

How fisher behavior can bias stock assessment: insights from an agent-based modeling approach

Steven Saul, Elizabeth N. Brooks, and David Die

Abstract: During stock assessment, fishery-dependent observations are often used to develop indices of abundance or biomass from catch per unit of effort (CPUE) and contribute catch at size or age information. However, fisher behavior, rather than scientific sampling protocols, determines the spatial and temporal locations of fishery-dependent observations. As a result, trends from fishery-dependent data may be a function of fishing activity rather than fish population changes. This study evaluates whether data collected from commercial fishing fleets in the Gulf of Mexico are representative of trends in fish population size. A coupled bioeconomic agent-based model was developed to generate simulated fishery data, which were used to populate an age-structured stock assessment. Comparison of stock assessment results with simulated fish population dynamics showed that management advice from assessment models based on fishery-dependent data could be biased. Assessment of fish with small home ranges harvested by fishing fleets that frequent the same fishing grounds could cause overestimation of fishing mortality. Not accounting for the spatial structure of the fishers or fish can cause biased estimates of population status.

Résumé : Dans le cadre d'évaluations de stocks, des observations dépendantes de la pêche sont souvent utilisées pour définir des indices d'abondance ou de biomasse à partir des captures par unité d'effort (CPUE) et fournissent de l'information sur les prises selon la taille ou l'âge. Ce sont toutefois les comportements des pêcheurs, plutôt que des protocoles d'échantillonnage scientifiques, qui déterminent l'emplacement dans l'espace et le temps d'observations dépendantes de la pêche. Les tendances révélées par les données dépendantes de la pêche peuvent donc être une fonction de l'activité de pêche plutôt que de changements dans les populations de poissons. L'étude tente d'établir si les données tirées de flottes de pêche commerciale dans le golfe du Mexique sont représentatives des tendances de la taille des populations de poissons. Un modèle qui jumelle des approches bioéconomique et multiagents a été mis au point pour générer des données de pêche simulées qui ont été utilisées comme intrants pour une évaluation des stocks structurée par âge. Une comparaison des résultats de l'évaluation des stocks à la dynamique simulée des populations de poissons montre que les avis de gestion tirés de modèles d'évaluation reposant sur des données dépendantes de la pêche pourraient être biaisés. L'évaluation de poissons caractérisés par de petits domaines vitaux pêchés par des flottes de pêche qui fréquentent les mêmes lieux de pêche pourrait entraîner une surestimation de la mortalité par pêche. La non-prise en compte de la structure spatiale des pêcheurs ou des poissons peut se traduire par des estimations biaisées de l'état des populations. [Traduit par la Rédaction]

Introduction

The importance of understanding human behavior in the context of fisheries management has been well acknowledged (Branch et al. 2006; Fulton et al. 2011). Fisher behavior has often been discussed with respect to avoiding unforeseen responses by fishing fleets and (or) the ecosystem to different fisheries policies (Girardin et al. 2017; Salas and Gaertner 2004; Wilen et al. 2002). Less attention, however, has been given to the influence that fisher behavior might have on stock assessments, which are often the tool that informs catch limits or other aspects of fisheries management (Fulton et al. 2011). Fisher behavior can affect stock assessments because it determines the spatial and temporal locations of fishery-dependent observations, often a primary input to stock assessment (Sethi et al. 2010; Nguyen and Leung 2013).

Many studies have evaluated the impact of specific fishing behavior changes in response to changes in policy (Dharmawan et al. 2017; Said et al. 2018; Seung 2017), the environment (Tommasi et al. 2017), technology (Herrmann et al. 2017), or market conditions (Guillotreau et al. 2017). Such behavioral changes are thought to aid in maximiz-

ing fisher revenue by allocating their limited fishing effort in what fishers perceive to be an economically efficient manner (Hilborn 1985; Lane 1988; Salas et al. 2004). However, even in the absence of specific drivers of fishing effort, such as periods of market and regulatory stability, the daily operational decisions of fishers are still focused on allocating their fishing effort to fulfill orders and make a profit. As such, fisher behavior, rather than scientific sampling protocols, determines the spatial and temporal locations of fishery-dependent observations.

Fishery-dependent observations are not equivalent to those collected from statistically designed fishery-independent sampling (Mesnil et al. 2009; Reimer et al. 2017). However, both fishery-dependent and fishery-independent observations are often used to fit stock assessment models (Maunder and Piner 2015). In stock assessment models, fishery-dependent observations are often used to develop indices of abundance or biomass that are assumed to be proportional to fish abundance or biomass trends over time (Maunder et al. 2006). Fishery-dependent observations also provide catch at size (or age) information, which are required for

Received 19 January 2019. Accepted 1 August 2020.

S. Saul. Arizona State University, College of Integrative Sciences and Arts, Polytechnic Campus, 6073 S. Backus Mall, Mail Code 2780, Mesa, AZ 85212, USA.
E.N. Brooks. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, USA.

D. Die. University of Miami, Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Cswy., Miami, FL 33149, USA.

Corresponding author: Steven Saul (email: steven.saul@asu.edu).

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from copyright.com.

many types of assessment models. As a result of targeting and profit-oriented decisions, trends in abundance and population size structure derived from these data may be a function of fishing activity rather than fish population changes. To minimize the influence of exogenous processes on fishery-dependent data, statistical approaches are used to remove effects of fishing on catch per unit of effort (CPUE) so that the remaining trend reflects actual changes in fish abundance (Bishop et al. 2000, 2004; Maunder and Punt 2004).

However, even when variables that may explain some drivers of fisher behavior are available in the data, the interactions between fisher behavior and fish populations are complex, nonlinear, and cannot be simply standardized away (Ye and Dennis 2009; Monk et al. 2018). For example, some approaches have been proposed to address time–area interactions that can bias CPUE indices (Walters 2003; Campbell et al. 2014; Dolder et al. 2018). Unfortunately, data are often collected at spatial scales that are too large to capture underlying spatial–temporal trends in abundance, and therefore space–time interactions are not often considered when standardizing. Stock assessments based on a CPUE index that is inappropriately standardized are likely to provide biased results that may lead to inaccurate management advice and threaten fishery sustainability, individual livelihood, and fishery-dependent communities and cultures (Bishop 2006; Benson and Stephenson 2018).

This study investigated how day-to-day decisions about fishing operations could affect fishery-dependent data and the results of stock assessments that use fishery-dependent information. The purpose of the study was to determine whether, and to what degree, fisher behavior and the spatial interplay between fish and fishers contributes to stock assessment model uncertainty and to what degree such dynamics affect stock status determination. A bioeconomic, spatially explicit, agent-based simulation model of the reef fish fishery on the West Florida Shelf (Gulf of Mexico located off the west coast of Florida) was developed as an operating model to address this question. We hypothesize that the use of fishery-dependent data in stock assessments for the species and fisheries modeled would cause more pessimistic stock status metrics compared with the status of the simulated populations. Our hypothesis was premised on the fact that the fish species simulated have a strong bottom habitat association, are not highly migratory, and that the fishing fleets operate in repeated locations and predictable ways.

To test this hypothesis, the simulation model replicated daily behaviors of the fish and fishers under conditions of constant catchability for 20 years. Fishery-dependent data generated by the simulated fleets in the model were used to conduct stock assessments on each of the four species in the simulation. Indices of biomass were calculated in several different ways, and an assessment model was fit to each index standardization scenario. In addition, the use of catch at length data from the simulated fishery was compared with using selectivity-filtered data on the known size structure of the simulated population to see whether catch at length data contained any bias. Stock status determination was compared across scenarios and with the actual stock status in the simulation model.

Methods

Simulation model architecture

The reef fish fishery on the West Florida Shelf targets a complex of bottom-dwelling species including groupers (*Epinephelus* spp. and *Mycteroperca* spp.), amberjacks (*Seriola* spp.), triggerfish (*Balistes* spp.), porgies (*Sparidae* spp.), tilefish (*Malicanthidae* spp.), and snapper (*Lutjanus* spp.) species (Darcy and Gutherz 1984). The West Florida Shelf habitat is characterized by areas of calcium carbonate hard bottom and some live coral interspersed among

areas of soft substrate, across a wide continental shelf (~100 nautical miles (1 n.mi. = 1.852 km) in some locations from the shore to shelf edge; Phillips et al. 1990; Ward and Tunnell 2017). This fishery was selected for study because assessments of Gulf of Mexico reef fish are heavily reliant on catch and effort information from the commercial fishing industry. Four economically important reef fish species were modeled in the simulation: red grouper (*Epinephelus morio*), gag grouper (*Mycteroperca microlepis*), mutton snapper (*Lutjanus analis*), and red snapper (*Lutjanus campechanus*). The two primary commercial fishing fleets were explicitly represented in the model as individual agents: the handline fleet (also called the vertical line or bandit fleet), which consists of vessels using lines with baited hooks on a reel; and the bottom longline fleet, which consists of vessels that lay a longline across bottom habitat with baited hooks (Scott-Denton and Williams 2013). In addition, remaining fishing mortality from recreational vessels, together with minor commercial gear types (i.e., fish traps and spear fishing), was also modeled as an instantaneous mortality rate at age.

An agent-based modeling approach was applied to develop the simulation (Farmer and Foley 2009; An 2012; Bonabeau 2002). There are a growing number of examples from fisheries science in which agent-based modeling was the approach of choice (Bastardie et al. 2014; Little et al. 2009; Perez et al. 2009). The four fish species and the two primary commercial fishing fleets were simulated as agents. Each individual fishing vessel was represented as its own agent, while each fish represented 25 individuals at birth, all with the same properties, to accommodate computer memory and processing limitations (Parry and Evans 2008). The numbers of individuals each fish super-agent represented decreased exponentially over time as fish died from natural and fishing mortality. Fish abundances were modeled to match estimates in recent stock assessments, and the number of simulated fishing vessels matched those currently registered. Vessel numbers (290 handline and 74 longline vessels) reflected those with reef fish permits, actively participating in the fishery at the time. Port locations were represented in the model, and simulated vessels were assigned probabilistically to each port along the west coast of Florida, based on the characteristics and fishing power of vessels at that port, as reported by the logbook data.

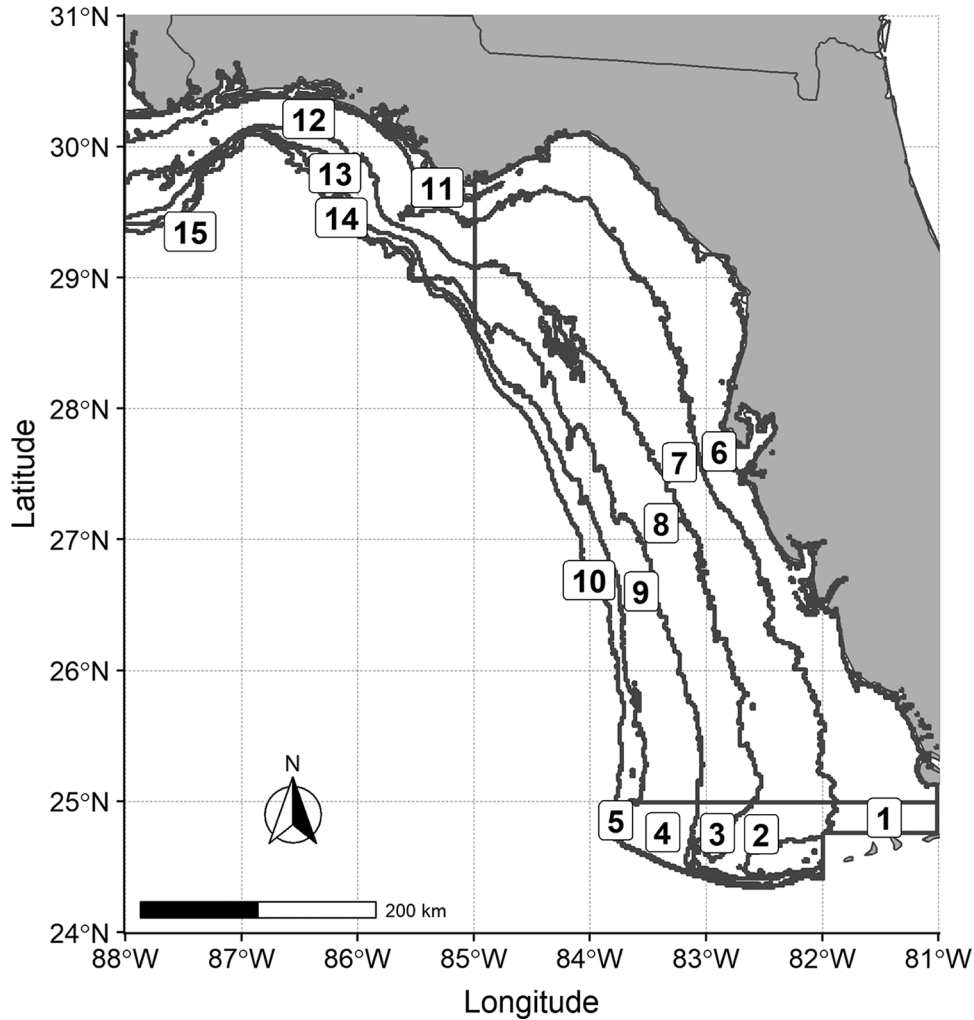
Biological dynamics

The spatial distribution of fish in the simulation was generated by combining three sets of estimates: computed stock size from stock assessment models, fishery-dependent CPUE, and fishery-independent estimates of spatial autocorrelation in relative abundance derived from video survey data (Saul et al. 2013). Each of the four species represented in the simulation are routinely assessed, and the most recent stock assessment models at the time the simulation model was developed were used to provide life history, age distribution, and population abundance inputs (SEDAR 2005, 2006a, 2006b, 2008). Stock assessment estimates were made for the entire northern Gulf of Mexico occurring within the United States Exclusive Economic Zone. The simulation model, however, only represented the eastern half of US Gulf of Mexico waters. Therefore, standardized CPUE indices were estimated spatially to partition the fraction of species abundance that occurred in the study area. A second set of standardized spatial CPUE indices were used to distribute fish occurring on the West Florida Shelf among 15 spatial strata defined by the intersection of 20 m depth contours with 25°N and 85°W (Fig. 1).

