Producing distribution maps for informing ecosystem-based fisheries management using a comprehensive survey database and spatio-temporal models

Arnaud Grüss[1*], James T. Thorson[2], Elizabeth A. Babcock[1] and Joseph H. Tarnecki[3]

[1]Department of Marine Biology and Ecology, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL, 33149, USA

[2]Fisheries Resource Assessment and Monitoring Division (FRAM), Northwest Fisheries Science Center, National Marine Fisheries Service (NMFS), NOAA, 2725, Montlake Boulevard E, Seattle, WA 98112, USA

[3]Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 100 8th Ave SE, St. Petersburg, FL 33701, USA

Type of article: Original article

Manuscript length
Abstract (299 words), Core text (6,651 words), References (60)
7 figures, 4 tables, 1 box
4 figures, 3 tables and 2 appendices appearing in the Supplementary material.

**** Corresponding author***
Dr. Arnaud Grüss
Department of Marine Biology and Ecology
Rosenstiel School of Marine and Atmospheric Science, University of Miami
4600 Rickenbacker Causeway
Miami, FL, 33149
United States of America
Telephone: (01) 305 421 4262
Email: agruss@rsmas.miami.edu

ABSTRACT

Ecosystem-based fisheries-management (EBFM) is increasingly used in the United States (U.S.), including in the Gulf of Mexico (GOM). Producing distribution maps for marine organisms is a critical step in the implementation of EBFM. In particular, distribution maps are important inputs for many spatially-explicit ecosystem models, such as OSMOSE models, as well as for biophysical models used to predict annual recruitment anomalies due to oceanographic factors. In this study, we applied a recently proposed statistical modelling framework to produce distribution maps for: (1) younger juveniles (ages 0-1) of red snapper (*Lutjanus campechanus*), red grouper (*Epinephelus morio*) and gag (*Mycteroperca microlepis*), so as to be able to define the potential larval settlement areas of the three species in a biophysical model; and (2) the functional groups and life stages represented in the OSMOSE model of the West Florida Shelf ("OSMOSE-WFS"). This statistical modelling framework consists of: (1) compiling a large database blending all of the encounter/non-encounter data of the GOM collected by the fisheries-independent and fisheries-dependent surveys using random sampling schemes, referred to as the "comprehensive survey database"; (2) employing the comprehensive survey database to fit spatio-temporal binomial generalized linear mixed models (GLMMs) that integrate the confounding effects of survey and year; and (3) using the predictions of the fitted spatio-temporal binomial GLMMs to generate distribution maps. This large endeavour allowed us to produce distribution maps for younger juveniles of red snapper, red grouper and gag and nearly all of the other functional groups and life stages represented in OSMOSE-WFS, at different seasons. Using Pearson residuals, the probabilities of encounter predicted by all spatio-temporal binomial GLMMs were demonstrated to be reasonable. Moreover, the results obtained for younger juvenile fish concur with the literature, provide additional

insights into the spatial distribution patterns of these life stages, and highlight important future research avenues.

Key words: distribution maps; ecosystem-based fisheries management (EBFM); spatially-explicit ecosystem models; biophysical models; comprehensive survey database; generalized linear mixed models (GLMMs)

Introduction

Ecosystem-based fisheries-management (EBFM) is increasingly being used in the United States (U.S.), including in the Gulf of Mexico (GOM) (Levin *et al.*, 2014; Samhouri *et al.*, 2014; Grüss *et al.*, 2017a; Harvey *et al.*, 2017). Producing distribution maps for marine organisms is a critical step in the implementation of EBFM (Mace *et al.*, 2001; MSFCMA, 2007). In particular, distribution maps are important inputs for a number of spatially-explicit ecosystem models, such as applications of the OSMOSE (Shin and Cury, 2001, 2004) and Atlantis (Fulton *et al.*, 2004, 2011) modelling platforms, as well as for biophysical models used to predict annual recruitment anomalies due to oceanographic factors, such as the Connectivity Modelling System (CMS; Paris *et al.*, 2013). In ecosystem models, distribution maps and simulated movement patterns (e.g., seasonal migrations) are used to allocate the biomasses of modelled marine organisms over space; in this way, distribution maps influence patterns of spatial overlap between functional groups and, consequently, trophic interactions between these functional groups (Grüss *et al.*, 2016a). In biophysical models such as the CMS, distribution maps are needed to define spatial patterns of egg production and the potential larval settlement areas of the species under consideration (Karnauskas *et al.*, 2013a, 2013b; Grüss *et al.*, 2014b).

The production of distribution maps for spatially-explicit ecosystem and biophysical models has generally relied on simplistic methodologies (Grüss *et al.*, 2016a). Two exceptions to this general pattern are the methodologies developed by Drexler and Ainsworth (2013) for the Atlantis model of the GOM ("Atlantis-GOM") and Grüss *et al.* (2014a) for the OSMOSE model of the West Florida Shelf ("OSMOSE-WFS"). Drexler and Ainsworth (2013) generated distribution maps for Atlantis-GOM from the predictions of negative binomial generalized additive models (GAMs) fitted to a groundfish trawl survey dataset. Grüss *et al.* (2014) produced distribution maps for OSMOSE-WFS using

the predictions of delta GAMs fitted to a groundfish trawl, a video, or a bottom longline survey dataset. While Drexler and Ainsworth (2013) and Grüss *et al.* (2014a)'s methodologies represent improvements over previous methodologies for generating distribution maps for spatially-explicit ecosystem models, they also have limitations. First, Drexler and Ainsworth (2013) and Grüss *et al.* (2014a) relied on a limited amount of survey data for some functional groups, which led in some cases to unreliable predictions of spatial distributions. Then, Drexler and Ainsworth (2013) and Grüss *et al.* (2014a) employed survey data that were not appropriate in some cases (e.g., groundfish trawl survey data for some pelagic functional groups). Finally, Drexler and Ainsworth (2013) and Grüss *et al.* (2014a)'s approaches were not geospatial and, therefore, resulted in substantial, unmodelled spatial patterns in GAM residuals for many functional groups.

Grüss *et al.* (2016a) proposed a novel statistical modelling framework that addresses the limitations of Drexler and Ainsworth (2013) and Grüss *et al.* (2014a)'s methodologies. Grüss *et al.* (2016a)'s proposed statistical modelling framework consists of: (1) compiling a large database blending all of the encounter/non-encounter data of the U.S. GOM collected by the fisheries-independent and fisheries-dependent surveys that use random sampling schemes (i.e., that do not use fixed-station designs or do not compile fisheries catch time series for specific areas of the GOM), referred to as the "comprehensive survey database"; (2) employing the comprehensive survey database to fit binomial statistical models that integrate the confounding effects of "gear" (where each gear type specifies a survey dataset) and year; and (3) using the predictions of the fitted binomial statistical models to produce distribution maps for the U.S. GOM. Grüss *et al.* (2016a)'s methodology is particularly appropriate for generating distribution maps for groupers (Epinephelidae), as demonstrated in a previous study (Grüss *et al.*, 2017b). In Grüss *et al.* (2017b), spatio-temporal binomial generalized linear mixed models (GLMMs)

were developed, using a blending of encounter/non-encounter data for red grouper (*Epinephelus morio*) and gag (*Mycteroperca microlepis*) collected by six fisheries-independent and three fisheries-dependent surveys of the U.S. GOM. Then, the predictions of fitted spatio-temporal binomial GLMMs were employed to generate probability of encounter maps for the older juvenile (ages $1-3$) and adult (ages 3+) stages of red grouper and gag. Grüss *et al.* (2017b) showed that the predictions of their spatio-temporal binomial GLMMs were reasonable. Yet, the authors found that, in the case of adult gag, observed frequency of encounter for samples with highest predicted encounter probability was considerably smaller than the estimated 95% confidence interval for these samples; this result was attributed to the relatively limited amount of data available to the authors for adult gag, which yielded low observed frequency of encounter for the highest probability samples.

In the present study, we apply Grüss *et al.* (2016a)'s statistical modelling framework to produce distribution maps for: (1) the younger juveniles (ages 0-1) of red snapper (<22.9 cm TL), red grouper (<14.8 cm TL) and gag (<20 cm TL), so as to delineate the potential larval settlement areas of the three species in the CMS biophysical model; and (2) the functional groups represented in the OSMOSE-WFS ecosystem model. All these distribution maps were generated using the predictions of spatio-temporal binomial GLMMs fitted to the comprehensive survey database that we compiled for the U.S. GOM (hereafter often simply referred to as "GOM"). First, we report the development of the comprehensive survey database, which gathered a sufficient amount of encounter/non-encounter data coming from 37 different survey datasets to generate distribution maps for the younger juveniles of red snapper, red grouper and gag, and nearly all of the functional groups represented in OSMOSE-WFS. Then, we produce and evaluate distribution maps, with a focus on younger juveniles of red snapper, red grouper and gag.

Finally, we use these distribution maps to estimate the percentages of spatial overlap between younger juveniles of red snapper, red grouper and gag and the older juvenile and adult stages of red grouper and gag in the West Florida Shelf region, so as to revisit a contentious result of the latest published versions of OSMOSE-WFS (Grüss *et al.*, 2016b, 2016c).

Material and methods

Study areas

The GOM is a Large Marine Ecosystem bordered by the U.S., Mexico and Cuba (NOS, 2008). The U.S. GOM is bounded on the east by the West Florida Shelf, on the north by the states of Mississippi, Alabama and Louisiana, and on the west by the state of Texas. The area of the West Florida Shelf considered in the OSMOSE-WFS model excludes the Florida Keys and Dry Tortugas (Figures 1 and 2a).

Study functional groups, species and life stages

Younger juveniles of red snapper, red grouper and gag

Red snapper, red grouper and gag are demersal fish characterized by small home ranges and high site fidelity (Bullock and Smith, 1991; Workman *et al.*, 2002; Coleman *et al.*, 2010, 2011). The three species undertake several ontogenetic migrations during their life cycle (Mullaney Jr, 1994; Gallaway *et al.*, 2009; Saul *et al.*, 2012; Carruthers *et al.*, 2015). The first of these ontogenetic migrations occurs when fish reach age 1 (i.e., when they transition from the younger juvenile to the older juvenile stage). At around one year of age, red snapper migrates to deeper, higher-relief areas (Szedlmayer and Conti, 1999; Gallaway *et al.*, 2009), while red grouper and gag migrate from nearshore shallow areas to inshore reefs (Koenig and Coleman, 1998; Switzer *et al.*, 2012).

