobster as percent of total in the conservation zone, the general use zone, and the deep wall reef. Histograms show distribution of percentages across 50 simulated datasets. Data were simulated using the reference departure rate (0.3), without return of deep reef migrants to shallow areas, equal effort distribution, and fishing mortality of 1.5 yr-1.
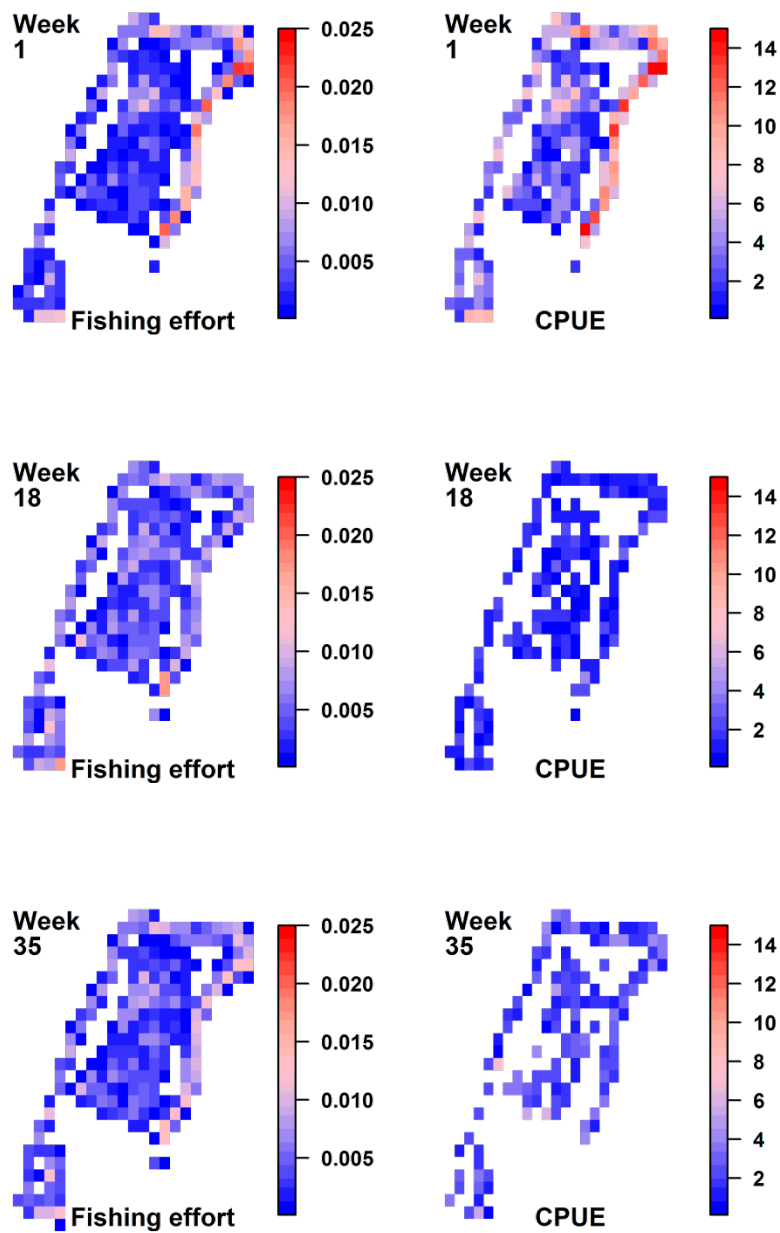
Figure D4. Spatial patterns of fishing effort (as a fractions of total effort) and catch-per-unit-effort (CPUE) at the beginning (week 1), mid-point (week 18) and end (week 35) of the simulated fishing season. Effort distributed in proportional to spiny lobster abundance. Plots show only nonzero values, illustrating the spatial depletion of the population by the fishery as the fishing season progresses.