CPUE abundance indices for each species and gear type were estimated using commercial logbook data by applying generalized linear models with a delta-lognormal approach (Pennington 1983, 1996; Lo et al. 1992). A binomial model was used to model whether the species of interest was encountered on a fishing trip, and a lognormal model was used to model the CPUE using records with nonzero catches for the species of interest. These two models were combined (eq. 1), where w represents the probability of a zero observations, and $f(y)$ represents the mean of the lognormal

Fig. 1. Map of the West Florida Shelf showing the 15 areas for which spatial catch per unit effort (CPUE) were estimated, as determined by the intersection of 20 m depth contours and 25°N, 85°W. Map features and land designation are from the R project using the ggplot, ggplot2, and sf packages (R Core Team 2018). Lines indicating the 15 areas were developed using data from NOAA’s National Centers for Environmental Information.

Spatial CPUE Estimation Strata



distribution fit to positive observations, where y is the observed catch (Maunder and Punt 2004):

$$(1) \quad \Pr(Y = y) = \begin{cases} w, & y = 0 \\ (1 - w)f(y), & \text{otherwise} \end{cases}$$

Predictive variables considered in the binomial and lognormal components were area, depth, month, year, and all first-level interactions. Results from these two models were combined to generate the index (Hinton and Maunder 2004).

Fish species within each of these 15 large spatial strata were distributed across grid cells within each stratum by computing the spatial autocorrelation of individuals. Each grid cell in the simulation represented one-minute latitude by one-minute longitude, which were ~1.15 km². Fishery-independent video survey data observations were used to calculate an empirical variogram, to which a spherical relationship was fit (eq. 2), where $\rho(u)$ (eq. 3) is a monotonic decreasing function:

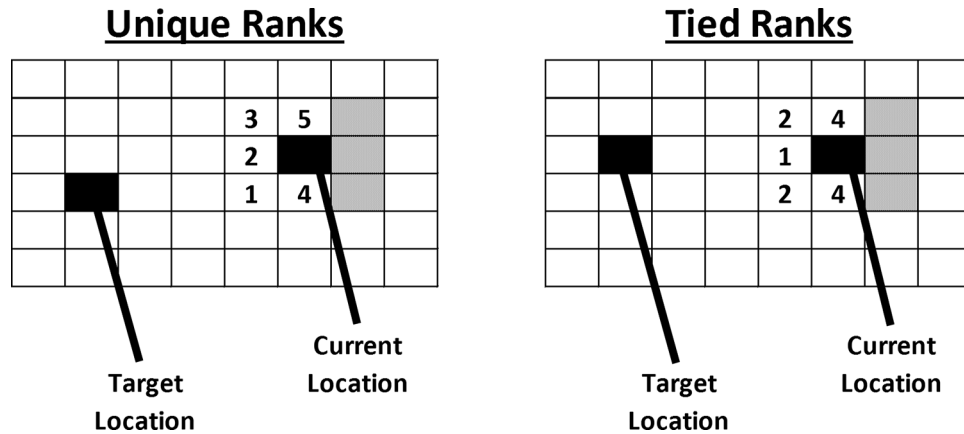
$$(2) \quad V_Y(u) = \Gamma^2 + \sigma^2[1 - \rho(u)]$$

$$(3) \quad \rho(u) = \begin{cases} 1 - \frac{3}{2}\left(\frac{u}{\varphi}\right) + \frac{1}{2}\left(\frac{u}{\varphi}\right)^3 & \text{for } 0 \leq u \leq \varphi \\ 0 & \text{for } u > \varphi \end{cases}$$

The spherical variogram has three parameters: the nugget (Γ^2), partial sill (σ^2), and range (φ). The variable u in the equations represents the binned distance between data points. Estimated spherical model covariance was Cholesky-decomposed and used to simulate a Gaussian random field across the grid in each of the 15 large spatial strata. For this application, the probability of abundance y in each grid cell n was a function of a Gaussian stochastic process with Cholesky-decomposed covariance matrix \mathbf{M} :

$$(4) \quad P(y_1, \dots, y_n) dy_1 \dots dy_n = \frac{1}{2\pi\sqrt{\det(\mathbf{M})}} \times \exp\left[-\frac{(y_1, \dots, y_n)\mathbf{M}^{-1}\begin{pmatrix} y_1 \\ \vdots \\ y_n \end{pmatrix}}{2}\right] dy_1, \dots, dy_n$$

Fig. 2. Schematic illustrating how grid cells adjacent to the grid cell a migrating fish is located in are ranked given their distance to the target location, where the fish will terminate its migration. Grayed grid cells illustrate the inability of fish to move in the direction from whence they came.



This approach was used to initialize the placement of fish at the start of the model and guide the placement of new recruits in adjacent nursery habitat. As a stochastic process, the fine-scale distribution of fish within each of the 15 large spatial areas was simulated at the start of each simulation model run (Saul et al. 2013).

Recruited age-0 fish were placed in nursery habitat, where nursery habitat was assumed as nearshore shallow water between 0 and 20 m. The nursery habitat location where fish were assigned was adjacent to their predestined adult location, meaning within the same integer band of latitude or longitude (depending on its location in the Gulf of Mexico given the Gulf’s curved coastline). This ensured that fish followed a sensible ontogenetic migration trajectory. The ontogenetic movement of fish from juvenile to adult habitat was modeled as a biased random walk (Saul et al. 2012). The onset of maturity cued simulated fish to begin ontogenetic migration. Newly recruited age-0 fish agents were assigned a predestined adult habitat location, based on the Gaussian random field computation, to which they migrated if they survived.

Only forward directional movement was permitted. Each time step that a fish migrated, the distance between its current location and predestined adult habitat location was calculated, and the neighboring grid cells at the time were ranked one through five; the three grid cells behind the fish agent were excluded (Fig. 2). If distances were the same, equal ranks were applied. An exponential probability function (p_i) was applied to each rank, r_i , where n is the number of distance options (five) and $\lambda = 1/n$:

$$(5) \quad p_i = \frac{\lambda \exp(-\lambda r_i)}{\sum_{i=1}^n \lambda \exp(-\lambda r_i)}$$

Given the bathymetric pattern of increasing depth from inshore to offshore across the West Florida Shelf, a directional bias was incorporated. As fish j moved further offshore, it evaluated the ratio of the depth of its current location $D_{j,t}$ at time t to the depth of their target location D_{tar} :

$$(6) \quad p_{direct_{j,t}} = \left(\frac{D_{j,t}}{D_{tar}} \right)^C$$

The constant C is a scalar that determined the steepness of the probability function and the sign of its slope. If the directional movement probability value was larger than the probability value for the highest ranked grid cell, the directional movement probability was substituted for this value, and remaining grid cell probabilities were rescaled, so all summed to one (Saul et al. 2012).

Conventional empirical tagging data were used to develop a gamma distribution of movement speed from the distance traveled and time at large between the time of tagging and time of recapture (eq. 7). Migration speed of an individual fish j at the time of recruitment R was a continuous random variable, $S_{j,R}$, selected from this gamma distribution and represented the number of cells a fish can move in a daily time step in the simulation. To apply the continuous random variable $S_{j,R}$ to discretized space and time in the simulation, movement speed (in units of grid cells per simulation day) could only advance a fish to the next grid cell when greater than one. Therefore, an intermediary variable, $S_{j,t}$, was used for each time step t and fish j to capture the remainder of unused movement speed from the previous time period ($S_{j,t-1}$). Daily speed selected for that individual fish ($S_{j,R}$) was added to the unused movement speed each day. When the value of the intermediary movement speed ($S_{j,t}$) was greater than one, movement length ($L_{j,t}$), the discrete number of grid cells a fish moved each day, was calculated as the mathematical floor of the intermediary movement speed, and the fish would move this number of grid cells (Saul et al. 2012).

$$(7) \quad \left. \begin{aligned} L_{j,t} &= \lfloor S_{j,t} \rfloor \\ \Delta S_{j,t} &= S_{j,t} - L_{j,t} \\ S_{j,t} &= \Delta S_{j,t-1} + S_{j,R} \end{aligned} \right\} S_{j,t} \geq 1$$

$$\left. \begin{aligned} L_{j,t} &= 0 \\ S_{j,t} &= S_{j,t-1} + S_{j,R} \end{aligned} \right\} S_{j,t} < 1$$

Parameters describing fish life history (animal growth, natural mortality, recruitment, maturity, fecundity, and meristic conversions), gear selectivity, and current numbers at age were used from the most up-to-date stock assessments for each species at the time of simulation model development. The numbers of fish in each age group at the start of the simulation was determined from the number at age in the terminal year of the stock assessments (refer to online Supplementary material, Tables S.5 though S.8¹).

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0025>.

Sequential hermaphroditism was modeled for red and gag grouper based on the last assessment for these species and was implemented in the assessment component of the current study using the logistic relationship within Stock Synthesis (eq. 9), where P_{female} is the proportion female at age a , the minimum and maximum ages modeled are a_{min} and a_{max} , respectively, δ is the inflection point, σ represents the standard deviation, ω represents the maximum value, and $\Phi_{0,1}(x)$ is the cumulative normal distribution value at x (Methot and Wetzell 2013):

$$(8) \quad P_{\text{female}} = \frac{\omega}{\Phi_{0,1}\left(\frac{a_{\text{max}} - \delta}{\sigma}\right) - \Phi_{0,1}\left(\frac{a_{\text{min}} - \delta}{\sigma}\right)} \times \left[\Phi_{0,1}\left(\frac{a - \delta}{\sigma}\right) - \Phi_{0,1}\left(\frac{a_{\text{min}} - \delta}{\sigma}\right) \right]$$

Life history parameters for each functional form and each species simulated can be found in the online Supplementary material (Tables S.1 through S.8¹). Fish grew in size according to a von Bertalanffy function (eq. 9), where L_t is the length at age t , L_∞ is the asymptotic length, k is the growth rate, and t_0 is the y intercept of the curve:

$$(9) \quad L_t = L_\infty \{1 - \exp[-k(t - t_0)]\}$$

Maturity was modeled using a length-based logistic function (eq. 10), where M_L is the maturity at length L , M_∞ is the asymptotic maturity, k is the maturity rate, and γ is the y intercept of the curve.

$$(10) \quad M_L = \frac{M_\infty}{1 + \exp[-k(L - \gamma)]}$$

Surviving fish graduated to the next age cohort at the start of each calendar year. Natural mortality values were modeled as age-dependent (except for red snapper) and used the same values provided by each stock assessment (Supplementary material, Tables S.5 through S.8¹). Spawning stock biomass was measured as either total weight or grams of gonad weight of mature female fish (see Tables S.1–S.4¹), and the stock–recruitment function followed a Beverton–Holt relationship (eq. 11), where R is the number of recruited fish, h is the steepness parameter, R_0 is the number of recruited fish when the population is at virgin conditions, and SS is the spawning stock biomass. The parameter ϕ represents the virgin spawning fish per recruit (eq. 12), such that E_{age} is the product of maturity and fecundity at each age, a_r is the age of recruitment, MaxAge is the maximum age modeled, and M is natural mortality at age j :

$$(11) \quad R = \frac{4hR_0SS}{R_0\phi(1 - h) + (5h - 1)SS}$$

$$(12) \quad \phi = \sum_{\text{age}=a_r}^{\text{MaxAge}} E_{\text{age}} \prod_{j=a_r}^{\text{age}-1} \exp(-M_j)$$

Recruitment occurred at the start of each simulation year. Note that for some of the species, parameterization of the Beverton–Holt stock–recruitment function varied from eq. 12; details can be found in the online Supplementary material, Tables S.1 through S.4¹.