163 The habitats of younger juveniles of red snapper, red grouper and gag differ.
164 Younger juvenile red snappers are distributed over low-relief areas, characterized by
165 patches of rubble, debris, or relic shell beds associated with sand and mud (Szedlmayer and
166 Conti, 1999; Gallaway *et al.*, 2009). Younger juvenile red groupers do not require specific
167 habitats; they are found in estuaries, in inshore hard bottom areas and on seagrass beds
168 (Moe, 1969; Koenig and Coleman, 1999; Coleman *et al.*, 2010). By contrast, younger
169 juvenile gags are dependent on high-salinity estuaries (Koenig and Coleman, 1998;
170 Fitzhugh *et al.*, 2005; Switzer *et al.*, 2012), where they inhabit primarily seagrass beds, but
171 also mangroves, oyster reefs, jetties and seawalls (Hastings, 1979; Bullock and Smith,
172 1991; Koenig and Coleman, 1998, 1999; Casey *et al.*, 2007). Recently, Ingram *et al.*
173 (2013) combined three fisheries-independent databases to produce abundance indices for
174 younger juvenile gag for the eight regions of the GOM where the life stage is consistently
175 found: (1) Saint Andrew Bay; (2) Saint Joe Bay; (3) Turkey Point; (4) the Mid Big Bend;
176 (5) Cedar Key; (6) Tampa Bay; (7) Sarasota Bay; and (8) Charlotte Harbor (Figure 2b).
177
178 *Functional groups of the OSMOSE-WFS model*
179 OSMOSE is a spatially-explicit individual-based, multispecies modelling approach,
180 which simulates the entire life cycle of several (typically 10-15) high trophic level (HTL)
181 functional groups and is forced by fields of biomass for low trophic level (LTL) functional
182 groups (Shin and Cury, 2001, 2004 ; Grüss *et al.*, 2016b). Distribution maps are provided
183 to OSMOSE at each modelled time step to allocate the biomasses of HTL and LTL groups
184 over space. When the distribution of a given HTL functional group or of a given life stage
185 of a HTL functional group remains static during seasonal or yearly time frames, the
186 individuals of this functional group or life stage move to model cells immediately adjacent
187 to their current cell according to a random walk. In OSMOSE, a parameter determines the

188 range of random walk movements of HTL functional groups and life stages and, therefore,
189 can account for the fact that some HTL functional groups and life stages have lower site
190 fidelity than others; however, this parameter is usually set to its default value of 1.0 cell
191 (but see Halouani *et al.*, 2016). Contrary to most ecosystem modeling platforms, OSMOSE
192 does not use a diet matrix, but rather makes the assumption that predation is an
193 opportunistic process and that a predator will feed on any prey item if: (1) the predator and
194 the potential prey overlap over space, as determined by distribution maps defined for
195 specific functional groups, life stages and seasons; (2) there is size adequacy between the
196 predator and the potential prey, as determined by "predator/prey size ratios"; and, (3) the
197 potential prey is accessible to the predator, in relation to its vertical distribution and
198 morphology, as determined by "accessibility coefficients" (Grüss *et al.*, 2016b; Fu *et al.*,
199 2017). OSMOSE is a stochastic modelling approach, because it: (1) uses distribution maps
200 to distribute only a limited number of HTL individuals over space at run time; (2)
201 implements random walk movement when the distribution of HTL individuals remains
202 static; and (3) employs a stochastic mortality algorithm to compute the mortality rates of
203 HTL functional groups (Grüss *et al.*, 2016b).
204 OSMOSE-WFS is an application of the OSMOSE modelling approach with a
205 spatial resolution of 0.18° and a monthly time step, which describes the trophic structure of
206 the West Florida Shelf ecosystem in the 2000s (Figure 2a). Three versions of OSMOSE-
207 WFS have been developed and undergone validation (Grüss *et al.*, 2015, 2016b, 2016c).
208 Twelve HTL fish and invertebrate functional groups are represented in OSMOSE-WFS.
209 The model is forced by biomass fields for seven LTL functional groups, consisting of
210 phytoplankton, zooplankton, and five LTL benthic groups (Figure 3). The designation of
211 functional groups as either HTL or LTL groups in OSMOSE-WFS was based on the food
212 web structure described in another ecosystem model of the West Florida Shelf ("WFS Reef

213 fish Ecopath"; Chagaris, 2013). The OSMOSE-WFS functional groups considered in this
214 study include the twelve HTL functional groups and the five LTL benthic groups (Table
215 1).
216 Some of the HTL functional groups represented in OSMOSE-WFS are made of
217 only one species of high economic importance. This is the case for the "red snapper", "red
218 grouper" and "gag" functional groups.
219
220 ***Compilation of a comprehensive survey database for the GOM***
221 We requested data for the period of 2000-2016 from the different federal and state
222 agencies, universities and non-governmental organizations that either collect survey data in
223 the GOM using random sampling schemes, or randomly sample fisheries operations in the
224 GOM with observer programs. We received a total of 37 different datasets, including 29
225 fisheries-independent and eight fisheries-dependent datasets (Table 2 and Supplementary
226 Table S1).
227 We conducted a literature review to determine: (1) for which life stages of the HTL
228 functional groups represented in OSMOSE-WFS we should produce distribution maps; and
229 (2) whether we should produce annual or seasonal maps for the different HTL functional
230 groups/life stages and LTL functional groups represented in OSMOSE-WFS
231 (Supplementary Table S2). It was necessary to generate distribution maps for different life
232 stages of a given HTL functional group when the literature review revealed that this
233 functional group undertakes ontogenetic migrations, i.e., changes habitats as it grows older
234 (e.g., red snapper; Gallaway *et al.*, 2009).
235 Next, we extracted the following information from each of the 37 survey datasets
236 for each functional group/life stage: (1) the latitudes and longitudes at which the sampling
237 events took place; (2) the years and months during which the sampling events took place;

and (3) whether the functional group/life stage under consideration was encountered or not during the sampling events (0's and 1's). Encounters/non-encounters for life stages of HTL groups were obtained using the body size estimates collected during surveys and body length benchmarks (e.g., body length at sexual maturity) from FishBase and SeaLifeBase (Froese and Pauly, 2015; Palomares and Pauly, 2015). As we extracted information for the functional groups and life stages, we gauged the quality of each of the 37 survey datasets (e.g., does the survey have a high or a low spatio-temporal resolution?), so as to identify those survey datasets that should not be used to fit spatio-temporal binomial GLMMs for the data-rich functional groups and life stages (Table 2).

For younger juveniles of red snapper, red grouper and gag and each of the other functional groups and life stages represented in OSMOSE WFS, we determined which surveys to employ when fitting spatio-temporal binomial GLMMs. To select survey data from the comprehensive survey database for a given functional group/life stage and season, we applied the following rules: (1) survey datasets with fewer than 50 encounters should be excluded for modelling exercises (Leathwick *et al.*, 2006; Austin, 2007; Grüss *et al.*, 2017b); (2) years with fewer than five encounters should be excluded from modelling exercises (Grüss *et al.*, 2017b); and (3) a survey dataset that we gauged to be of low quality should be excluded from modelling exercises in situations that are not data-limited. Future research could explore changes to criteria (1) and (2), but they are unlikely to greatly affect results given that they serve to exclude surveys with little information.

Statistical modelling

We describe our statistical modelling approach briefly here and refer the reader to the Supplementary Appendix S3 for details. Our statistical modelling framework was based on the spatio-temporal delta GLMM approach of Thorson *et al.* (2015), which can be

implemented using the R package *SpatialDeltaGLMM* (https://github.com/nwfsc-assess/geostatistical_delta-GLMM). Our spatio-temporal binomial GLMMs predict probabilities of encounter, and spatial residuals in probability of encounter are Gaussian Markov random fields that are approximated using 1000 "knots", for the sake of computational convenience. The location of knots is determined, for each functional group/life stage, via the application of a *k*-means algorithm to the locations of the data of the comprehensive survey database; this *k*-means algorithm distributes knots spatially taking into account the sampling intensity of the different surveys considered for a given functional group/life stage.

Our spatio-temporal binomial GLMMs are fitted to the comprehensive survey database, following the equation:

$$g(p_i) = \sum_{t=1}^{n_t} \beta_t Y_{i,t} + \sum_{g=1}^{n_g} \gamma_g G_{i,g} + \varepsilon_{J(i)} \quad (1)$$

where p_i is the probability of encounter at site *s(i)*; g represents the logit link function between p_i and each random and fixed effect provided at the right side of the equation; $\varepsilon_{J(i)}$ are the random effects of the spatial residuals in probability of encounter at the nearest knot to sample *i*, *J(i)*, on the logit scale; $\sum_{t=1}^{n_t} \beta_t Y_{i,t}$ is the fixed effect of year on p_i on the logit scale; and $\sum_{g=1}^{n_g} \gamma_g G_{i,g}$ is the effect of gear (i.e., research survey) on p_i on the logit scale, which is treated as a random effect through the implementation of restricted maximum likelihood (REML). Regarding the fixed effect of year, $Y_{i,t}$ is a design matrix where $Y_{i,t}$ is one for the year t during which sample *i* was collected and zero otherwise; β_t is an intercept that varies among years; and n_t is the number of sampling years for the functional group/life stage under consideration. Regarding the random effect of gear, $G_{i,g}$ is a design matrix where $G_{i,g}$ is one for the gear g used to collect sample *i* and zero otherwise; γ_g is a gear effect (where $\gamma_g = 0$ for the gear g with the largest sample size for

a given functional group/life stage; this constraint is imposed for identifiability of all year effects β_t); and n_g is the number of sampling gears for the functional group/life stage under consideration. Finally, the random effects of the spatial residuals in probability of encounter are Gaussian Markov random fields that follow a multivariate normal distribution:

$$\boldsymbol{\varepsilon} \sim MN(\boldsymbol{\mu}, \boldsymbol{\Sigma}) \quad (2)$$

where MN is the multivariate normal distribution; $\boldsymbol{\mu}$ is the expected value at each site, which we fixed to zero; and $\boldsymbol{\Sigma}$ is a covariance matrix for $\boldsymbol{\varepsilon}$ at each site. The covariance between sites *s* and *s'* is assumed to be stationary and to follow a Matérn distribution (with smoothness $\nu = 1$):

$$\Sigma(s, s') = \sigma_\varepsilon^2 . Matérn(\|\mathbf{H}(s - s')\|; \kappa) \quad (3)$$

where σ_ε is the standard deviation of $\boldsymbol{\varepsilon}$; $\mathbf{H}$ is the linear transformation representing anisotropy; $(s - s') = (x - x', y - y')$ is the difference in eastings and northings between sites *s* and *s'*; $\|\mathbf{H}(s - s')\|$ is the distance between sites after having accounted for anisotropy (Cressie and Wikle, 2015; Thorson *et al.*, 2015); and κ is the range parameter, which governs the distance over which covariance reaches 10% of its pointwise value (Thorson *et al.*, 2016). The Matérn distribution is a distribution that is commonly employed to characterize the statistical covariance between the measurements made at two distant sites (Minasny and McBratney, 2005). The Matérn covariance is stationary as used here, because it depends solely on distances between sites. It can be isotropic if distances are Euclidian distances, or follow geometric anisotropy as is the case here; geometric anisotropy is a condition where autocorrelation between locations varies with both distance and direction.