Fleet dynamics

Fishing mortality from the commercial handline and longline fleets was a function of the decision-making behaviors of the vessel agents. The remaining fraction of fishing mortality from other

less important commercial gear types (i.e., fish traps and commercial spearfishing), together with recreational fishing mortality, was modeled as one combined instantaneous rate at age, uniformly across the spatial and temporal extent of the simulation (Supplementary material, Tables S.5 through S.8¹). Landings from this remaining fishing mortality were included in the stock assessment models. Tables S.9 and S.10 in the Supplementary material¹ provide the mathematical relationships and parameters used to initialize the characteristics of the boats that make up the simulated handline and longline fishing fleets; these characteristics are used as part of each vessel’s decision-making process as described below.

Behavior of commercial handline and longline vessel agents was represented by three primary decisions: participation, site choice, and when to return to port (Little et al. 2008). Locations to select for the site choice modeling were determined by partitioning the region into 45 areas, using the intersection of 20 m depth contours with bands of equal, integer latitude and longitude (Fig. 3). Participation and return to port decisions were statistically modeled daily using binomial logistic models, while site choice was modeled using multinomial mixed logistic models:

$$(13) \quad l_{ij} = \ln\left(\frac{P_{ij}}{1 - P_{ij}}\right) = a_j + b_{1j}X_{1i} + b_{2j}X_{2i} + \dots + b_{kj}X_{ki}$$

The linear predictor of a logit model (l) is the natural logarithmic function of the ratio between the probability (P) that on a given choice occasion (i), a decision is made, and the probability that on that same choice occasion, it is not ($1 - P$). Let j represent each possible choice that can be made on a given choice occasion. If the model was binomial, then j equaled 2, such as whether to take a fishing trip on a given day or to return to port on a given day once out fishing. The linear predictor can be directly calculated for each decision and choice occasion, where a is the intercept, b represents predictor parameters, and X are the temporal, spatial, and vessel-level characteristics, k , of that choice occasion (eq. 13).

The models were fit using maximum likelihood:

$$(14) \quad LL(\mathbf{b}) = \sum_{k=1}^N \sum_{j=1}^J \left(y_{kj} \sum_{q=0}^Q X_{kq} b_{qj} \right) - n_k \ln\left(1 + \sum_{j=1}^{J-1} \exp \sum_{q=0}^Q X_{kq} b_{qj} \right)$$

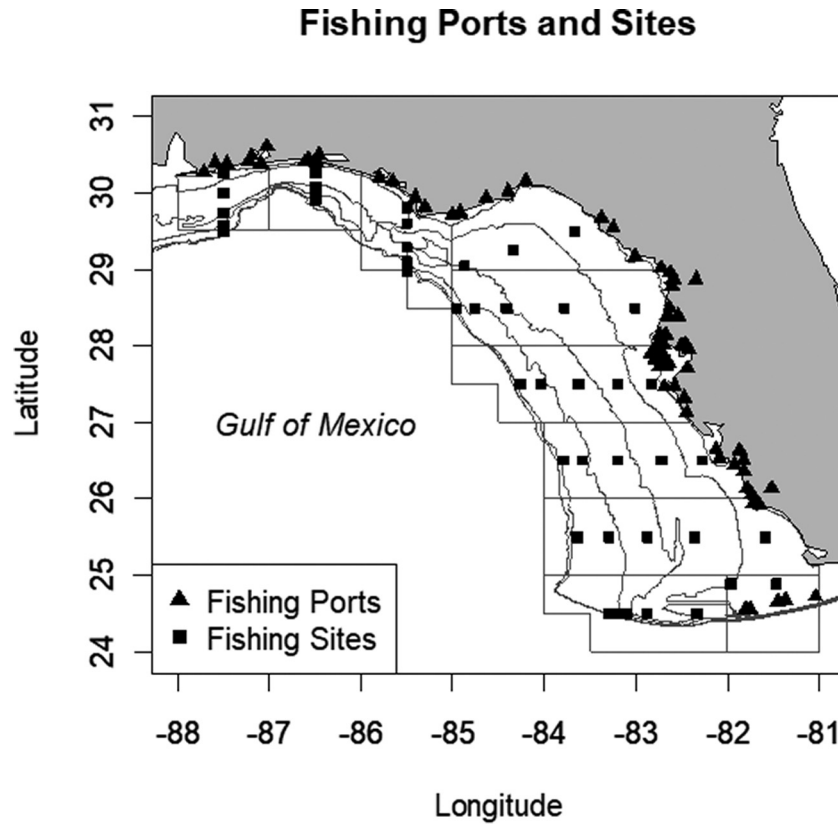
Unknown values in vector \mathbf{b} represent known fixed constant values for each y , and q represents each independent variable. Parameters for the three decision models were incorporated into the simulation and used together with the state variables of each site, vessel, day, and choice occasion combination to compute the probability of making each decision:

$$(15) \quad P_{ij} = \frac{\exp l_{ij}}{1 + \sum_{j=1}^{J-1} \exp l_{ij}}$$

The simulation model used this together with a random number draw to determine the choice a vessel would make. Once a vessel agent selected a fishing site, it randomly chose a grid cell within that fishing site polygon in which to start fishing.

Discrete choice models were fit to panel datasets, which were developed by combining logbook observations with other datasets containing information that could influence fisher decision-making, such as weather, vessel characteristics, fish and fuel price, regulations, and quota (Saul and Die 2016). The decision to start a trip on a given day was determined by seasonal regulatory

Fig. 3. Map of the West Florida Shelf showing the 45 sites that fishers could select from when modeling site choice. The centroid of each site is denoted by a black square and represents the intersection of 20 m depth contours with integer lines of latitude and longitude. Black triangles represent the locations of fishing ports along the coast. Map features and land designation are from the R project using the maps and sf packages (R Core Team 2018). Port locations (triangles) are from the NOAA fisheries landings program, and fishing sites (squares) are the approximate centroid of each polygon displayed.



closures for groups of species, fuel price, wind speed, and frequency of trips spent commercial fishing (some vessels participated in both the recreational and commercial fishery). Once out fishing, vessels tested daily to see whether they would return to port. The factors a vessel considered when deciding whether to return to port were seasonal regulatory closures, fuel price, fish price, the day of the week (not permitted to land on weekends), and the ratio of current catch volume relative to total fish hold capacity. Finally, the site choice decision considered distance from port, expected revenue, wind speed, habit, and fuel cost. Parameter values from choice model fits can be found in Tables S.10 through S.18 in the online Supplementary material¹.

Catchability and selectivity

To model the capture of an individual fish by a fishing vessel agent within a grid cell of the simulation, a catchability parameter (q) was calculated. Catchability in this context represented an average probability of catching an individual fish within the spatial extent of a grid. Landings information was converted to estimated numbers of fish caught (using age-length-weight data). Average catch of fish in numbers of fish per day ($\bar{C}_{\text{number} \cdot \text{day}^{-1}}$) was calculated by dividing the catch in number (C_{number}) by the total number of days (Days) that the fleet fished in a year:

$$(16) \quad \bar{C}_{\text{number} \cdot \text{day}^{-1}} = \frac{C_{\text{number}}}{\text{Days}}$$

Years 2005 and 2006 were used for these calculations. Let the number of available fish in the population, $N_{\text{available}}$, refer to the fish in the population that are over the size limit and vulnerable

to be caught by a particular fishing gear (either handline or longline) based on that gear’s selectivity vector at age. From these, the average catchability coefficient (\bar{q}) was computed to represent catchability per day. To translate this catchability into a value that represents the probability of catching one fish in one grid cell, on one day, we divided the catchability by the average fraction of the population available to be caught that resides in one grid cell:

$$(17) \quad \bar{q} = \frac{\bar{C}_{\text{number} \cdot \text{day}^{-1}}}{N_{\text{available}}}$$

Let \bar{D} represent the average density of available fish within one grid cell, where g is the total number of grid cells that fish can occupy:

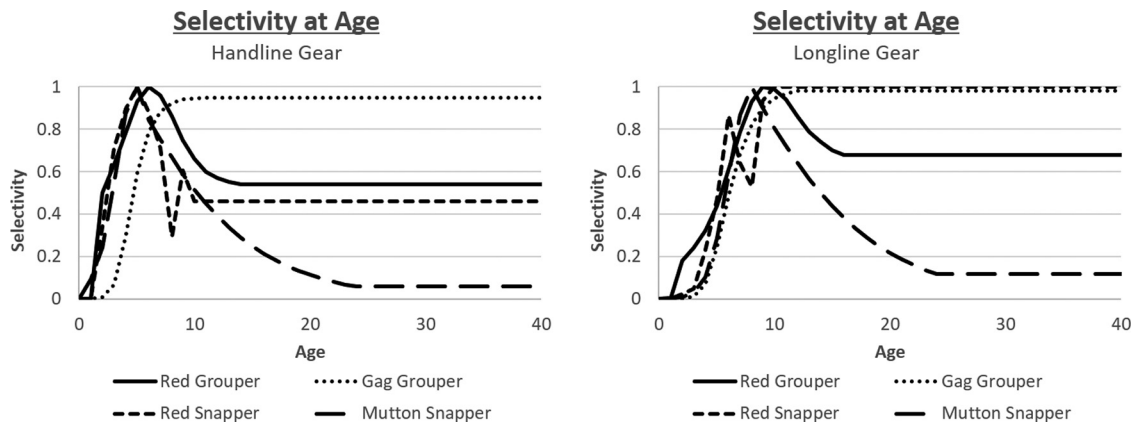
$$(18) \quad \bar{D} = \frac{N_{\text{available}}}{g}$$

Using this density, the average fraction of fish located within each grid cell (\bar{f}) was calculated as the density divided by the total number of available fish:

$$(19) \quad \bar{f} = \frac{\bar{D}}{N_{\text{available}}}$$

The average probability of catching an individual fish within a grid cell was calculated by dividing the stock-wide average catchability by the average fraction of the population within a grid cell:

Fig. 4. Line charts showing the selectivity at age (in years) used in the simulation model for each species and fleet as part of the fishing process. Selectivity at age patterns were those fit by the stock assessments used to parameterize the simulation model.



$$(20) \quad \bar{p} = \frac{\bar{q}}{f}$$

The average probability of catching an individual fish was applied to each fish within the same grid cell as the vessel. Selectivity was parameterized in the simulation using the functions and estimated parameters determined in the most recent stock assessments. Selectivity was modeled using a variety of functional forms, depending on the species and fishing gear (Fig. 4). Once a simulated fish was captured, knife-edge retention was applied according to the minimum size limit for that species: 20, 13, 24, and 16 inches (1 inch = 2.5 cm), for red grouper, red snapper, gag grouper, and mutton snapper, respectively. It was assumed that all vessel agents were compliant with the regulations throughout the simulation. Discarding occurred for fish captured below the size limit, and the discard mortality rates from the most recent stock assessments were applied to determine the survival of the released fish.

Fishing vessels could fish multiple grid cells on a given day. This was simulated by probabilistically selecting the number of locations a vessel will fish each simulated day by sampling from the empirical distribution as computed from observer data. To decide which grid cell to visit next, the simulated vessel would select a random direction from its current location. Then, a distance to travel was determined by sampling from the empirical distribution of distance between fishing sites in a day from the observer data; the vessel would then travel to the grid cell that distance away. When a vessel fished in multiple locations on a given day, the catchability probability was divided evenly among the different locations on that day.

To generate fleet heterogeneity, the catchability probability value (\bar{p}) was scaled to the calculated relative fishing power of each individual vessel (Marchal et al. 2002). The agent-based simulation model was run for a 20-year projection. The simulation model was run 50 times using different random number seeds. All runs produced similar population and catch trends, with variability among them due to the stochastic nature of the simulation model. From this set of runs, data from one that best approximated the median population trajectory and median catch values from the set was used to develop the inputs to the stock assessments. Simulated fishing vessels generated logbook data at the end of each trip, analogous to the information that fishers are required to submit to NOAA Fisheries. It was assumed that fishers honestly reported their information on their logbook forms and that catch information was complete. Length and age measurements were made for all fish caught by the commercial and recreational sectors, and no aging or measurement error was assumed.

Simulation model validation

Pattern-oriented modeling was used to validate the agent-based simulation model. This approach uses “multiple patterns observed in real systems to guide design of model structure” (Grimm et al. 2005). Different from equation-based deterministic models, agent-based models do not contain an objective function and consequently cannot be minimized or maximized, and therefore model fit cannot be determined using statistical approaches such as Akaike’s information criterion (AIC; Burnham and Anderson 2004). Instead, the best-fit model was considered the one that produced patterns most closely matched to the analogous patterns observed in the real system (Grimm et al. 2005, 2006). Simulated and real patterns across time and space of fish and fishing effort were compared with one another both qualitatively and quantitatively as reported in Saul et al. (2013) and presented in Figs. S.9 and S.10 in the Supplementary material¹.

CPUE estimation

Data collected from the vessel agents were used to conduct a stock assessment for each fish species. The simulation model produced logbook data from the two commercial fleets, landings from all three fleets, a complete census of each fish caught and its life history characteristics, discards, time series of abundance each day, annual maps of spatial abundance, biomass, catch and fishing effort by fleet, spawning stock biomass and recruits each year, and the size distribution of each species’ population. Reporting was assumed to be accurate. Results from the stock assessment were compared with the actual population data from the simulation.

CPUE indices of biomass (pounds per hook hour; 1 pound = 0.45 kg) were computed for both the simulated handline and longline fleets in three different ways for each species. These three indices are hereinafter referred to as “typical standardization”, “extended standardization”, and “perfect information”. The first two methods, typical and extended standardization, applied the delta-lognormal approach as described earlier (Lo et al. 1992). The third approach (perfect information) derived an index that perfectly tracked biomass by normalizing the annual biomass trend in the simulation to its mean. Each of these three indices were used to compare the effects of alternative approaches for index development on stock assessment model results.

The typical standardization approach used variables that were available in the actual logbook data and typically used in the Southeast Region to standardize fishery-dependent CPUE for stock assessments. These variables included year, area (as blocks of latitude and longitude), month or season, and days away at sea (days away for the binomial model only). The extended standardization approach

also tested some additional variables: the number of locations fished each year by the vessel, travel time to and from port, fish price, vessel travel speed, vessel length, red snapper allocation (i.e., 0, 200, or 2000 pounds per vessel), the capacity of the fish hold, and days away on a trip (only included in the binomial portion of the model). The inclusion of variables in both the typical and extended CPUE standardization models were evaluated using a forward stepwise approach.

Stock assessment of simulated fisheries

At the end of the 20-year simulation, single species, age- and size-structured stock assessment models were developed for each of the four species represented in the simulation model using Stock Synthesis, version 3.24P (Methot and Wetzel 2013). For each species, four different stock assessment models were configured to test hypotheses about the inclusion and treatment of fishery-dependent data. Each assessment model configuration tested a different biomass index scenario (using the typical, extended, and perfect information), where the fourth model tested the inclusion of perfect catch at size information by using data that comes from the population size structure and is adjusted for selectivity and retention. All other data inputs and parameter starting conditions were kept the same to test how fisher behavior could bias CPUE and affect stock assessment. Each assessment included 20-year time series of CPUE, landings, discards, and catch at length. Two fishery-dependent indices of biomass were included, one from the simulated handline fleet and the other from the simulated bottom longline fleet. Landings from three fleets were included in the model: the commercial handline, commercial longline, and the combined recreational and remaining commercial fishing mortality.

Catch at size from the simulated handline and longline commercial fleets was included in three of the four assessment model scenarios. Every simulated fish caught was used to provide catch at size information to the assessment model to avoid introducing sampling bias. Life history parameters, including von Bertalanffy growth, maturity, fecundity, and natural mortality, were assumed to be known from empirical studies, and the parameters for these relationships were fixed in the stock assessment to those used in the simulation model. One exception to this was that for all species, allowing Stock Synthesis to estimate the minimum and (or) maximum size growth function parameters improved the fit to the composition data. Selectivity, catchability, retention, Beverton-Holt stock-recruitment function parameters, and fishing mortality were estimated by Stock Synthesis. Sequential hermaphroditism was modeled in Stock Synthesis for the red and gag grouper species to capture in the assessment their ability to gender switch in the simulation model. Maximum likelihood was used to fit the relative abundance, landings, discards, and size composition data in stock assessment models.

For each species, a base model configuration was selected through constructing multiple Stock Synthesis models to explore different functional forms for selectivity and retention, as well as different starting values and bounds for the stock-recruitment function. Base model selection was determined using AIC (Burnham and Anderson 2004). To test base model stability, we performed jitter analyses (i.e., running the assessment model from several sets of starting values). The results of the jittered runs were very similar to the base model results, except that the parameters representing initial fishing mortality for each fleet were highly sensitive to the starting values and bounds provided for all species. Since these parameters could not be estimated, we iteratively manually tuned them until the estimates of catch in the first year provided a good match to catch from the first year of the simulated time series.

Stock status was calculated using the maximum sustainable yield (MSY) proxy for this fishery (30% of spawning potential ratio (SPR)) for each assessment model and from the simulation model itself. Overfishing was defined as the current level of fishing mor-

tality relative to its SPR 30% reference point, while overfished was defined as the current level of biomass relative to its SPR 30% reference point. Estimated stock status for all four CPUE standardizations, plus the case with perfect length composition, were compared to evaluate how changes to a trend in CPUE or catch size composition due to fishing operation decision-making could affect these estimates.

Results

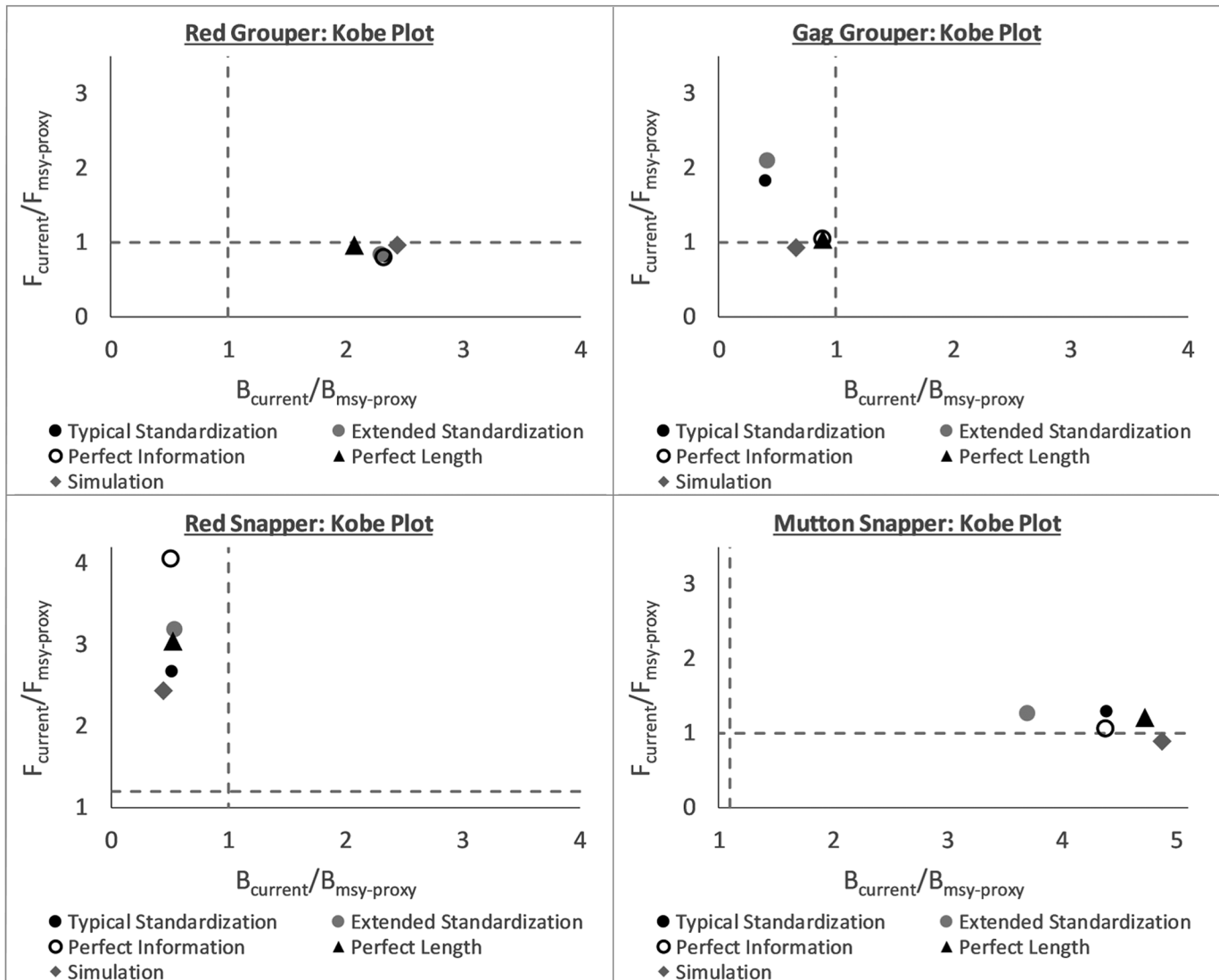
The spatial placement of reef fish in the simulation model was compared with the distribution of benthic habitat features found in the Gulf of Mexico (see Saul et al. 2013). Modeled fish life history and movement were compared with tagging data, while the biological characteristics of actual commercial catches were compared with catches simulated by the model (see Saul et al. 2012). Fishing operations in the simulation were validated by comparing simulated landings, trip duration, average number of trips per vessel each year, and total number of trips per year with these actual metrics from logbook data (Supplementary material, Figs. S.2 to S.8¹). Spatial patterns of simulated catch were compared with actual spatial catch distributions estimated by combining vessel monitoring system (VMS) data with logbook data for red grouper and gag grouper; comparative spatial VMS plots were not available for red snapper or mutton snapper catches (Supplementary material, Figs. S.9 and S.10¹).

When determining a base stock assessment model for each species, the functional forms and associated parameters most difficult to estimate (after fixing the initial F) were those associated with the stock-recruitment function and selectivity functions. Table S.19¹ in the Supplementary material shows the different combinations of stock assessment model configurations that were developed and their respective AIC values. Parameters controlling sequential hermaphroditism were estimated in the stock assessments for red grouper and gag grouper. The parameter of the stock-recruitment function that represents virgin recruitment was estimable for all four species; for gag grouper and red snapper, the steepness parameter was able to be estimated and the form of the stock-recruitment relationship was correctly identified. For stock assessment model configurations where the steepness parameter was not able to be estimated, this value was fixed to the value used in the agent-based operating model. In addition, for some species, the stock-recruitment function parameter governing recruitment error and deviations was not able to be estimated and in these cases was fixed at the value used in the base run from the most recent stock assessment for that species.

For each of the four stock assessment model configurations as applied to each species, (typical index, extended index, perfect information index, and perfect information in both the index and length composition), stock status was computed (Fig. 5). Stock status from the perfect information index and perfect information in both the index and length composition scenarios estimated nearly the same status for gag grouper, although the status did not match the true status from the simulation. For the other three species, the perfect information index and perfect information in both the index and length composition scenarios estimated stock status values that were comparatively closer to that of the simulation. Stock status results for red grouper were similar across all scenarios.

Conclusions about overfishing from the four assessment models also differed in some cases from the actual stock status of the simulation itself. For gag grouper, red snapper, and mutton snapper, overfishing from the assessment models exceeded the actual degree of overfishing that occurred in the simulation (Fig. 5). Standard deviation estimates for benchmarks were generally small (Table 1), illustrating that differences between benchmark estimates among assessment model configuration scenarios were

Fig. 5. Kobe plots from the assessment models of the four species. Each plot contains stock status as determined from assessment models that used the typical, extended, and perfect information indices of biomass and the assessment model that also incorporated perfect catch at length information. Population status from the simulation model itself is also included. The x axis represents the ratio of biomass at the end of the time series to the biomass level at spawning potential ratio (SPR) 30% ($B_{\text{current}}/B_{\text{msy-proxy}}$), while the y axis represents the ratio of fishing mortality at the end of the time series to the fishing mortality level at SPR 30% ($F_{\text{current}}/F_{\text{msy-proxy}}$). Note that the x axis of the mutton snapper plot and the y axis of the red snapper plot both start at 1 to accommodate the high biomass and fishing mortality ratio values. Both axes are scaled the same as the other plots to compare the differences in assessment outcomes.



outside of uncertainty bounds. Red grouper was an exception and calculated higher standard deviations for the biomass benchmark, making it difficult to discern whether there were actual differences in this benchmark for this species between stock assessment scenarios. Most of the variability in stock status from the different scenarios for gag grouper and mutton snapper occurred in the biomass ratio estimates.

For gag grouper, red grouper, and red snapper, one or both CPUE indices showed some evidence of hyperdepletion at the start of the time series, which could cause higher estimates of fishing mortality (Fig. 6). Although fishing effort for both handline and longline gears was distributed across most areas of the study site, fishing vessel agents demonstrated a strong preference for repeated site selection (Fig. 7). Simulation model scenarios showed that handline vessels aggregated their fishing effort predominantly in the central part of the region, with additional areas of higher fishing effort off the Florida Panhandle, and offshore from more

populated areas (such as the Tampa area, which occurs at $\sim 27.5^{\circ}\text{N}$, 83°W). Two somewhat concentrated spatial groups of fishing effort emerged from the longline fleet behavior (Fig. 7). This established local depletion conditions, and fishery-dependent data reflected the population trends in these locally depleted areas, rather than the population trends across the entire region.

Catch at length data were also a function of the repeated site selection and local depletion conditions, which caused the size distribution of the catch to be smaller than that of the overall population, even when the size distribution of the total population was adjusted for selectivity and retention. The two species most affected by local depletion, red grouper and gag grouper, had their largest portion of log-likelihood error attributed to fitting the catch at length information (Table 2). The CPUE and catch at length components of the log-likelihood for all four species indicated that no real improvement in model fit was gained from using the available population size structure corrected for

Table 1. Depletion ($B_{\text{current}}/B_{\text{msy-proxy}}$) and fishing mortality ($F_{\text{current}}/F_{\text{msy-proxy}}$) benchmark estimates from the different stock assessment model configurations.