We estimated the fixed effect of year through maximum marginal likelihood while integrating across the random effects of gear and $\boldsymbol{\varepsilon}$; maximum marginal likelihood was

approximated via the Laplace approximation implemented in the Template Model Builder (Kristensen *et al.*, 2016). Firstly, the probability of the random effects was approximated through the use of the stochastic partial differential equation approximation (*Lindgren et al.*, 2011) for Gaussian Markov random fields with anisotropy described in Thorson *et al.* (2015). Secondly, the marginal likelihood was maximized through conventional non-linear optimization in R (R Core Development Team, 2013).

To evaluate GLMM fits, we calculated Pearson residuals for the samples considered for each functional group/life stage, as described in Supplementary Appendix S3.

Production of distribution maps and analyses

We produced probability of encounter maps for the U.S. GOM for younger juveniles of red snapper, red grouper and gag and the other functional groups and life stages represented in the OSMOSE-WFS ecosystem model, using the fitted spatio-temporal binomial GLMMs. To produce these maps, we first defined prediction grids for each of the functional groups/life stages. To do so, we constructed a spatial grid covering the whole U.S. GOM (Figure 4a). Then, we generated prediction grids for each of the functional groups/life stages, based on the ranges of bottom depth, latitude and longitude at which the functional groups/life stages are encountered by surveys (Figures 4b-d and Supplementary Figure S4). To determine the bottom depth at which the different functional groups/life stages are encountered by surveys, we constructed a raster of bottom depth with a resolution of 0.18° from the SRTM30 PLUS global bathymetry grid, which we obtained from the Gulf of Mexico Coastal Observing System (http://gcoos.tamu.edu/). The way we defined prediction grids for the functional groups and life stages represented in OSMOSE-WFS is reasonable, because the survey data that we used to fit spatio-temporal binomial

GLMMs for all these functional groups/life stages - except younger juvenile gag - cover the whole U.S. GOM (Supplementary Figure S5). Based on the criteria established above, only three fisheries-independent surveys conducted on the West Florida Shelf (FLBAY, FLHAUL, and FLTRAWL; Table 2) provided a reasonable amount of encounter/non-encounter data for younger juvenile gag; the data provided by the three surveys cover the eight regions of the West Florida Shelf where younger juvenile gag is consistently found according to Ingram *et al.* (2013) (Supplementary Figure S5).

To produce the probability of encounter maps for the U.S. GOM for the different functional groups/life stages, we assumed that the Gaussian Markov random field in each cell of a prediction grid is equal to the value of the random field at the nearest knot. First, for each of the functional groups/life stages, we constructed a probability of encounter map for each sampling year, using the fitted spatio-temporal binomial GLMM for that functional group/life stage. Then, we averaged the probability of encounter maps for each individual sampling year to obtain one long-term probability of encounter map for each functional group/life stage.

We used the long-term probability of encounter maps for the U.S. GOM for the different functional groups/life stages to generate distribution maps for the OSMOSE-WFS ecosystem model (Figure 2a). Since the prediction grids and the OSMOSE-WFS model have the same spatial resolution (0.18°), we did not need to average the probabilities of encounter predicted for the whole U.S. GOM according to OSMOSE-WFS grid cells. However, we rescaled probabilities so that their sum across OSMOSE-WFS grid cells is 1.0 (hereafter referred to as “probabilities of presence”); we needed to do this so that our distribution maps are useable in OSMOSE.

Below, we report the production and evaluation of distribution maps for the functional groups and life stages represented in OSMOSE-WFS, with a focus on younger

juveniles of red snapper, red grouper and gag. Moreover, we estimate the mean bottom depth at which younger juveniles of red snapper, red grouper and gag are encountered from their long-term probability of encounter maps for the U.S. GOM and the map of bottom depth (weighted average). Finally, we estimate the percentages of spatial overlap between younger juveniles of red snapper, red grouper and gag and the older juvenile and adult stages of red grouper and gag in the region covered by the OSMOSE-WFS model. The percentage of spatial overlap between younger juvenile stage *i* and older juvenile or adult stage *j* ($SO_{i,j}$) is evaluated as (Drapeau *et al.*, 2004; Brodeur *et al.*, 2008):

$$SO_{i,j} = \frac{N_{i,j}}{N_i}.100 \quad (4)$$

where $N_{i,j}$ is the number of cells of the OSMOSE-WFS model that are hotspots of both stages *i* and *j*; and N_i is the number of cells of the OSMOSE-WFS model that are hotspots of stage *i*; here, the hotspots of a given stage *s* are the cells of the OSMOSE-WFS model where the probability of presence of stage *s* is equal to or greater than the mean probability of presence of stage *s* over the entire spatial domain of OSMOSE-WFS (Brodeur *et al.*, 2008, 2014). The *SO* metric describes how older and adult grouper stages are distributed spatially in relation to younger juveniles of red snapper, red grouper and gag; it serves as a proxy of the exposure of younger juvenile fish to older juvenile and adult grouper stages, which represent potential predators of younger juvenile fish in OSMOSE-WFS (*Grüss et al.*, 2016b, 2016c).We evaluate the *SO* metric to revisit a contentious result obtained with the latest published versions of OSMOSE-WFS; the latest versions of OSMOSE-WFS predicted younger juvenile red snapper to be preyed upon by older juveniles and adults of red grouper and gag, which is something that is not reported in the literature (Grüss *et al.*, 2016b, 2016c).

Results

383 ***Compilation of a comprehensive survey database for the GOM***

384 The datasets and sampling years included in the comprehensive survey database for
385 the GOM varied greatly from one functional group/life stage to another (Supplementary
386 Table S2). We were able to follow the criteria established in the Material and methods for
387 all functional groups and life stages, except younger juvenile red grouper. In the case of
388 younger juvenile red grouper, encounters were so scarce that we retained two research
389 survey datasets with fewer than 50 encounters (Table 3). We were able to compile data to
390 generate nearly all the distribution maps that should ideally be produced according to our
391 literature review reported in Supplementary Table S2 (e.g., three maps for red grouper,
392 since the species undertake two ontogenetic migrations during its life cycle, one at age 1
393 and the other at age 3; Saul *et al.*, 2012; Carruthers *et al.*, 2015). However, due to data
394 availability, we were unable to compile data to generate seasonal distribution maps for
395 juveniles and adults of king mackerel (*Scomberomorus cavalla*) or annual maps for
396 juveniles and adults of reef omnivores. Moreover, since the OSMOSE-WFS ecosystem
397 model is not sex-structured, we did not compile data for males and females of adult gag
398 and large crabs, but rather for the entire populations of adult gag and large crabs. Finally,
399 due to a dearth of data for meiofauna and small infauna, we were unable to compile data to
400 generate distribution maps for these two LTL benthic functional groups. The only research
401 survey that encountered meiofauna and small infauna was the DGOMB fisheries-
402 independent survey, which has a low spatio-temporal resolution and was therefore gauged
403 to be of low quality for the purpose of this study (Table 2). Following Okey and
404 Mahmoudi (2002), we assumed that the spatial distributions of meiofauna and small
405 infauna are identical to that of small mobile epifauna (Supplementary Table S2).

406 Younger juvenile red snapper was encountered both in the eastern GOM (i.e., on
407 the West Florida Shelf) and in the western GOM (Table 3). For younger juvenile red

snapper, one observer program (OBSSHRIMP: 12,270 encounters) and three fisheries-independent surveys (SMALLPEL: 166 encounters; TRAWL: 4,144; TXTRAWL: 1,480) were retained for the comprehensive survey database. In these four datasets, the percentage of younger juvenile red snappers encountered in the eastern GOM varied between 0 (TXTRAWL) and 7.9% (OBSSHRIMP).

In the case of younger juvenile red grouper, a total of three fisheries-independent survey datasets were retained for the comprehensive survey database: FLTRAWL (59 encounters), TRAWL (44), and FLHAUL (29) (Table 3). The three surveys encountered younger juvenile red grouper on the West Florida Shelf only.

Younger juvenile gag was more frequently encountered than younger juvenile red grouper (Table 3). For younger juvenile gag, three fisheries-independent surveys conducted in West Florida waters were retained for the comprehensive survey database: FLHAUL (532 encounters), FLTRAWL (348), and FLBAY (87).

Statistical modelling

For all the functional groups/life stages, we found that none of the parameters H, κ and σ_ε hit an upper or lower bound, that the absolute value of the final gradient for each of these parameters was smaller than 0.002, and that the Hessian matrix was positive definite (Supplementary Table S6). Thus, there was no evidence of non-convergence for any of the functional groups and life stages.

For all the functional groups and life stages, observed encounter frequencies for either low or high probability samples were usually within or extremely close to the 95% confidence interval for predicted probability of encounter (Supplementary Figure S7). However, in the cases of older juvenile red snapper and the sardine-herring-scad complex in spring-summer, observed encounter frequency for the highest probability samples

tended to be noticeably smaller than the 95% confidence interval for predicted probability of encounter (Supplementary Figure S7). Yet, the GLMMs for these two groups did not systematically over- or underestimate probability of encounter in any area of the U.S. GOM (Supplementary Figure S8).