Species	Scenario	B		F	
		Ratio	SE	Ratio	SE
Red grouper	Typical index	2.33	0.13	0.82	0.03
	Extended standardization	2.29	0.13	0.85	0.03
	Perfect information	2.32	0.13	0.81	0.03
	Simulation	2.44	0.13	0.97	0.02
	Perfect length	2.07	0.12	0.97	0.03
Gag grouper	Typical index	0.40	0.01	1.83	0.04
	Extended standardization	0.41	<0.01	2.11	0.03
	Perfect information	0.88	0.04	1.05	0.06
	Simulation	0.66	0.04	0.92	0.08
	Perfect length	0.89	0.04	1.05	0.06
Red snapper	Typical index	0.52	0.05	2.46	0.02
	Extended standardization	0.54	0.05	3.00	0.04
	Perfect information	0.51	0.01	3.86	0.02
	Simulation	0.44	0.02	2.23	0.03
	Perfect length	0.53	<0.01	2.84	0.04
Mutton snapper	Typical index	4.29	0.09	1.28	0.03
	Extended standardization	3.59	0.09	1.27	0.03
	Perfect information	4.28	0.11	1.06	0.03
	Simulation	4.77	0.11	0.89	0.07
	Perfect length	4.63	0.10	1.20	0.03

Fig. 6. Time series plots comparing the typical and extended estimated trends in catch per unit effort for the handline (HL) and longline (LL) gear types, with the actual trend in biomass, referred to as perfect information. All trends are normalized to their respective means for comparison purposes.

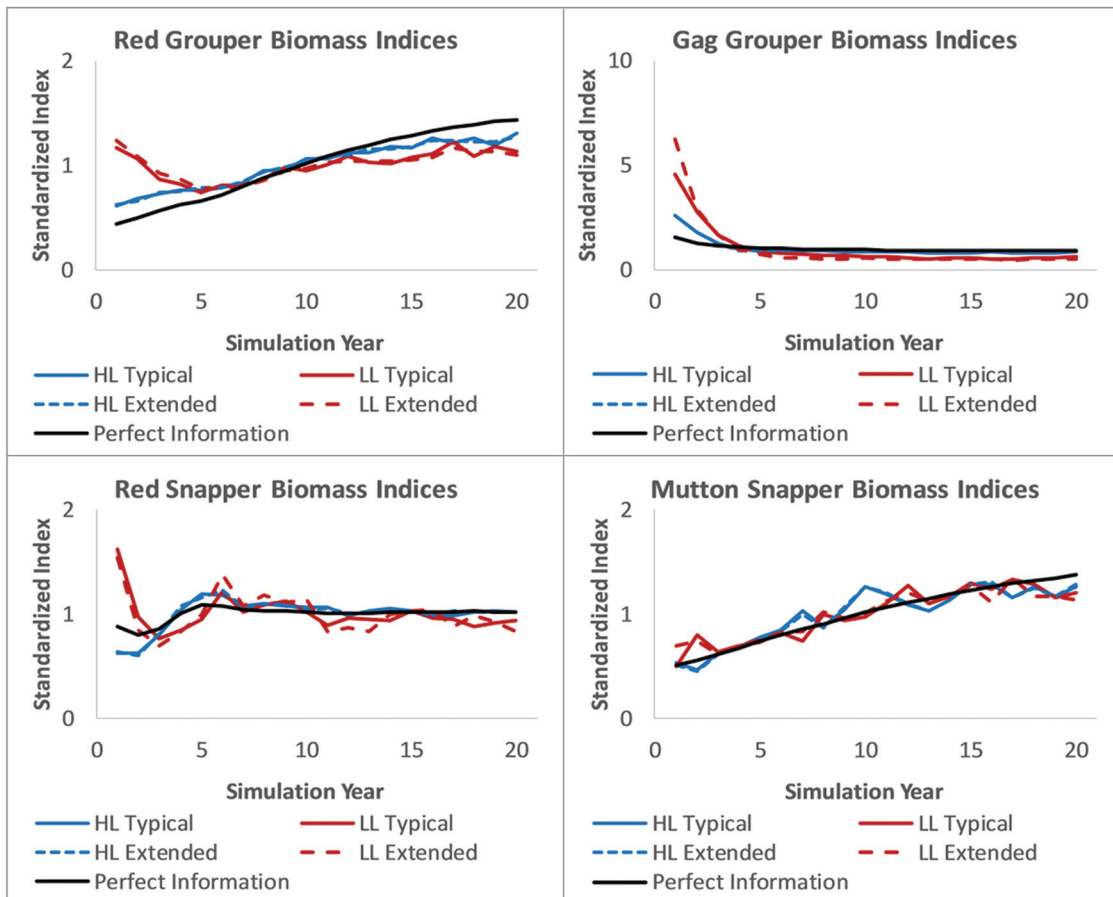


Fig. 7. Maps illustrating the average spatial distribution of fishing effort for the handline and longline fleets during the simulation. Map features and land designation are from the R project maps package (R Core Team 2018). Spatial data displayed is output from the simulation model.

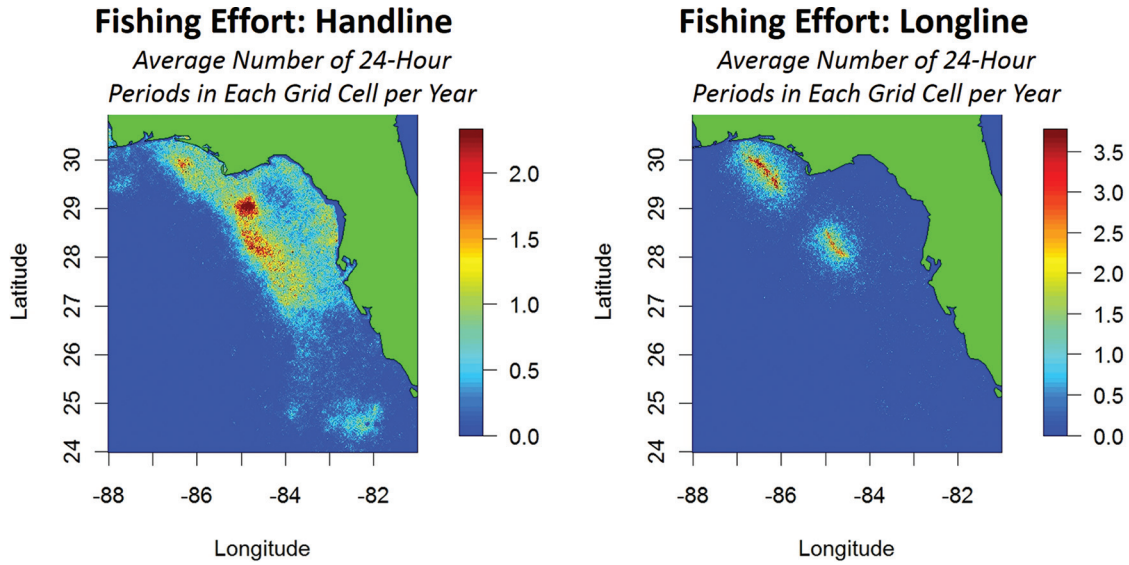


Table 2. The percentage of partial log-likelihood for the stock assessment model fits to catch per unit effort and catch at length.

Species	CPUE scenario	Log-likelihood from CPUE (%)	Log-likelihood from catch at length (%)
Red grouper	Typical index	1.08	69.58
	Extended index	0.52	97.61
	Perfect information	3.30	68.17
	Perfect info. and length	1.72	65.52
Gag grouper	Typical index	7.52	34.80
	Extended index	11.07	68.43
	Perfect information	2.89	73.12
	Perfect info. and length	2.86	73.52
Red snapper	Typical index	3.68	0.37
	Extended index	16.84	3.54
	Perfect information	21.83	1.91
	Perfect info. and length	21.41	0.18
Mutton snapper	Typical index	7.02	0.04
	Extended index	6.50	0.05
	Perfect information	0.22	0.05
	Perfect info. and length	0.33	0.07

selectivity instead of the catch at length from the simulated fishery (Table 2). Neither the assessment model with the perfect information index nor the assessment model with both the perfect information index and the population length structure (adjusted for selectivity) were able to properly recreate the population size structure of the simulated populations (Fig. 8).

The inclusion of additional factors in the index standardization was not able to account for a difference between the index and simulated biomass time series (Fig. 6). CPUE trends from the typical standardization were nearly identical to trends produced by the extended standardization. Thus, incorporating additional factors that would be available in the data from the fishing vessels, and that could potentially reflect fisher behavior, did not improve the alignment of the standardized index with the simulation trends in biomass. The incorporation of additional factors into CPUE standardization for some fleets and species reduced the amount of deviance left unexplained (Fig. 9).

The Euclidean distance (a measure of similarity) between the perfect information index and the typical or extended index re-

Table 3. Euclidean distance between the perfect information index and either the typical or extended indices.

Species	Distance (perfect, typical)	Distance (perfect, extended)
Handline		
Red grouper	0.52	0.52
Gag grouper	1.20	1.21
Red snapper	0.38	0.39
Mutton snapper	0.47	0.46
Longline		
Red grouper	1.21	1.30
Gag grouper	3.61	5.21
Red snapper	0.85	0.89
Mutton snapper	0.43	0.49

Note: Smaller values indicate closer agreement between indices.

vealed that the extended index was not closer to the normalized biomass trend in comparison with the typical index (Table 3). For handline gear, the typical and extended indices were similar distances apart from the biomass trends, while for longline gear, the extended index was more different from the biomass trends compared with the typical index. When additional, fisher behavior-related factors were incorporated, more variability was explained by the lognormal regression for positive catch trips compared with the binomial model for proportion of zero catch trips. This, however, did not always translate to a CPUE index that better correlated with biomass. For example, the two red snapper standardized indices — typical and extended — for both handline and longline data agreed well with one another and with the trends in available biomass in the simulation, despite the “extended” lognormal index explaining ~30% more variance (Fig. 9).

Discussion

This study demonstrated that fisher behavior could alter the outcome of a stock assessment by influencing fishery-dependent observations and, as a result, the calculation of indices and inference of population size or age structure, both of which inform population trends over time. In this study, changes in catchability over time were not simulated because regulations, technology, and fishing power were all held constant throughout the simulation. However, different from typical fisheries models, the daily behavioral decision-making process that fishers used to operate

Fig. 8. Comparison of population size structure from the simulation (points) and estimated population size structure from the perfect information index assessment model, and the assessment model that incorporated the perfect information index and the population size structure adjusted for selectivity. Note that the figure for gag grouper has both the dashed and solid lines plotted on top of one another.

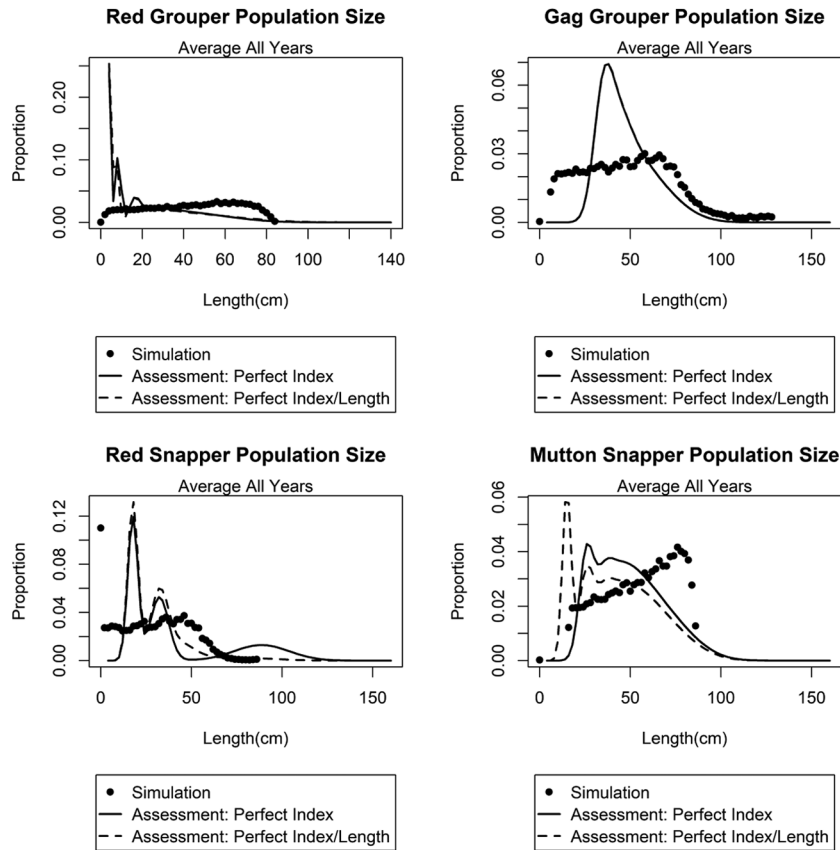
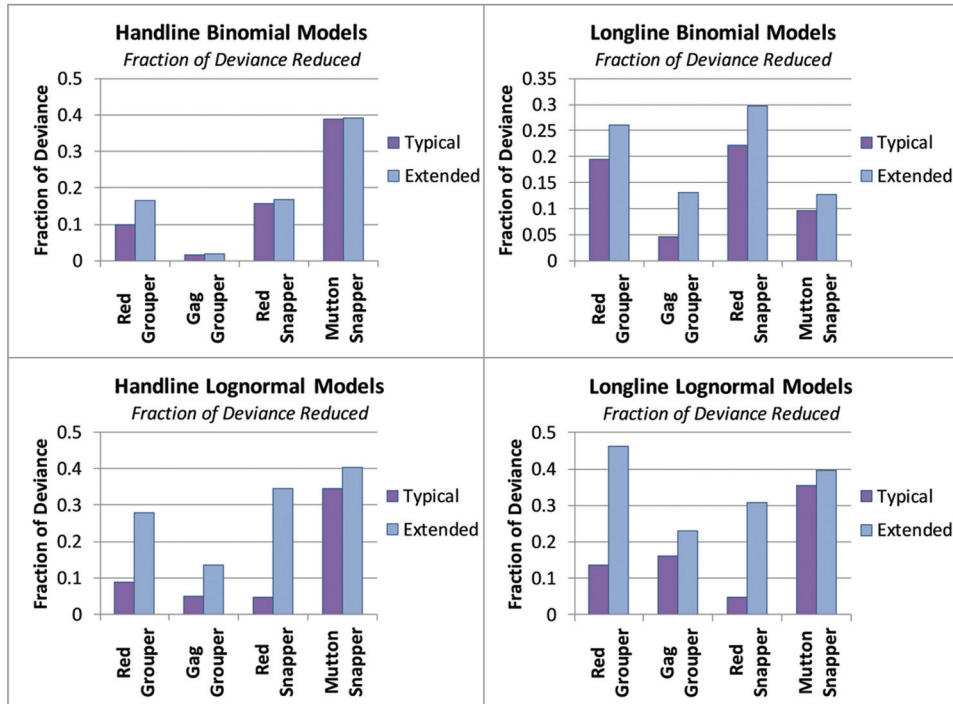