Distribution maps

The spatio-temporal binomial GLMM of younger juvenile red snapper predicted the life stage to be encountered all over the GOM, primarily at bottom depths ranging from 20 to 60 m (43 m on average; Figure 5a). We found the probability of encounter of younger juvenile red snapper to be much higher in the western than in the eastern GOM. In the eastern GOM, the probability of encounter of the life stage is highest near the Florida Keys and Dry Tortugas. In the western GOM, hotspots of probability of encounter for the life stage include the mid-shelf zone offshore Alabama and the Texas continental shelf.

Younger juvenile red grouper is encountered from Apalachicola, Florida, to the southern West Florida Shelf, at 24 m water depth on average (Figure 5b). Its probability of encounter is highest in the southern part of the Apalachee Bay, as well as from Sarasota, Florida, to the southern West Florida Shelf, in waters shallower than 40 m.

The spatio-temporal binomial GLMM of younger juvenile gag predicted the life stage to be encountered in all of the eight regions of the West Florida Shelf where the life stage has been consistently found over the recent years (Ingram *et al.*, 2013) (Figure 6). We found that younger juvenile gag is encountered at a bottom depth of 8 m on average. The probability of encounter of the life stage is highest in Tampa Bay (Figure 6b). It is also relatively high in St. Andrew Bay and Sarasota Bay, while it is lowest in St. Joe Bay and Cedar Key.

457 The distribution maps that we produced from GLMM predictions for the functional
458 groups and life stages represented in OSMOSE-WFS - including younger juveniles of red
459 snapper, red grouper and gag – are shown in Figure 7. These distribution maps allowed us
460 to evaluate percentages of spatial overlap (*SO*'s) between younger juveniles of red snapper,
461 red grouper and gag and the older juvenile and adult stages of red grouper and gag (Table
462 4). We found that younger juvenile red grouper is the stage most exposed to older juvenile
463 red grouper (*SO* = 78%), followed by younger juvenile gag (42%) and younger juvenile
464 red snapper (36%). The spatial distribution of adult red grouper strongly overlaps with
465 those of younger juvenile red grouper (*SO* = 81%) and younger juvenile red snapper (*SO* =
466 70%). Younger juvenile gag is the stage most exposed to older juvenile gag (*SO* = 72%),
467 followed by younger juvenile red snapper (21%) and younger juvenile red grouper (19%).
468 Finally, younger juvenile red snapper is the stage most exposed to adult gag (*SO* = 26%),
469 followed by younger juvenile gag (14%) and younger juvenile red grouper (8%).
470
471 **Discussion**
472 In this study, we applied the framework proposed in Grüss *et al.* (2016a) to
473 construct a database blending all of the encounter/non-encounter data of the GOM
474 collected by the fisheries-independent surveys and fisheries-dependent observer programs
475 using random sampling schemes (i.e., a "comprehensive survey database" for the GOM),
476 and to produce distribution maps for younger juveniles of red snapper, red grouper and gag
477 and the other functional groups and life stages represented in the OSMOSE-WFS
478 ecosystem model. The spatio-temporal binomial GLMMs that we fit in the present study
479 allowed us to generate maps for nearly all the functional groups and life stages represented
480 in OSMOSE-WFS, except four LTL functional groups (phytoplankton, zooplankton,
481 meiofauna, and small infauna). The probabilities of encounter predicted by all spatio-

482 temporal binomial GLMMs were demonstrated to be reasonable (Supplementary Figures
483 S7 and S8). In particular, model fits for adult gag were greatly improved in this study
484 compared to a previous study applying Grüss *et al.* (2016a)'s framework (Grüss *et al.*,
485 2017b); in Grüss *et al.* (2017b), adult gag observed frequency of encounter for the highest
486 probability samples was considerably smaller than the 95% confidence interval for
487 predicted probability of encounter, which was not the case in the present study. This result
488 stems from the consideration of additional survey datasets in the present study.
489 The compilation of a comprehensive survey database for the GOM allowed us to fit
490 spatio-temporal binomial GLMMs to then produce distribution maps for younger juveniles
491 of red snapper, red grouper and gag for the CMS biophysical model, as well as distribution
492 maps for almost all the functional groups and life stages represented in the OSMOSE-WFS
493 ecosystem model. Without the comprehensive survey database, it would have been
494 impossible to generate distribution maps for some of these functional groups and life
495 stages, particularly the younger juveniles of red grouper and gag. The functional groups for
496 which we were unable to produce distribution maps using the comprehensive survey
497 database included two LTL benthic functional groups, meiofauna and small infauna, which
498 were both encountered only by the DGOMB survey in the GOM; DGOMB is a fisheries-
499 independent survey that collected data at a limited number of sites during the summer
500 months of the period 2000-2002 in the offshore areas of the GOM only (Rowe and
501 Kennicutt, 2009). Here, we assumed that the spatial distributions of meiofauna and small
502 infauna are identical to that of small mobile epifauna, based on Okey and Mahmoudi
503 (2002). In the previous versions of the OSMOSE-WFS model (Grüss *et al.*, 2015, 2016b,
504 2016c), since we had no data for meiofauna, small infauna and small mobile epifauna, we
505 assumed a uniform spatial distribution for the three LTL functional groups. We
506 recommend the initiation of new research surveys targeting small benthic organisms in

both the inshore and offshore areas of the GOM, so as to collect encounter/non-encounter data for meiofauna, small infauna and similar animals and fill in current gaps in the comprehensive survey database. More generally, the comprehensive survey database should be viewed as a dynamic platform, which should be regularly updated as new data are collected by the research surveys of the GOM that use random sampling schemes (Grüss *et al.*, 2016a). The functional groups for which we were unable to produce distribution maps using the comprehensive survey database also included phytoplankton and zooplankton. For those, no research survey data can be employed to fit statistical models and then generate distribution maps. To generate monthly distribution maps for phytoplankton and zooplankton, we used, respectively, SeaWiFS (Sea-viewing Wide Field-of-view Sensor) chlorophyll a concentration data (http://oceancolor.gsfc.nasa.gov/SeaWiFS/) and zooplankton biomass estimates from the SEAPODYM ocean model (Lehodey *et al.*, 2010) (Supplementary Appendix S9).

The spatio-temporal binomial GLMMs that we fitted for the functional groups and life stages represented in OSMOSE-WFS yielded reasonable predictions (Supplementary Figures S7 and S8). Yet, we found that observed encounter frequency for the highest probability samples tended to be noticeably smaller than the 95% confidence interval for predicted encounter probability in the cases of older juvenile red snapper and the sardine-herring-scad complex in spring-summer (Supplementary Figure S7). We did not integrate environmental covariates in spatio-temporal binomial GLMMs in the present study, because previous unpublished and published work (e.g., Drexler and Ainsworth, 2013; Farmer and Karnauskas, 2013; Grüss *et al.*, 2014a) suggests that non-geospatial statistical models that integrate environmental covariates result in substantial, unmodelled spatial patterns in residuals for fish and invertebrates of the GOM. However, we suspect that integrating environmental covariates in the spatio-temporal binomial GLMM of some

functional groups/life stages (e.g., natural and artificial physical habitats and vertical relief in the case of older juvenile red snapper; Szedlmayer and Lee, 2004; Wells, 2007; Gallaway *et al*., 2009) may improve model fits. Therefore, we recommend future studies to explore this issue.

The results obtained for younger juveniles of red snapper, red grouper and gag in this study concur with the literature, provide additional insights into the spatial distribution patterns of these life stages, and highlight important future research avenues (Box 1). Importantly, producing distribution maps for younger juveniles of red snapper, red grouper and gag, as well as for the older juvenile and adult stages of the three species, allowed us to revisit a contentious result obtained with the latest published versions of the OSMOSE-WFS model (Grüss *et al.*, 2016b, 2016c). As explained earlier, in OSMOSE, diet compositions are not determined a *priori*, but rather emerges from model simulations, and predation is controlled by spatial distributions, predator/prey size ratios and the accessibility of prey to predators (Grüss *et al.*, 2016b; Fu *et al.*, 2017). In Grüss *et al.* (2016b, 2016c), due to the predator/prey size ratios (estimated from the literature), accessibility coefficients (determined from expert opinion) and distribution maps (constructed in Grüss *et al.* (2014b)) fed into OSMOSE-WFS, older juveniles and adults of red grouper and gag were predicted to prey upon younger juvenile red snapper. Such predation events are, however, not reported in the empirical literature. Because the distribution maps generated in Grüss *et al.* (2014b) are uncertain for a number of reasons listed in the Introduction, the predictions made in Grüss et al. (2016b, 2016c) that younger juvenile red snapper is preyed upon by older juveniles of adults of red grouper and gag were surprizing. The robust GLMMs fitted to the comprehensive survey database for the GOM in this study predict that: (1) the spatial distributions of younger juvenile red snapper and adult red grouper strongly overlap; (2) younger juvenile red snapper is more exposed

557 to adult gag than younger juveniles of red grouper and gag, which are both prey items of
558 adult gag according to the literature (Grüss *et al.*, 2016b, 2016c); and (3) the percentages of
559 spatial overlap between younger juvenile red snapper and older juveniles of red grouper
560 and gag are relatively small but non-negligible. Therefore, the present study shows that it is
561 reasonable to hypothesize that older juveniles and adults of red grouper and gag prey upon
562 younger juveniles of red snapper. To investigate this hypothesis further, future diet surveys
563 should collect additional stomachs for older juveniles and adults of red grouper and gag.
564 Such surveys should ideally be conducted using spearfishing rather than the gears
565 classically used to sample groupers in the GOM (e.g., longline), which result in stomachs
566 being everted when fish ascend from the depths. Moreover, because the fish ingested by
567 groupers are often unidentifiable, even to the family level, advanced DNA
568 (deoxyribonucleic acid) barcoding techniques should be used to identify precisely the
569 different fish prey of older juveniles and adults of red grouper and gag (Dahl *et al.*, 2017).
570 The framework employed in the present study is valuable for producing distribution
571 maps and functional relationships for different types of spatially-explicit ecosystem models
572 (Grüss *et al.*, 2016a), as well as for parameterizing biophysical models used to inform
573 EBFM. The spatio-temporal binomial GLMM approach used in this study can be
574 employed to generate distribution maps for any spatially-explicit ecosystem model whose
575 entire spatial domain is sampled by the research surveys included in the comprehensive
576 survey database (Grüss *et al.*, 2016a). Geospatial statistical models cannot be used to
577 construct accurate distribution maps for spatially-explicit ecosystem models whose entire
578 spatial domain is not sampled by the surveys included in the comprehensive survey
579 database (e.g., spatially-explicit ecosystem models for the entire GOM Large Marine
580 Ecosystem); for such spatially-explicit ecosystem models, it is necessary to extrapolate the
581 spatial distributions of marine organisms to unsampled areas. Binomial GAMs

582 characterized by a few covariates and smooth relationships between environmental
583 parameters and functional groups/life stages are appropriate for such spatially-explicit
584 ecosystem models (Drexler and Ainsworth, 2013; Mannocci *et al.*, 2017). The widely-used
585 Ecospace modelling platform does not employ distribution maps to allocate the biomasses
586 of modelled functional groups/life stages over space, but rather a "habitat capacity model",
587 which defines the spatial distribution of species dynamically based on relationships
588 between abiotic environmental variables and functional groups/life stages (Christensen *et*
589 *al.*, 2014). The habitat capacity model of Ecospace applications of the GOM can be
590 parameterized using functional relationships established by fitting binomial GAMs to the
591 comprehensive survey database (Grüss *et al.*, 2016a). The framework applied in this study
592 is also useful to parameterize biophysical models designed to predict annual recruitment
593 anomalies due to oceanographic factors for assessed species, such as the CMS (Karnauskas
594 *et al.*, 2013a, 2013b; Grüss *et al.*, 2014b). In the present study, we focused on the
595 production of distribution maps for younger juvenile fish for defining larval settlement
596 areas in biophysical models. The framework applied in this study can also be employed to
597 generate maps of egg production from distribution maps for adult life stages, under the
598 assumption that egg production is proportional to the probability of encounter of adult fish
599 (Grüss *et al.*, 2014b).
600
601 **Supplementary data**
602 Supplementary material is available at the *ICESJMS* online version of the manuscript.
603
604 **Acknowledgments**
605 This work was funded in part by the Florida RESTORE Act Centers of Excellence
606 Research Grants Program, Subagreement No. 2015-01-UM-522, and the National Oceanic

607 and Atmospheric Administration's RESTORE Act Science Program under award
608 NA15NOS4510233 to the University of Miami. This manuscript has cleared an internal
609 review at the NOAA Northwest Fisheries Science Center. We are grateful to Isaac Kaplan,
610 the NOAA internal reviewer, as well as to the Editor and two anonymous reviewers, whose
611 comments have improved the quality of the present manuscript. We would like to thank
612 Walt Ingram for having provided us with shapefiles for the eight regions of the West
613 Florida Shelf where younger juvenile gag has been consistently found over the recent
614 years. We are grateful to the following people for having provided us with data for the
615 comprehensive survey database for the Gulf of Mexico: Adam G. Pollack, Alisha Gray,
616 April Cook, Beverly Sauls, Brandi Noble, Chris Gardner, Christy Pattengill-Semmens,
617 Doug DeVries, Elizabeth Scott-Denton, Evan John Anderson, Fernando Martinez-Andrade,
618 Gilbert Rowe, Jeff Rester, Jill Hendon, John Carlson, John Mareska, Kelly Fitzpatrick,
619 Kenneth Brennan, Lawrence Beerkircher, Matthew A. Nuttall, Matthew D. Campbell,
620 Mike Brainard, Mike Harden, Nicole Smith, Rick Burris, Steve Turner, Theodore S.
621 Switzer, Tim MacDonald, and Tracey T. Sutton. The PCTRAP, PCVIDEO, GULFSPAN,
622 OBSLL, OBSVL, OBSSHRIMP, OBSGILL, SBLOP and POP data products were
623 produced without the involvement of NOAA Fisheries staff, and NOAA Fisheries cannot
624 vouch for the validity of these products. The TRAWL and INBLL data were produced
625 without the involvement of SEAMAP partners. Therefore, SEAMAP and its partners
626 cannot vouch for the validity of these products. The FLBAY, FLHAUL, FLOBS,
627 FLPURSE, FLTRAP, FLTRAWL and FLVIDEO data products were produced without the
628 involvement of FWC – FWRI staff, and FWC – FWRI cannot vouch for the validity of
629 these products. The ALGILL data products were produced without the involvement of
630 AMRD staff, and AMRD cannot vouch for the validity of these products; a portion of the
631 provided data was funded through a Fish and Wildlife Service Sport Fish Restoration

Program grant. The MSGILL and MSHAND data products were produced without the involvement of USM GCRL staff, and USM GCRL staff cannot vouch for the validity of these products; the collection of MSGILL data was funded through a collaboration with the Mississippi Department of Marine Resources by a U.S. Fish and Wildlife Service Sport Fish Restoration Program grant. The LAVL data products were produced without the involvement of LDWF staff and, therefore, LDWF cannot vouch for the validity of these products. Many thanks to Patrick Lehodey, Beatriz Calmettes, Chris Koenig, Gary Fitzhugh, Matt Love, Michael Drexler, Skyler R. Sagarese, John F. Walter III, Mary Christman, and David Gloeckner for having provided help or advice at different levels of this study.

References

Austin, M. 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. Ecological modelling, 200: 1–19.

Brodeur, R. D., Suchman, C. L., Reese, D. C., Miller, T. W., and Daly, E. A. 2008. Spatial overlap and trophic interactions between pelagic fish and large jellyfish in the northern California Current. Marine Biology, 154: 649–659.

Brodeur, R. D., Barceló, C., Robinson, K. L., Daly, E. A., and Ruzicka, J. J. 2014. Spatial overlap between forage fishes and the large medusa *Chrysaora fuscescens* in the northern California Current region. Marine Ecology Progress Series, 510: 167–181.

Bullock, L. H., and Smith, G. B. 1991. Seabasses (Pisces: Serranidae). Memoirs of the Hourglass Cruises VIII (II) Florida Marine Research Institute. Department of Natural Resources, St. Petersburg, Florida, USA.

Carruthers, T. R., Walter, J. F., McAllister, M. K., Bryan, M. D., and Wilberg, M. 2015. Modelling age-dependent movement: an application to red and gag groupers in the Gulf of Mexico. Canadian Journal of Fisheries and Aquatic Sciences, 72: 1159–1176.

Casey, J. P., Poulakis, G. R., and Stevens, P. W. 2007. Habitat use by juvenile gag, *Mycteroperca microlepis* (Pisces: Serranidae), in subtropical Charlotte Harbor, Florida (USA). Gulf and Caribbean Research, 19: 1–9.

Chagaris, D. D. 2013. Ecosystem-based evaluation of fishery policies and tradeoffs on the West Florida Shelf. PhD thesis, University of Florida, Gainesville, Florida.

Christensen, V., Coll, M., Steenbeek, J., Buszowski, J., Chagaris, D., and Walters, C. J. 2014. Representing variable habitat quality in a spatial food web model. Ecosystems, 17: 1397–1412.

Coleman, F. C., Koenig, C. C., Scanlon, K. M., Heppell, S., Heppell, S., and Miller, M. W. 2010. Benthic habitat modification through excavation by red grouper, *Epinephelus morio*, in the northeastern Gulf of Mexico. The Open Fish Science Journal, 3.

Coleman, F. C., Scanlon, K. M., and Koenig, C. C. 2011. Groupers on the edge: shelf edge spawning habitat in and around marine reserves of the northeastern Gulf of Mexico. The Professional Geographer, 63: 456–474.

Cressie, N., Wikle, C.K., 2015. Statistics for spatio-temporal data. John Wiley & Sons, Hoboken, NJ.

Dahl, K. A., Patterson, W. F., Robertson, A., and Ortmann, A. C. 2017. DNA barcoding significantly improves resolution of invasive lionfish diet in the Northern Gulf of Mexico. Biological Invasions, doi: 10.1007/s10530-017-1407-3.

Drapeau, L., Pecquerie, L., Fréon, P., and Shannon, L. J. 2004. Quantification and representation of potential spatial interactions in the southern Benguela ecosystem. African Journal of Marine Science, 26: 141–159.

Drexler, M., and Ainsworth, C. H. 2013. Generalized additive models used to predict species abundance in the Gulf of Mexico: an ecosystem modeling tool. PLoS ONE, 8: e64458.

Farmer, N. A., and Karnauskas, M. 2013. Spatial distribution and conservation of speckled hind and warsaw grouper in the Atlantic Ocean off the southeastern US. PloS One., 8: e78682.

Fitzhugh, G. R., Koenig, C. C., Coleman, F. C., Grimes, C. B., and Sturges, W. 2005. Spatial and temporal patterns in fertilization and settlement of young gag (*Mycteroperca microlepis*) along the West Florida Shelf. Bulletin of Marine Science, 77: 377–396.

Froese, R., and Pauly, D. 2015. A Global Information System on Fishes, Fishbase, http://www.fishbase.org.

Fu, C., Olsen, N., Taylor, N., Grüss, A., Batten, S., Liu, H., Verley, P., *et al.* 2017. Spatial and temporal dynamics of predator-prey species interactions off western Canada. ICES Journal of Marine Science, doi: 10.1093/icesjms/fsx056.

Fulton, E. A., Parslow, J. S., Smith, A. D., and Johnson, C. R. 2004. Biogeochemical marine ecosystem models II: the effect of physiological detail on model performance. Ecological Modelling, 173: 371–406.

Fulton, E. A., Link, J. S., Kaplan, I. C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., *et al.* 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish and Fisheries, 12: 171–188.

Gallaway, B. J., Cole, J. G., Meyer, R., and Roscigno, P. 1999. Delineation of essential habitat for juvenile red snapper in the northwestern Gulf of Mexico. Transactions of the American Fisheries Society, 128: 713–726.

Gallaway, B. J., Szedlmayer, S. T., and Gazey, W. J. 2009. A life history review for red snapper in the Gulf of Mexico with an evaluation of the importance of offshore petroleum platforms and other artificial reefs. Reviews in Fisheries Science, 17: 48–67.

Grüss, A., Karnauskas, M., Sagarese, S. R., Paris, C. B., Zapfe, G., Walter III, J. F., Ingram, W., *et al.* 2014a. Use of the Connectivity Modeling System to estimate the larval dispersal, settlement patterns and annual recruitment anomalies due to oceanographic factors of red grouper (*Epinephelus morio*) on the West Florida Shelf. SEDAR42-DW-03, SEDAR, North Charleston, SC. 24 pp.