Fig. 9. Comparison of the fraction of deviance reduced by the typical and extended standardizations for the handline and longline fleets, where the extended standardization generalized linear models incorporated additional factors related to fisher decision-making. [Colour online.]



their business was explicitly represented in this simulation study. This is infrequently considered a source of uncertainty or bias in fisheries population modeling. The location and timing of fishery-dependent data collection are governed by the behaviors and decision-making patterns of fishers, which are not concerned with statistical sampling designs. As a result, fishery-dependent data are not equivalent to data collected through a scientific survey approach (Chen and Rajakaruna 2003). If fishery-dependent data are not representative of the whole population, and instead reflect localized dynamics, this can lead to biased indices and biased size distributions and ultimately lead to biased estimates of stock status (Wiedenmann et al. 2017; Goethel and Berger 2017).

A disproportionality between CPUE indices and abundance or biomass over time (Harley et al. 2001) and approaches for handling this (Maunder et al. 2006; Maunder and Punt 2004) have been explored through simulation studies (Swain and Sinclair 1994; Gillis and Peterman 1998) and by evaluating empirical data (Cooke and Beddington 1984; Richards and Schnute 1986; Rose and Leggett 1991). More recently, some work has been done to evaluate possible impacts to stock assessment of bias in fishery-dependent length frequency samples (Heery and Berkson 2009). Francis (2017) and Thorson et al. (2017) both discussed the utility of data and likelihood reweighting in stock assessment models, as well as the use of the Dirichlet-multinomial distribution to improve fits to length samples. The techniques described in these two studies could help improve assessment model fit under some circumstances, but additional research is needed. In our implementation, size composition data were weighted relative to their actual sample sizes (i.e., actual sample size divided by 1000).

Several behavioral patterns were observed that could contribute bias to fishery-dependent catch, effort, and length sampling data. Repeatedly fishing the same locations in the simulation caused local depletion of the population at frequently visited locations and underutilization of fish at locations visited less often; this was highly influenced by the habit parameter in the discrete choice model fits. Recurring visits to the same fishing locations are common in many fisheries (Holland and Sutinen 2000) and is driven by a need for supply predictability to satisfy species-specific catch requests within a specified timeframe (Saul and Die 2016). Data from fisheries that frequent the same locations could be biased by local depletion effects (Davies et al. 2014; Holland and Sutinen 2000).

In other locations that experienced little or no fishing pressure, a de facto “refugia effect” protected higher abundance and larger animals (Shephard et al. 2012). These lightly fished areas contributed to an increase in spawning stock biomass, recruitment, and population growth (see Supplementary material Figs. S.11 and S.12¹ for example; Dugan and Davis 1993). Without properly sampling areas of higher abundance or biomass, the effect of such areas on the stock cannot be properly accounted for in the assessment model (Marriott et al. 2017). Thus, in our study the stock assessments had a good understanding of the stock dynamics where fishing frequently occurred and a poor understanding of stock dynamics elsewhere across the range of the population (Kraak et al. 2009; Vinther and Eero 2013).

Our study demonstrated that the local depletion of gag grouper and red snapper led to hyperdepleted indices at the start of the time series and artificially pessimistic stock status estimates (Supplementary material Figs. S.12 and S.13¹). The spatial distribution of red grouper biomass (Supplementary material Fig. S.11¹) also showed the occurrence of local depletion resulting in hyperdepletion of the biomass index at the start of the time series; however, it did not alter the stock status criterion by very much. Fisheries assessment scientists should exercise caution with computing indices from fisheries-dependent data in fisheries that continually return to past locations for structure-oriented species, as the data may not reflect the dynamics of the stock across its entire spatial domain (Salthaug and Aanes 2003; Smith et al. 2009).

Walters (2003) and others (Gelfand et al. 2012) have shown that not accounting for imbalanced spatial sampling can lead to the development of indices that declined more rapidly than an index adjusted for spatial sampling bias. Other studies, like this one, also found that not addressing spatial complexities could affect biological reference points (Goethel and Berger 2017; Little et al. 2017). Recommendations made by Campbell (2015) regarding handling things like the imputation of missing values, handling outliers, the use of random effects, proper modeling of interactions, and weighted model fits could be applied to develop a more accurate index. Recent work applying VMS data has shown some success for correcting spatial bias and improving resource assessments (Cao et al. 2017).

Standardization of population indices is most successful when it accounts for differences in catchability across time (Wilberg et al. 2010). As a control in the simulation model, all aspects of catchability that could change over time, except for fisher behavior, were kept constant, such as environmental, biological, and management processes. The only changes made by the simulated fishers in the agent-based model were those made to fisher behavior through explicitly representing the decisions of when to fish, where to fish, and when to return to port. Wilberg et al. (2010) recommended that adjustments to account for changes in catchability be made through either the standardization of CPUE, down-weighting or ignoring an index, or through explicitly modeling catchability within the stock assessment model as a function of time and (or) space. In this study, efforts were made to include additional factors into the standardization of CPUE that would represent fisher behavior and could be collected as value added to already existing sampling approaches in place for this fishery. Although this approach did not necessarily result in an improved index or assessment outcome, it did change the unexplained deviance in some cases. This is because in this study, fisher behavior resulted in catch rate changes that CPUE indices interpreted as changes in abundance, causing a mismatch between the index and the true population trend.

In addition to the CPUE indices, the catch at length data included in the stock assessment models was also fishery-dependent and therefore also not representative of the population, even after filtering through selectivity functions in Stock Synthesis. The size distribution of fish caught in the simulation was also a function of spatial fishing location and local depletion. Therefore, neither the assessment model with the perfect information index nor the assessment model with both the perfect information index and the population length structure (adjusted for selectivity) were able to properly recreate the population size structure, resulting in inaccurate estimates of fishing mortality and biomass.

In this study, the spatial behavior of fishers also interacted with the spatial behavior of the fish. Only ontogenetic movements were represented by simulated fish and occurred at the onset of maturity. Once settled in adult habitat, fish no longer moved in the simulation. Life histories of the species modeled suggest limited adult movements, with species constrained to areas of essential habitat that match their life history stage and spawning strategy for long periods of time (Coleman et al. 2000). Red snapper exhibits high residence times in certain habitats prior to moving to another location (Patterson and Cowan 2003; Karnauskas et al. 2016), gag grouper and mutton snapper seasonally migrate to spawn in aggregations (Coleman et al. 1996; Burton et al. 2005), while red grouper is largely sedentary and does not relocate to spawn (Harter et al. 2017; Ellis 2019). If the species modeled moved around on a more regular basis, such that the populations were spatially well mixed, we suspect that the calculated indices and stock assessment results would have more closely represented simulated population conditions (Rose and Kulka 1999; Alós et al. 2018).

Simplifying assumptions were required when developing both the agent-based simulation model, as well as the Stock Synthesis

assessment models. Neither the simulation nor the stock assessment models included the behaviors or drivers of markets, supply chains, or firms with influential effects that trickle down to affect fisher behavior and thus population dynamics (Nightingale 2011). Fisher behavior was also “statistically fixed” in the agent-based model, meaning that all fisher agents within the same fleet used the same set of discrete choice model-fitted parameters to make decisions (Saul and Die 2016). Learning was not directly represented in the simulation model but was indirectly modeled through the inclusion of a variable indicating the frequency that individuals fished in a location. It is important to acknowledge that the results of this study may not mirror the real world because the simulation and assessment models may be different from the real world. Nevertheless, broad spatial patterns of the resulting simulated fishing effort showed reasonable similarity with observed data.

Finally, the assessment models were not able to successfully capture the size structure of the simulated populations, even when the selectivity-filtered true length composition of the population was used in the assessment models. This indicates that the catch at size data from the simulated fishery were probably not driving the difference between the stock status of the simulation and that calculated by the assessment models. Examination of assessment model output figures indicated that all stock assessment models fit well to the size composition data, and nearly all selectivity and retention function parameters were well estimated. As such, there was no indication (other than our knowledge from the simulation) that the assessment model’s estimation of population size structure was misaligned with that of the simulation.

This is a concern, because it means that the model diagnostics cannot alert us to a mismatch between the fishery data and the population. Research suggests that information contained in the size composition data that would help improve the estimates of absolute abundance and time trends in abundance could be incorrect (Minte-Vera and Uosaki 2017). In our study, the Stock Synthesis assessment model assumed a well-mixed population where all individuals within the same size class experience the same fishing mortality rate. However, the interacting spatial structures of the fish populations and fishing fleets produced spatially different fishing mortality rates. This inability to identify this phenomenon led to the error observed in the assessment models (Cao et al. 2020). Further research is recommended to evaluate under what conditions this may occur and how it could be detected and corrected in actual assessments.

Conclusions

This study demonstrated that fisher behavior could introduce bias to fishery stock assessments through the inclusion of fishery-dependent data and spatial differences in fishing mortality. This could occur at the intersection of several processes: when (i) the spatial decision-making patterns of fishers, and therefore their fishing effort, does not randomly sample the spatial distribution of the fish, (ii) the spatial distribution of the fish is patchily distributed and the fish exhibit some degree of site fidelity for substantial periods of their life history, and (iii) fishers repeatedly visit the same fishing locations causing local depletion. Under these conditions, fishery-dependent data provides stock assessment models with disproportionately more information from the places heavily visited by fishers and less information from the places lightly fished. Owing to local depletion effects, the structure of the population in heavily visited locations is different from the average population structure across the spatial domain.

Because of data limitations, the use of fishery-dependent data in stock assessments is inevitable in most applications. Spatially re-weighting fishery-dependent data (Maunder et al. 2020; Walter et al. 2014; Walters 2003) and including indices of abundance or

biomass from scientific surveys, as is often done, could help provide stock assessments with a more accurate reconstruction of the population. In addition, recent work combining logbook data with vessel monitoring system data in the Gulf of Mexico corrected for sampling bias and found that indices provided a more robust estimate of abundance trends (Ducharme-Barth et al. 2018). When considering data collection for stock assessment, locations that are undersampled should be considered for additional sampling effort to provide stock assessment models with spatially balanced inputs. Spatially structured stock assessment models provide the ability to model some degree of spatial heterogeneity in the fish and fishers (Methot and Wetzel 2013; Maunder et al. 2020), which could help address some of this issue. In many cases, however, spatial assessment models can only be fit at coarse spatial scales and may not be able to address spatial dynamics occurring at fine scales (Maunder et al. 2020).

When using assessment results to develop advice for fisheries management, spatially explicit management strategy evaluation tools (Punt et al. 2016) that explore the bioeconomic trade-offs of different management actions can help mitigate any negative effects of stock assessment uncertainty (Bailey et al. 2019). Interdisciplinary work is recommended between fisheries scientists and fisheries economists that finds ways to quantitatively merge stock assessment and fisher behavior modeling.

Acknowledgements

This work was funded by the NOAA – Sea Grant Population Dynamics Fellowship Grant Award NA080AR4170763, NOAA Cooperative agreement NA17RJ1226 through University of Miami, and an International Light Tackle Tournament Association Scholarship. This manuscript has benefited greatly from the feedback of several peer reviewers and the editorial assistant.