Grüss, A., Drexler, M., and Ainsworth, C. H. 2014b. Using delta generalized additive models to produce distribution maps for spatially explicit ecosystem models. Fisheries Research, 159: 11–24.

Grüss, A., Schirripa, M. J., Chagaris, D., Drexler, M., Simons, J., Verley, P., Shin, Y.-J., *et al.* 2015. Evaluation of the trophic structure of the West Florida Shelf in the 2000s using the ecosystem model OSMOSE. Journal of Marine Systems, 144: 30–47.

Grüss, A., Babcock, E. A., Sagarese, S. R., Drexler, M., Chagaris, D. D., Ainsworth, C. H., Penta, B., *et al.* 2016a. Improving the spatial allocation of functional group biomasses in spatially-explicit ecosystem models: insights from three Gulf of Mexico models. Bulletin of Marine Science, 92: 473–496.

Grüss, A., Schirripa, M. J., Chagaris, D., Velez, L., Shin, Y.-J., Verley, P., Oliveros-Ramos, R., *et al.* 2016b. Estimating natural mortality rates and simulating fishing scenarios for Gulf of Mexico red grouper (*Epinephelus morio*) using the ecosystem model OSMOSE-WFS. Journal of Marine Systems, 154: 264–279.

Grüss, A., Harford, W. J., Schirripa, M. J., Velez, L., Sagarese, S. R., Shin, Y.-J., and Verley, P. 2016c. Management strategy evaluation using the individual-based, multispecies modeling approach OSMOSE. Ecological Modelling, 340: 86–105.

Grüss, A., Rose, K. A., Simons, J., Ainsworth, C. H., Babcock, E. A., Chagaris, D. D., De Mutsert, K., et al. 2017a. Recommendations on the use of ecosystem modeling for informing ecosystem-based fisheries management and restoration outcomes in the Gulf of Mexico. Marine and Coastal Fisheries, doi: 10.1080/19425120.2017.1330786.

Grüss, A., Thorson, J. T., Sagarese, S. R., Babcock, E. A., Karnauskas, M., Walter, J. F., and Drexler, M. 2017b. Ontogenetic spatial distributions of red grouper (*Epinephelus morio*) and gag grouper (*Mycteroperca microlepis*) in the US Gulf of Mexico. Fisheries Research, 193: 129–142.

Halouani, G., Lasram, F. B. R., Shin, Y.-J., Velez, L., Verley, P., Hattab, T., Oliveros-Ramos, R., *et al.* 2016. Modelling food web structure using an end-to-end approach in the coastal ecosystem of the Gulf of Gabes (Tunisia). Ecological Modelling, 339: 45–57.

Harvey, C. J., Kelble, C. R., and Schwing, F. B. 2017. Implementing "the IEA": using integrated ecosystem assessment frameworks, programs, and applications in support of operationalizing ecosystem-based management. ICES Journal of Marine Science, 74: 398–405.

Hastings, R. W. 1979. The origin and seasonality of the fish fauna on a new jetty in the northeastern Gulf of Mexico. Bulletin of the Florida State Museum, Biological Science, 24: 1–22.

Ingram, G. W., Pollack, A., and McEachron, L. 2013. Summary of fishery-independent surveys of juvenile gag grouper in the Gulf of Mexico. SEDAR33-AW06. SEDAR, North Charleston, SC. 20 pp.

Johnson, D. R., Perry, H. M., and Lyczkowski-Shultz, J. 2013. Connections between Campeche Bank and red snapper populations in the Gulf of Mexico via modeled larval transport. Transactions of the American Fisheries Society, 142: 50–58.

Karnauskas, M., Walter, J. F., and Paris, C. B. 2013a. Use of the Connectivity Modeling System to estimate movements of red snapper (*Lutjanus campechanus*) recruits in the northern Gulf of Mexico. SEDAR31-AW10. SEDAR, North Charleston, SC, 20 pp.

Karnauskas, M., Zapfe, G., Grüss, A., Walter III, J. F., and Schirripa, M. J. 2013b. Use of the Connectivity Modeling System to estimate movements of gag grouper (*Mycteroperca microlepis*) recruits in the northern Gulf of Mexico.SEDAR33-DW18. SEDAR, North Charleston, SC 12 pp.

Koenig, C. C., and Coleman, F. C. 1998. Absolute abundance and survival of juvenile gags in sea grass beds of the northeastern Gulf of Mexico. Transactions of the American Fisheries Society, 127: 44–55.

Koenig, C. C., and Coleman, F. C. 1999. Recruitment indices and seagrass habitat relationships of the early juvenile stages of gag, gray snapper, and other

economically important reef fishes in the eastern Gulf of Mexico. Final Report, MARFIN Award No. NA57FF0055.
Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., and Bell, B. 2016. TMB: automatic differentiation and Laplace approximation. Journal of Statistical Software, 70: 1–21.
Leathwick, J. R., Elith, J., and Hastie, T. 2006. Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. Ecological modelling, 199: 188–196.
Lehodey, P., Murtugudde, R., and Senina, I. 2010. Bridging the gap from ocean models to population dynamics of large marine predators: a model of mid-trophic functional groups. Progress in Oceanography, 84: 69–84.
Levin, P. S., Kelble, C. R., Shuford, R. L., Ainsworth, C., Dunsmore, R., Fogarty, M. J., Holsman, K., *et al.* 2014. Guidance for implementation of integrated ecosystem assessments: a US perspective. ICES Journal of Marine Science, 71: 1198–1204.
Lindgren, F., Rue, H. avard, and Lindström, J. 2011. An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach. Journal of the Royal Statistical Society: Series B (Statistical Methodology), 73: 423–498.
Mace, P. M., Bartoo, N. W., Hollowed, A. B., Kleiber, P., Methot, R. D., Murawski, S. A., Powers, J. E., et al. 2001. Marine fisheries stock assessment improvement plan. Report of the National Marine Fisheries Service. National Task Force for Improving Fish Stock Assessments, US Department of Commerce and NOAA, 68 pp.
Mannocci, L., Roberts, J.J., Miller, D.L., Halpin, P.N., 2017. Extrapolating cetacean densities to quantitatively assess human impacts on populations in the high seas. Conservation Biology, 31: 601-614.
Minasny, B., and McBratney, A. B. 2005. The Matérn function as a general model for soil variograms. Geoderma, 128: 192–207.
Moe, M. A. 1969. Biology of the red grouper *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. Florida Department of Natural Resources Marine Research Laboratory Professional papers series, 10: 1–95.
Monk, M. H., Powers, J. E., and Brooks, E. N. 2015. Spatial patterns in species assemblages associated with the northwestern Gulf of Mexico shrimp trawl fishery. Marine Ecology Progress Series, 519: 1–12.
MSFCMA. 2007. Magnuson-Stevens Fishery Conservation and Management Act. U.S. Department of Commerce NOAA, National Marine Fisheries Service.
Mullaney Jr, M.D., 1994. Ontogenetic shifts in diet of gag, *Mycteroperca microlepis*,(Goode and Bean),(Pisces: Serranidae). Proceedings of the Gulf and Caribbean Fisheries Institute, 43: 432–445.
NOS. 2008. Gulf of Mexico at a Glance: U.S. National Ocean Service, Department of Commerce, National Oceanic and Atmospheric Administration. Washington, DC.
Okey, T. A., and Mahmoudi, B. 2002. An Ecosystem Model of the West Florida Shelf for use in Fisheries Management and Ecological Research: Volume II. Model Construction. Report of the Florida Marie Research Institute, St Petersburg, Florida, USA.
Palomares, M. L. D., and Pauly, D. 2015. SeaLifeBase. Available: http://http://www.sealifebase.org.
Paris, C. B., Helgers, J., Van Sebille, E., and Srinivasan, A. 2013. Connectivity Modeling System: A probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. Environmental Modelling & Software, 42: 47–54.

R Core Development Team. 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Rowe, G. T., and Kennicutt, M. C. 2009. Northern Gulf of Mexico continental slope habitats and benthic ecology study: Final report. OCS Study MMS 2009-039. 456 pp.

Samhouri, J. F., Haupt, A. J., Levin, P. S., Link, J. S., and Shuford, R. 2014. Lessons learned from developing integrated ecosystem assessments to inform marine ecosystem-based management in the USA. ICES Journal of Marine Science, 71: 1205–1215.

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. Transactions of the American Fisheries Society, 141: 1439–1452.

Shin, Y.-J., and Cury, P. 2001. Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. Aquatic Living Resources, 14: 65–80.

Shin, Y.-J., and Cury, P. 2004. Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. Canadian Journal of Fisheries and Aquatic Sciences, 61: 414–431.

Switzer, T. S., MacDonald, T. C., McMichael Jr, R. H., and Keenan, S. F. 2012. Recruitment of juvenile Gags in the eastern Gulf of Mexico and factors contributing to observed spatial and temporal patterns of estuarine occupancy. Transactions of the American Fisheries Society, 141: 707–719.

Switzer, T. S., Keenan, S. F., Stevens, P. W., McMichael Jr, R. H., and MacDonald, T. C. 2015. Incorporating Ecology into Survey Design: Monitoring the Recruitment of Age-0 Gags in the Eastern Gulf of Mexico. North American Journal of Fisheries Management, 35: 1132–1143.

Szedlmayer, S. T., and Conti, J. 1999. Nursery habitats, growth rates, and seasonality of age-0 red snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico. Fishery Bulletin, 97: 626–635.

Szedlmayer, S. T., and Lee, J. D. 2004. Diet shifts of juvenile red snapper (*Lutjanus campechanus*) with changes in habitat and fish size. Fishery Bulletin, 102: 366–375.

Szedlmayer, S. T., and Mudrak, P. A. 2014. Influence of age-1 conspecifics, sediment type, dissolved oxygen, and the Deepwater Horizon oil spill on recruitment of age-0 red snapper in the northeast Gulf of Mexico during 2010 and 2011. North American Journal of Fisheries Management, 34: 443–452.

Thorson, J. T., Shelton, A. O., Ward, E. J., and Skaug, H. J. 2015. Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for West Coast groundfishes. ICES Journal of Marine Science, 72: 1297–1310.

Thorson, J. T., Fonner, R., Haltuch, M. A., Ono, K., and Winker, H. 2016. Accounting for spatiotemporal variation and fisher targeting when estimating abundance from multispecies fishery data 1. Canadian Journal of Fisheries and Aquatic Sciences, 73: 1–14.