References

- Alós, J., Campos-Candela, A., and Arlinghaus, R. 2018. A modelling approach to evaluate the impact of fish spatial behavioural types on fisheries stock assessment. *ICES J. Mar. Sci.* **76**(2): 489–500. doi:10.1093/icesjms/tsy172.
- An, L. 2012. Modeling human decisions in coupled human and natural systems: review of agent-based models. *Ecol. Modell.* **24**: 25–36. doi:10.1016/j.ecolmodel.2011.07.010.
- Bailey, R.M., Carrella, E., Axtell, R., Burgess, M.G., Cabral, R., Drexler, M., et al. 2019. A computational approach to managing coupled human–environmental systems: the POSEIDON model of ocean fisheries. *Sustainability Sci.* **14**: 259–275. doi:10.1007/s11625-018-0579-9.
- Bastardie, F., Nielsen, J.R., and Miethe, T. 2014. DISPLACE: a dynamic, individual-based model for spatial fishing planning and effort displacement — integrating underlying fish population models. *Can. J. Fish. Aquat. Sci.* **71**(3): 366–386. doi:10.1139/cjfas-2013-0126.
- Benson, A.J., and Stephenson, R.L. 2018. Options for integrating ecological, economic, and social objectives in evaluation and management of fisheries. *Fish. Fish.* **19**(1): 40–56. doi:10.1111/faf.12235.
- Bishop, J. 2006. Standardizing fishery-dependent catch and effort data in complex fisheries with technology change. *Rev. Fish Biol. Fish.* **16**: 21–38. doi:10.1007/s11660-006-0004-9.
- Bishop, J., Die, D., and Wang, Y. 2000. Applications: A generalized estimating equation approach for analysis of the impact of new technology on a trawl fishery. *Aust. N.Z. J. Stat.* **42**(2): 159–177. doi:10.1111/1467-842X.00116.
- Bishop, J., Venables, W.N., and Wang, Y. 2004. Analysing commercial catch and effort data from a Penaeid trawl fishery: a comparison of linear models, mixed models and generalized estimating equations approaches. *Fish. Res.* **70**: 179–193. doi:10.1016/j.fishres.2004.08.003.
- Bonabeau, E. 2002. Agent-based modeling: methods and techniques for simulating human systems. *Proc. Natl. Acad. Sci. U.S.A.* **99**: 7280–7287. doi:10.1073/pnas.082080899. PMID:12011407.
- Branch, T.A., Hilborn, R., Haynie, A.C., Fay, G., Flynn, L., Griffiths, J., et al. 2006. Fleet dynamics and fishermen behavior: lessons for fisheries managers. *Can. J. Fish. Aquat. Sci.* **63**(7): 1647–1668. doi:10.1139/f06-072.
- Burnham, K.P., and Anderson, D.R. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Soc. Methods Res.* **33**(2): 261–304. doi:10.1177/0049124104268644.
- Burton, M.L., Brennan, K.J., Muñoz, R.C., and Parker, R.O. 2005. Preliminary evidence of increased spawning aggregations of mutton snapper (*Lutjanus analis*) at Riley’s Hump two years after establishment of the Tortugas South Ecological Reserve. *Fish. Bull.* **103**(2): 404–410.
- Campbell, M.S., Stehfest, K.M., Votier, S.C., and Hall-Spencer, J.M. 2014. Mapping

- fisheries for marine spatial planning: gear-specific vessel monitoring system (VMS), marine conservation and offshore renewable energy. *Mar. Pol.* **45**: 293–300. doi:10.1016/j.marpol.2013.09.015.
- Campbell, R.A. 2015. Constructing stock abundance indices from catch and effort data: some nuts and bolts. *Fish. Res.* **161**: 109–130. doi:10.1016/j.fishres.2014.07.004.
- Cao, J., Thorson, J.T., Richards, R.A., and Chen, Y. 2017. Spatiotemporal index standardization improves the stock assessment of northern shrimp in the Gulf of Maine. *Can. J. Fish. Aquat. Sci.* **74**(11): 1781–1793. doi:10.1139/cjfas-2016-0137.
- Cao, J., Thorson, J.T., Punt, A.E., and Szuwalski, C. 2020. A novel spatiotemporal stock assessment framework to better address fine-scale species distributions: development and simulation testing. *Fish. Fish.* **21**: 350–367. doi:10.1111/faf.12433.
- Chen, Y., and Rajakaruna, H. 2003. Quality and Quantity of Fisheries Information in Stock Assessment. In *Proceedings of the Third World Fisheries Congress: Feeding the World with Fish in the Next Millennium, the Balance Between Production and Environment*. Edited by B. Phillips, B. Megrey, and Z. Yingqi. American Fisheries Society Symposium, Bethesda, Maryland. pp. 411–424.
- Coleman, F.C., Koenig, C.C., and Collins, L.A. 1996. Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environ. Biol. Fishes*, **47**: 129–141. doi:10.1007/BF0005035.
- Coleman, F.C., Koenig, C.C., Huntsman, G.R., Musick, J.A., Eklund, A.M., McGovern, J.C., et al. 2000. Long-lived reef fishes: the grouper-snapper complex. *Fisheries*, **25**: 14–21. doi:10.1577/1548-8446(2000)025<0014:LRF>2.0.CO;2.
- Cooke, J.G., and Beddington, J.R. 1984. The relationship between catch rates and abundance in fisheries. *Math. Med. Biol.* **1**(4): 391–405. doi:10.1093/imammb/1.4.391.
- Darcy, G.H., and Guthertz, E.J. 1984. Abundance and density of demersal fishes on the West Florida Shelf, January 1978. *Bull. Mar. Sci.* **34**: 81–105.
- Davies, T.K., Mees, C.C., and Milner-Gulland, E.J. 2014. Modelling the spatial behavior of a tropical tuna purse sein fleet. *PLoS ONE*, **9**(12): e114034. doi:10.1371/journal.pone.0114037. PMID:25462165.
- Dharmawan, B., Böcher, M., and Krott, M. 2017. Failure of science-based win-win solution in fishery management: learnings from Segara Anakan waters, Central Java, Indonesia. *Ocean Coastal Manage.* **141**: 82–89. doi:10.1016/j.ocecoaman.2017.03.014.
- Dolder, P.J., Thorson, J.T., and Minto, C. 2018. Spatial separation of catches in highly mixed fisheries. *Sci. Rep.* **8**: 13886. doi:10.1038/s41598-018-31881-w. PMID:30224780.
- Ducharme-Barth, N.D., Shertzer, K.W., and Ahrens, R.N.M. 2018. Indices of abundance in the Gulf of Mexico reef fish complex: a comparative approach using spatial data from vessel monitoring systems. *Fish. Res.* **198**: 1–13. doi:10.1016/j.fishres.2017.10.020.
- Dugan, J.E., and Davis, G.E. 1993. Applications of marine refugia to coastal fisheries management. *Can. J. Fish. Aquat. Sci.* **50**(9): 2029–2042. doi:10.1139/f93-227.
- Ellis, R.D. 2019. Red grouper (*Epinephelus morio*) shape faunal communities via multiple ecological pathways. *Diversity*, **11**(6): 89. doi:10.3390/d11060089.
- Farmer, J.D., and Foley, D. 2009. The economy needs agent-based modelling. *Nature*, **460**: 685–686. doi:10.1038/460685a. PMID:19661896.
- Francis, R.I.C.C. 2017. Revisiting data weighting in fisheries stock assessment models. *Fish. Res.* **192**: 5–15. doi:10.1016/j.fishres.2016.06.006.
- Fulton, E.A., Smith, A.D.M., Smith, D.C., and van Putten, I.E. 2011. Human behaviour: the key source of uncertainty in fisheries management. *Fish. Fish.* **12**(1): 2–17. doi:10.1111/j.1467-2979.2010.00371.x.
- Gelfand, A., Sahu, S.K., and Holland, D.M. 2012. On the effect of preferential sampling in spatial prediction. *Environmetrics*, **23**(7): 565–578. doi:10.1002/env.2169. PMID:24077640.
- Gillis, D.M., and Peterman, R.M. 1998. Implications of interference among fishing vessels and the ideal free distribution to the interpretation of CPUE. *Can. J. Fish. Aquat. Sci.* **55**(1): 37–46. doi:10.1139/f97-206.
- Girardin, R., Hamon, K.G., Pinnegar, J., Poos, J.J., Thébaud, O., Tidd, A., Vermard, Y., and Marchal, P. 2017. Thirty years of fleet dynamics modelling using discrete-choice models: what have we learned? *Fish. Fish.* **18**(4): 638–655. doi:10.1111/faf.12194.
- Goethel, D.R., and Berger, A.M. 2017. Accounting for spatial complexities in the calculation of biological reference points: effects of misdiagnosing population structure for stock status indicators. *Can. J. Fish. Aquat. Sci.* **74**(11): 1878–1894. doi:10.1139/cjfas-2016-0290.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., et al. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science*, **310**(5750): 987–991. doi:10.1126/science.1116681. PMID:16284171.
- Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., et al. 2006. A standard protocol for describing individual-based and agent-based models. *Ecol. Modell.* **198**(1–2): 115–126. doi:10.1016/j.ecolmodel.2006.04.023.
- Guillotreau, P., Squires, D., Sun, J., and Compeán, G.A. 2017. Local, regional and global markets: what drives the tuna fisheries? *Rev. Fish Biol. Fish.* **27**: 909–929. doi:10.1007/s11160-016-9456-8.
- Harley, S.J., Myers, R.A., and Dunn, A. 2001. Is catch-per-unit-effort proportional to abundance? *Can. J. Fish. Aquat. Sci.* **58**(9): 1760–1772. doi:10.1139/f01-112.
- Harter, S.L., Moe, H., Reed, J.K., and David, A.W. 2017. Fish assemblages associated with red grouper pits at Pulley Ridge, a mesophotic reef in the Gulf of Mexico. *Fish. Bull.* **115**: 419–432. doi:10.7755/FB.115.3.11.
- Heery, E.C., and Berkson, J. 2009. Systematic errors in length frequency data and their effect on age-structured stock assessment models and management. *Trans. Am. Fish. Soc.* **138**(1): 218–232. doi:10.1577/T07-226.1.
- Herrmann, B., Sistiaga, M., Rindahl, L., and Tatone, I. 2017. Estimation of the effect of gear design changes on catch efficiency: methodology and a case study for a Spanish longline fishery targeting hake (*Merluccius merluccius*). *Fish. Res.* **185**: 153–160. doi:10.1016/j.fishres.2016.09.013.
- Hilborn, R. 1985. Fleet dynamics and individual variation: Why some people catch more fish than others. *Can. J. Fish. Aquat. Sci.* **42**(1): 2–13. doi:10.1139/f85-001.
- Hinton, M.G., and Maunder, M.N. 2004. Methods for standardizing CPUE and how to select among them. *Coll. Vol. Sci. Pap.* **56**: 169–177.
- Holland, D., and Sutinen, J.G. 2000. Location choice in New England trawl fisheries: old habits die hard. *Land Econ.* **76**: 133–149. doi:10.2307/3147262.
- Karnauskas, M., Walter, J.F., Campbell, M.D., Pollack, A.G., Drymon, J.M., and Powers, S. 2016. Red snapper distribution on natural habitats and artificial structures in the Northern Gulf of Mexico. *Mar. Coast. Fish.* **1**: 50–67. doi:10.1080/19425120.2016.1255684.
- Kraak, S.B.M., Daan, N., and Pastoors, M.A. 2009. Biased stock assessment when using multiple, hardly overlapping, tuning series if fishing trends vary spatially. *ICES J. Mar. Sci.* **66**(10): 2272–2277. doi:10.1093/icesjms/fsp179.
- Lane, D.E. 1988. Investment decision-making by fishermen. *Can. J. Fish. Aquat. Sci.* **45**(5): 782–796. doi:10.1139/f88-096.
- Little, L.R., Begg, G.A., Goldman, B., Ellis, N., Mapstone, B.D., Punt, A.E., et al. 2008. Modelling multi-species targeting of fishing effort in the Queensland Coral Reef Fin Fish Fishery. *Fishing and Fisheries Research Centre Technical Report No. 2*. Fishing and Fisheries Research Centre, James Cook University, Townsville.
- Little, L.R., Punt, A., Mapstone, B.D., Begg, G.A., Goldman, B., and Williams, A.J. 2009. An agent-based model for simulating trading of multi-species fisheries quota. *Ecol. Modell.* **220**(23): 3404–3412. doi:10.1016/j.ecolmodel.2009.08.004.
- Little, L.R., Punt, A.E., Tuck, G.N., and Mapstone, B.D. 2017. Exploring the effect of sampling, protogyny, and larval advection on stock estimates subject to no-take closures in a spatially complex coral reef line fishery on the Great Barrier Reef, Australia. *Can. J. Fish. Aquat. Sci.* **74**(11): 1950–1959. doi:10.1139/cjfas-2016-0349.
- Lo, N.C., Jacobson, L.D., and Squire, J.L. 1992. Indices of relative abundance from fish spotter data based on delta-lognormal models. *Can. J. Fish. Aquat. Sci.* **49**(12): 2515–2526. doi:10.1139/f92-278.
- Marchal, P., Ulrich, C., Korsbrekke, K., Pastoors, M., and Rackham, B. 2002. A comparison of three indices of fishing power on some demersal fisheries of the North Sea. *ICES J. Mar. Sci.* **59**(3): 604–623. doi:10.1006/jmsc.2002.1215.
- Marriott, R.J., Turlach, B.A., Murray, K., and Fairclough, D.V. 2017. Evaluation of spatiotemporal imputations for fishing catch rate standardization. *Can. J. Fish. Aquat. Sci.* **74**(9): 1348–1361. doi:10.1139/cjfas-2016-0182.
- Maunder, M.N., and Piner, K.R. 2015. Contemporary fisheries stock assessment: many issues still remain. *ICES J. Mar. Sci.* **72**(1): 7–18. doi:10.1093/icesjms/fsu015.
- Maunder, M.N., and Punt, A.E. 2004. Standardizing catch and effort data: a review of recent approaches. *Fish. Res.* **70**: 141–159. doi:10.1016/j.fishres.2004.08.002.
- Maunder, M.N., Sibert, J.R., Fonteneau, A., Hampton, J., Kleiber, P., and Harley, S.J. 2006. Interpreting catch per unit effort data to assess the status of individual stock and communities. *ICES J. Mar. Sci.* **63**(8): 1373–1385. doi:10.1016/j.icesjms.2006.05.008.
- Maunder, M.N., Thorson, J.T., Xu, H., Oliveros-Ramos, R., Hoyle, S.D., Tremblay-Boyer, L., et al. 2020. The need for spatio-temporal modeling to determine catch-per-unit effort based indices of abundance and associated composition data for inclusion in stock assessment models. *Fish. Res.* **229**: 105594. doi:10.1016/j.fishres.2020.105594.
- Mesnil, B., Cotter, J., Fryer, R.J., Needle, C.L., and Trenkel, V.M. 2009. A review of fishery-independent assessment models, and initial evaluation based on simulated data. *Aquat. Living Resour.* **22**(2): 207–216. doi:10.1051/alr/2009003.
- Methot, R.D., and Wetzel, C.R. 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. *Fish. Res.* **142**: 86–99. doi:10.1016/j.fishres.2012.10.012.
- Minte-Vera, C.V., Maunder, M.N., Aires-da-Silva, A.M., Satoh, K., and Uosaki, K. 2017. Get the biology right, or use size-composition data at your own risk. *Fish. Res.* **192**: 114–125. doi:10.1016/j.fishres.2017.01.014.
- Monk, C.T., Barbier, M., Romanczuk, P., Watson, J.R., Alós, J., Nakayama, S., et al. 2018. How ecology shapes exploitation: a framework to predict the behavioural response of human and animal foragers along exploration–exploitation trade-offs. *Ecol. Lett.* **21**: 779–793. doi:10.1111/ele.12949. PMID:29611278.
- Nguyen, Q., and Leung, P. 2013. Revenue targeting in fisheries. *Environ. Dev. Econ.* **18**(5): 559–575. doi:10.1017/S1355770X13000144.
- Nightingale, A.J. 2011. Beyond design principles: subjectivity, emotion, and the (ir)rational commons. *Soc. Nat. Resour.* **24**(2): 119–132. doi:10.1080/08941920903278160.
- Parry, H.R., and Evans, A.J. 2008. A comparative analysis of parallel processing