Wells, R. J. D. 2007. The effects of trawling and habitat use on red snapper and the associated community. Ph.D. thesis, Lousiana State University, Baton Rouge, Lousiana.

868 Workman, I., Shah, A., Foster, D., and Hataway, B. 2002. Habitat preferences and site
869 fidelity of juvenile red snapper (*Lutjanus campechanus*). ICES Journal of Marine
870 Science, 59: S43–S50.
871 http://gcoos.tamu.edu/
872 https://github.com/nwfsc-assess/geostatistical_delta-GLMM
873 http://oceancolor.gsfc.nasa.gov/SeaWiFS/

Tables

Table 1. Functional groups represented in the OSMOSE-WFS ecosystem model, including high trophic level (HTL) groups, whose entire life cycle is simulated in OSMOSE-WFS, and low trophic level (LTL) groups, whose biomass is used to force the model. Species of a given HTL group exhibit similar life history characteristics, body size ranges, diets and exploitation patterns. Some individual species constitute their own HTL group, as they are emblematic to the West Florida Shelf and of high economic importance. A reference species was identified for each of the HTL groups (indicated in bold).

Functional group	HTL or LTL group?	Species making up the functional group
King mackerel	HTL	**King mackerel (*Scomberomorus cavalla*)**
Amberjacks	HTL	**Greater amberjack (*Seriola dumerili*)**, banded rudderfish (*Seriola zonata*), lesser amberjack (*Seriola fasciata*), almaco jack (*Seriola rivoliana*)
Red grouper	HTL	**Red grouper (*Epinephelus morio*)**
Gag	HTL	**Gag (*Mycteroperca microlepis*)**
Red snapper	HTL	**Red snapper (*Lutjanus campechanus*)**
Sardine-herring-scad complex	HTL	**Scaled sardine (*Harengula jaguana*)**, Spanish sardine (*Sardinella aurita*), Atlantic thread herring (*Opisthonema oglinum*), round scad (*Decapterus punctatus*), menhaden (*Brevoortia* spp.)
Anchovies and silversides	HTL	**Bay anchovy (*Anchoa mitchilli*)**, striped anchovy (*Anchoa hepsetus*), silversides (Atherinidae spp.), alewife (*Alosa* spp.)
Coastal omnivores	HTL	**Pinfish (*Lagodon rhomboides*)**, spottail pinfish (*Diplodus holbrooki*), orange filefish (*Aluterus schoepfii*), fringed filefish (*Monacanthus ciliatus*), planehead filefish (*Monacanthus hispidus*), orangespotted filefish (*Cantherhines pullus*), honeycomb filefish (*Acanthostracion polygonius*), Atlantic spadefish (*Chaetodipterus faber*), scrawled cowfish (*Lactophrys quadricornis*), pufferfish (Tetraodontidae spp.)
Reef carnivores	HTL	**White grunt (*Haemulon plumieri*)**, black sea bass (*Centropristis striata*), rock sea bass (*Centropristis philadelphica*), belted sandfish (*Serranus subligarius*), longtail bass (*Hemanthias leptus*), butter hamlet (*Hypoplectus unicolor*), creole fish (*Paranthias furcifer*), splippery dick (*Halichoeres bivittatus*), painted wrasse (*Halichoeres caudalis*), yellowhead wrasse (*Halichoeres garnoti*), bluehead (*Thalassoma bifasciatum*), reef croaker (*Odontoscion dentex*), jackknife-fish (*Equetus lanceatus*), leopard toadfish (*Opsanus pardus*), scorpian fish (Scorpaenidae spp.), bigeyes (Priacanthidae spp.), littlehead porgy (*Calamus proridens*), jolthead porgy (*Calamus bajonado*), saucereye progy (*Calamus calamus*), whitebone progy (*Calamus leucosteus*), knobbed progy (*Calamus nodosus*), French grunt (*Haemulon flavolineatum*), Spanish grunt (*Haemulon macrostomum*), margate (*Haemulon album*), bluestriped grunt (*Haemulon sciurus*), striped grunt (*Haemulon striatum*), sailor's grunt (*Haemulon parra*), porkfish (*Anisotremus virginicus*), neon goby (*Gobiosoma oceanops*)
Reef omnivores	HTL	**Doctorfish (*Acanthurus chirurgus*)**, blue tang (*Acanthurus coeruleus*), blue angelfish (*Holacanthus bermudensis*), gray angelfish (*Pomacanthus arcuatus*), cherubfish (*Centropyge argi*), rock beauty (*Holacanthus tricolor*), cocoa damselfish (*Pomacentrus variabilis*), bicolor damselfish (*Pomacentrus partitus*), beau gregory (*Pomacentrus leocostictus*), yellowtail damselfish (*Microspathodon chrysurus*), seaweed blenny (*Parablennius marmoreus*), striped parrotfish (*Scarus croicensis*), bridled goby (*Coryphopterus glaucofraenum*), Bermuda chub (*Kyphossus sectarix*), combtooth blenny (*Chasmodes saburrae*), banded blenny (*Paraclinus fasciatus*), blenny (*Ophioblennius atlanticus*), barred blenny (*Hypleurochilus bermudensis*), sailfin blenny (*Emblemaria pandionis*), glass blenny (*Coralliozetus diaphanus*), saddled blenny (*Malacoctenus triangulatus*), hairy blenny (*Labrisomus nuchipinnis*), wrasse blenny (*Hemiemblemaria simulus*), twospot cardinalfish (*Apogon maculatus*), sponge cardinalfish (*Phaeoptyx xenus*), purple reeffish (*Chromis scotti*), yellowtail reeffish (*Chromis enchrysurus*), blue chromis (*Chromis cyanea*), jawfish (*Opistognathus aurifrons*), dusky jawfish (*Opistognathus whitehursti*), moustache jawfish (*Opistognathus lonchurus*), banded jawfish (*Opistognathus macrognathus*), jawfish (*Opistognathus nothus*), ocean surgeon (*Acanthurus bahianus*), banded butterfly (*Chaetodon striatus*), bank butterfly (*Chaetodon aya*), foureye butterfly (*Chaetodon*

		capristratus), longnose butterfly (*Chaetodon aculeatus*), reef butterfly (*Chaetodon sedentarius*), spotfin butterfly (*Chaetodon ocellatus*), French angel (*Pomacanthus paru*), queen angel (*Holacanthus ciliarus*), blue reef damsel (*Chromis cyaneus*), brown reef damsel (*Chromis multilineata*), orange damsel (*Pomacentrus planifrons*), scarletback damsel (*Pomacentrus fuscus*), sergeant major damsel (*Abudefduf saxatilis*), sunshine damsel (*Chromis insolatus*), longfin damselfish (*Pomacentrus diencaeus*), blue parrot (*Scarus coeruleus*), queen parrot (*Scarus vetula*), rainbow parrot (*Scarus guacamaia*), redband parrot (*Sparisoma aurofrenatum*), spotlight parrot (*Sparisoma viride*), midnight parrotfish (*Scarus coelestinus*), princess parrotfish (*Scarus taeniopterus*), Gulf surgeonfish (*Acanthurus randalli*), yellow chub (*Kyphosus incisor*), redtail parrotfish (*Sparisoma chrysopterum*), bucktooth parrotfish (*Sparisoma radians*), redfin parrotfish (*Sparisoma rubripinne*)
Shrimps	HTL	**Pink shrimp (*Farfantepenaeus duorarum*)**, white shrimp (*Litopenaeus setiferus*), mantis shrimp (*Squilla empusa*)
Large crabs	HTL	**Blue crab (*Callinectes sapidus*)**, stone crabs (*Menippe mercenaria* and *Menippe adina*), horseshoe crab (*Limulus polyphemus*), hermits crabs (*Pylopagurus operculatus* and *Clibanaris vittatus*), spider crab (*Stenocionops furcatus*), arrow crab (*Stenorynchus seticornis*)
Meiofauna	LTL	Harpacticoida spp., Kinorhyncha spp., Nematoda spp., Halacaridae spp., Nauplii spp., Cyclopoida spp., Gastrotricha spp., Acari spp., Tartigrada spp., Rotifera spp., Loricifera spp.
Small infauna	LTL	Aplacophora spp., Cumacea spp., Polychaeta spp.
Small mobile epifauna	LTL	Amphipoda spp., Isopoda spp., Mysidacea spp., Ostracoda spp., Tanaidacea spp., Turbellaria spp., Leptostraca spp., Cladocera spp.
Bivalves	LTL	Bivalvia spp.
Echinoderms and gastropods	LTL	Asteroida spp., Echinoidea spp., Gastropoda spp., Holothuroidea spp.
Zooplankton	LTL	Small phytoplankton, diatoms
Phytoplankton	LTL	Small copepods, large mesozooplankton

882

883 **Table 2.** Datasets included in the comprehensive survey database for the Gulf of Mexico
884 (GOM). Details about the datasets can be found in Supplementary Table S1.