- and super-individual methods for improving the computational performance of a large individual-based model. *Ecol. Modell.* **214**(2–4): 141–152. doi:10.1016/j.ecolmodel.2008.02.002.
- Patterson, W.F., and Cowan, J.H. 2003. Site fidelity and dispersion of red snapper associated with artificial reefs in the northern Gulf of Mexico. *Am. Fish. Soc. Symp.* **36**: 181–193.
- Pennington, M. 1983. Efficient estimators of abundance, for fish and plankton surveys. *Biometrics*, **39**(1): 281–286. doi:10.2307/2530830.
- Pennington, M. 1996. Estimating the mean and variance from highly skewed marine data. *Fish. Bull.* **94**: 498–505.
- Perez, P., Dray, A., Cleland, D., and Arias-González, J.E. 2009. An agent-based model to address coastal management issues in the Yucatan Peninsula, Mexico. In *The 18th World IMACS Congress and MODSIM09 International Congress on Modelling and Simulation*. Edited by R.S. Anderssen, R.D. Braddock, and L.T.H. Newham. Modelling and Simulation Society of Australia and New Zealand and International Association for Mathematics and Computers in Simulation, July 2009. pp. 72–79. ISBN:9780975840078.
- Phillips, N.W., Gettleton, D.A., and Spring, K.D. 1990. Benthic biological studies of the Southwest Florida Shelf. *Integr. Comp. Biol.* **30**: 65–75. doi:10.1093/icb/30.1.65.
- Punt, A.E., Butterworth, D.S., de Moor, C.L., De Oliveira, J.A.A., and Haddon, M. 2016. Management strategy evaluation: best practices. *Fish. Fish.* **17**(2): 303–334. doi:10.1111/faf.12104.
- R Core Team. 2018. R: a language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.R-project.org/>.
- Reimer, M.N., Abbott, J.K., and Wilen, J.E. 2017. Fisheries production: management, institutions, spatial choice, and the quest for policy invariance. *Mar. Resour. Econ.* **32**(2): 143–168. doi:10.1086/690678.
- Richards, L.J., and Schnute, J.T. 1986. An experimental and statistical approach to the question: is CPUE an index of abundance? *Can. J. Fish. Aquat. Sci.* **43**(6): 1214–1227. doi:10.1139/f86-151.
- Rose, G.A., and Kulka, D.W. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. *Can. J. Fish. Aquat. Sci.* **56**(S1): 118–127. doi:10.1139/f99-207.
- Rose, G.A., and Leggett, W.C. 1991. Effects of biomass-range interactions on catchability of migratory demersal fish by mobile fisheries: an example of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **48**(5): 843–848. doi:10.1139/f91-100.
- Said, A., Tzanopoulos, J., and MacMillan, D. 2018. The contested commons: the failure of EU fisheries policy and governance in the Mediterranean and the crisis enveloping the small-scale fisheries of Malta. *Front. Mar. Sci.* **5**: 300. doi:10.3389/fmars.2018.00300.
- Salas, S., and Gaertner, D. 2004. The behavioural dynamics of fishers: management implications. *Fish. Fish.* **5**(2): 153–167. doi:10.1111/j.1467-2979.2004.00146.x.
- Salas, S., Sumaila, U.R., and Pitcher, T. 2004. Short-term decisions of small-scale fishers selecting alternative target species: a choice model. *Can. J. Fish. Aquat. Sci.* **61**(3): 374–383. doi:10.1139/f04-007.
- Salthaug, A., and Aanes, S. 2003. Catchability and the spatial distribution of fishing vessels. *Can. J. Fish. Aquat. Sci.* **60**(3): 259–268. doi:10.1139/f03-018.
- Saul, S., and Die, D. 2016. Modeling the decision-making behavior of fishers in the reef fish fishery on the West Coast of Florida. *Hum. Dimens. Wildl.* **21**(6): 567–586. doi:10.1080/10871209.2016.1198853.
- Saul, S., Die, D., Brooks, E.N., and Burns, K. 2012. An individual-based model of ontogenetic migration in reef fish using a biased random walk. *Trans. Am. Fish. Soc.* **141**(6): 1439–1452. doi:10.1080/00028487.2012.697091.
- Saul, S., Walter, J.F., Die, D.J., Naar, D.F., and Donahue, B.T. 2013. Modeling the spatial distribution of commercially important reef fishes on the West Florida Shelf. *Fish. Res.* **143**: 12–20. doi:10.1016/j.fishres.2013.01.002.
- Scott-Denton, E., and Williams, J.A. 2013. Observer coverage of the 2010–2011 Gulf of Mexico reef fish fishery. US Dept. Comm., NOAA Tech. Memo. NMFS-SEFSC-646.
- SEDAR. 2005. Southeast Data, Assessment, and Review: Stock Assessment Report of SEDAR 7: Gulf of Mexico Red Snapper. SEDAR7, 1 Southpark Circle #306, Charleston, SC 29414, USA.
- SEDAR. 2006a. Southeast Data, Assessment, and Review: Stock Assessment Report of SEDAR 12: Gulf of Mexico Red Grouper. SEDAR12, 1 Southpark Circle #306, Charleston, SC 29414.
- SEDAR. 2006b. Southeast Data, Assessment, and Review: Stock Assessment Report of SEDAR 10: Gulf of Mexico Gag Grouper. SEDAR10, 1 Southpark Circle #306, Charleston, SC 29414.
- SEDAR. 2008. Southeast Data, Assessment, and Review: Stock Assessment Report of SEDAR 15A: South Atlantic and Gulf of Mexico Mutton Snapper. SEDAR15A, 1 Southpark Circle #306, Charleston, SC 29414.
- Sethi, S.A., Branch, T.A., and Watson, R. 2010. Global fishery development patterns are driven by profit but not trophic level. *Proc. Natl. Acad. Sci. U.S.A.* **107**(27): 12163–12167. doi:10.1073/pnas.1003236107. PMID:20566867.
- Seung, C.K. 2017. A multi-regional economic impact analysis of Alaska salmon fishery failures. *Ecol. Econ.* **138**: 22–30. doi:10.1016/j.ecolecon.2017.03.020.
- Shephard, S., Gerritsen, H., Kaiser, M.J., and Reid, D.G. 2012. Spatial heterogeneity in fishing creates *de facto* refugia for endangered Celtic Sea elasmobranchs. *PLoS ONE*, **7**: e0049307. doi:10.1371/journal.pone.0049307. PMID:23166635.
- Smith, M.D., Sanchirico, J.N., and Wilen, J.E. 2009. The economics of spatial-dynamic processes: applications to renewable resources. *J. Environ. Econ. Manage.* **57**(1): 104–121. doi:10.1016/j.jeeem.2008.08.001.
- Swain, D.P., and Sinclair, A.F. 1994. Fish distribution and catchability: what is the appropriate measure of distribution? *Can. J. Fish. Aquat. Sci.* **51**(5): 1046–1054. doi:10.1139/f94-104.
- Thorson, J.T., Johnson, K.F., Method, R.D., and Taylor, I.G. 2017. Model-based estimates of effective sample size in stock assessment models using the Dirichlet-multinomial distribution. *Fish. Res.* **192**: 84–93. doi:10.1016/j.fishres.2016.06.005.
- Tommasi, D., Stock, C.A., Pegion, K., Vecchi, G.A., Method, R.D., Alexander, M.A., and Checkley, D.M., Jr. 2017. Improved management of small pelagic fisheries through seasonal climate prediction. *Ecol. Appl.* **27**(2): 378–388. doi:10.1002/eap.1458. PMID:28221708.
- Vinther, M., and Eero, M. 2013. Quantifying relative fishing impact on fish populations based on spatio-temporal overlap of fishing effort and stock density. *ICES J. Mar. Sci.* **70**(3): 618–627. doi:10.1093/icesjms/fst001.
- Walter, J.F., Hoening, J.M., and Christman, M.C. 2014. Reducing bias and filling in spatial gaps in fishery-dependent catch-per-unit-effort data by geostatistical prediction, I. Methodology and Simulation. *North Am. J. Fish Manage.* **34**(6): 1095–1107. doi:10.1080/02755947.2014.932865.
- Walters, C. 2003. Folly and fantasy in the analysis of spatial catch rate data. *Can. J. Fish. Aquat. Sci.* **60**(12): 1433–1436. doi:10.1139/f03-152.
- Ward, C.H., and Tunnell, J.W. 2017. Habitats and biota of the Gulf of Mexico: an overview. In *Habitats and biota of the Gulf of Mexico: before the Deepwater Horizon Oil Spill*. Edited by C. Ward. Springer, New York.
- Wiedenmann, J., Wilberg, M., Sylvia, A., and Miller, T. 2017. An evaluation of acceptable biological catch (ABC) harvest control rules designed to limit overfishing. *Can. J. Fish. Aquat. Sci.* **74**(7): 1028–1040. doi:10.1139/cjfas-2016-0381.
- Wilberg, M.J., Thorson, J.T., Linton, B.C., and Berkson, J. 2010. Incorporating time-varying catchability into population dynamic stock assessment models. *Rev. Fish. Sci.* **18**(1): 7–24. doi:10.1080/10641260903294647.
- Wilen, J.E., Smith, M.D., Lockwood, D., and Botsford, L.W. 2002. Avoiding surprises: Incorporating fisherman behavior into management models. *Bull. Mar. Sci.* **70**(2): 553–575.
- Ye, Y., and Dennis, D. 2009. How reliable are the abundance indices derived from commercial catch–effort standardization? *Can. J. Fish. Aquat. Sci.* **66**(7): 1169–1178. doi:10.1139/F09-070.

Copyright of Canadian Journal of Fisheries & Aquatic Sciences is the property of Canadian Science Publishing and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.