Name of the survey	Alias	Fisheries-independent or fisheries-dependent survey?	Quality of the survey	Why considered to be of high or low quality?
Alabama Marine Resources Division (AMRD) Fisheries Assessment and Monitoring Program (FAMP) Gillnet Survey	ALGILL	Fisheries-independent	High quality	Has a high spatio-temporal resolution
National Marine Fisheries Service (NMFS) Bottom Longline Survey	BLL	Fisheries-independent	High quality	Has a high spatio-temporal resolution
Deep Pelagic Nekton Dynamics of the Gulf of Mexico (DEEPEND) Survey	DEEPEND	Fisheries-independent	Low quality	Has a low spatio-temporal resolution; the data available to us were collected at a limited number of sites over two months of two consecutive years (May and August) in the offshore areas of north-central GOM only
Northern GOM Continental Slope Habitats and Benthic Ecology Study (DGoMB) Survey	DGOMB	Fisheries-independent	Low quality	Has a low spatio-temporal resolution; collected data at a limited number of sites during the summer months of the period 2000-2002 in the offshore areas of the GOM only
NMFS Expanded Annual Stock Assessment (EASA) Survey – Longline	EASALL	Fisheries-independent	High quality	Has a high spatial resolution
NMFS EASA Survey – Vertical Line	EASAVL	Fisheries-independent	High quality	Has a high spatial resolution
Fish and Wildlife Research Institute (FWRI) Bay Seine Survey	FLBAY	Fisheries-independent	High quality	Has a high spatio-temporal resolution
FWRI Haul Seine Survey	FLHAUL	Fisheries-independent	High quality	Has a high spatio-temporal resolution
FWRI For-Hire At-Sea Observer Program	FLOBS	Fisheries-dependent	High quality	Has a high spatio-temporal resolution
FWRI Purse Seine Survey	FLPURSE	Fisheries-independent	High quality	Has a high spatio-temporal resolution
FWRI Reef Fish Trap Survey	FLTRAP	Fisheries-independent	High quality	Has a high spatio-temporal resolution
FWRI Trawl Survey	FLTRAWL	Fisheries-independent	High quality	Has a high spatio-temporal resolution
FWRI Reef Fish Video Survey	FLVIDEO	Fisheries-independent	High quality	Has a high spatio-temporal resolution
Gulf of Mexico Fisheries Information Network (GulfFIN) Head Boat Port Sampling Program	GULFFINPORT	Fisheries-dependent	Low quality	Has a high spatial resolution; however, the geographic coordinates associated with some of the GULFFINPORT data are located inland (due to fishers unwilling to share the geographic coordinates of their fishing locations)
NMFS Gulf of Mexico Shark Pupping and Nursery (GULFSPAN) Survey	GULFSPAN	Fisheries-independent	High quality	Has a high spatio-temporal resolution
Southeast Area Monitoring and Assessment Program (SEAMAP) Gulf of	INBLL	Fisheries-independent	High quality	Has a high spatio-temporal resolution

Mexico Inshore Bottom Longline Survey				
Louisiana Department of Wildlife and Fisheries (LDWF) Vertical Line Survey	LAVL	Fisheries-independent	High quality	Has a high spatio-temporal resolution
Mississippi Department of Marine Resources (MDMR) Sport Fish Shark Gillnet Survey	MSGILL	Fisheries-independent	Low quality	Has a high spatio-temporal resolution; however, teleosts were documented by number caught in each panel in later years only
MDMR Sport Fish Shark Handline Survey	MSHAND	Fisheries-independent	High quality	Has a high spatio-temporal resolution
MDMR Fisheries Assessment and Monitoring (FAM) Trawl Survey	MSTRAWL	Fisheries-independent	High quality	Has a high spatio-temporal resolution
NMFS Southeast Gillnet Observer Program	OBSGILL	Fisheries-dependent	Low quality	Has a high spatio-temporal resolution; however, some of the OBSGILL data were collected in very close proximity (using different panels of the same gear)
Reef Fish Bottom Longline Observer Program	OBSLL	Fisheries-dependent	High quality	Has a high spatio-temporal resolution
Southeastern Shrimp Fisheries Observer Coverage Program	OBSSHRIMP	Fisheries-dependent	High quality	Has a high spatio-temporal resolution
Reef Fish Vertical Line Observer Program	OBSVL	Fisheries-dependent	High quality	Has a high spatio-temporal resolution
NMFS Panama City Trap Survey	PCTRAP	Fisheries-independent	High quality	Has a high spatio-temporal resolution
NMFS Panama City Video Survey	PCVIDEO	Fisheries-independent	High quality	Has a high spatio-temporal resolution
NMFS Pelagic Observer Program	POP	Fisheries-dependent	High quality	Has a high spatio-temporal resolution
Reef Environmental Education Foundation (REEF) Fish Survey Project	REEF	Fisheries-independent	High quality	Has a high spatio-temporal resolution
NMFS Shark Bottom Longline Observer Program	SBLOP	Fisheries-dependent	High quality	Has a high spatio-temporal resolution
NMFS Small Pelagics Survey	SMALLPEL	Fisheries-independent	High quality	Has a high spatio-temporal resolution
SEAMAP Groundfish/Trawl Survey	TRAWL	Fisheries-independent	High quality	Has a high spatio-temporal resolution
Texas Parks and Wildlife Department (TPWD) Bottom Longline Survey	TXBLL	Fisheries-independent	High quality	Has a high spatio-temporal resolution
TPWD Gillnet Survey	TXGILL	Fisheries-independent	High quality	Has a high spatio-temporal resolution
TPWD Seine Survey	TXSEINE	Fisheries-independent	High quality	Has a high spatio-temporal resolution
TPWD Trawl Survey	TXTRAWL	Fisheries-independent	High quality	Has a high spatio-temporal resolution
SEAMAP Reef Fish Video Survey	VIDEO	Fisheries-independent	High quality	Has a high spatio-temporal resolution
SEAMAP Gulf of Mexico Vertical Longline Survey	VL	Fisheries-independent	High quality	Has a high spatio-temporal resolution

885

886 **Table 3.** Number of encounters and regional percentages of younger juveniles (ages 0-1)
887 of red snapper (*Lutjanus campechanus*), red grouper (*Epinephelus morio*) and gag
888 (*Mycteroperca microlepis*) collected within the U.S. Gulf of Mexico by fisheries-
889 independent surveys and observer programs that use random sampling schemes. Datasets
890 are as defined in Table 2. % East = percentage of encounters east of 87°W (i.e., percentage
891 of encounters on the West Florida Shelf).

Fish life stage	Dataset	Number of encounters	% East
Younger juvenile red snapper	EASAVL	3	0
	FLOBS	7	100
	FLTRAP	3	33.3
	OBSSHRIMP	12,270	7.9
	OBSVL	19	19
	PCTRAP	8	100
	SBLOP	4	100
	SMALLPEL	166	1.2
	TRAWL	4,144	3.5
	TXTRAWL	1,480	0
	VIDEO	7	42.9
	VL	10	0
Younger juvenile red grouper	FLBAY	2	100
	FLHAUL	29	100
	FLOBS	1	100
	FLTRAWL	59	100
	SBLOP	4	100
	TRAWL	44	100
Younger juvenile gag	FLBAY	87	100
	FLHAUL	532	100
	FLPURSE	28	100
	FLTRAWL	348	100

892 **Table 4.** Percentages of spatial overlap between younger juveniles (ages 0-1) of red
893 snapper (*Lutjanus campechanus*), red grouper (*Epinephelus morio*) and gag (*Mycteroperca*
894 *microlepis*) and older juveniles (ages 1-3) and adults (ages 3+) of red grouper and gag.
895

Younger juvenile life stage	**Older juvenile or adult life stage**	**Percentage of spatial overlap**
Younger juvenile red snapper	Older juvenile red grouper	36%
	Adult red grouper	70%
	Older juvenile gag	21%
	Adult gag	26%
Younger juvenile red grouper	Older juvenile red grouper	78%
	Adult red grouper	81%
	Older juvenile gag	19%
	Adult gag	8%
Younger juvenile gag	Older juvenile red grouper	42%
	Adult red grouper	25%
	Older juvenile gag	72%
	Adult gag	14%

Figure captions

Figure 1. Map of the Gulf of Mexico. Depth contours are labeled in 20−, 40−, 60−, 80−, 100−, 200−, and 1000−m contours. Important features are labeled and include: the West Florida Shelf, the Apalachee Bay (**a**), Dry Tortugas (**b**), and the Florida Keys (**c**). MS = Mississippi - AL = Alabama. The black dashed-dotted line delineates the U.S. exclusive economic zone, while the black dashed rectangle delineates the spatial domain of the OSMOSE-WFS ecosystem model.

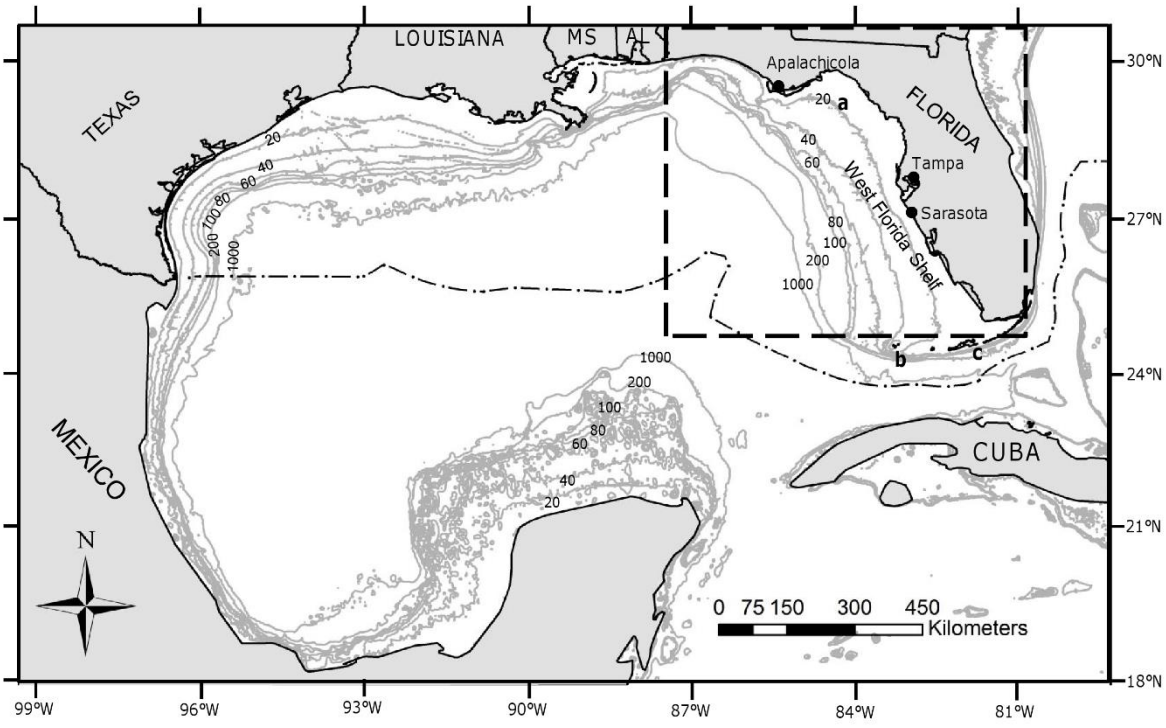


Figure 2. Maps of the West Florida Shelf in the Gulf of Mexico showing: **(a)** the spatial cells of the OSMOSE-WFS ecosystem model (filled in dark grey); and **(b)** the regions where younger juveniles (ages 0-1) of gag (*Mycteroperca microlepis*) have been consistently found over the recent years (Ingram *et al.*, 2013).

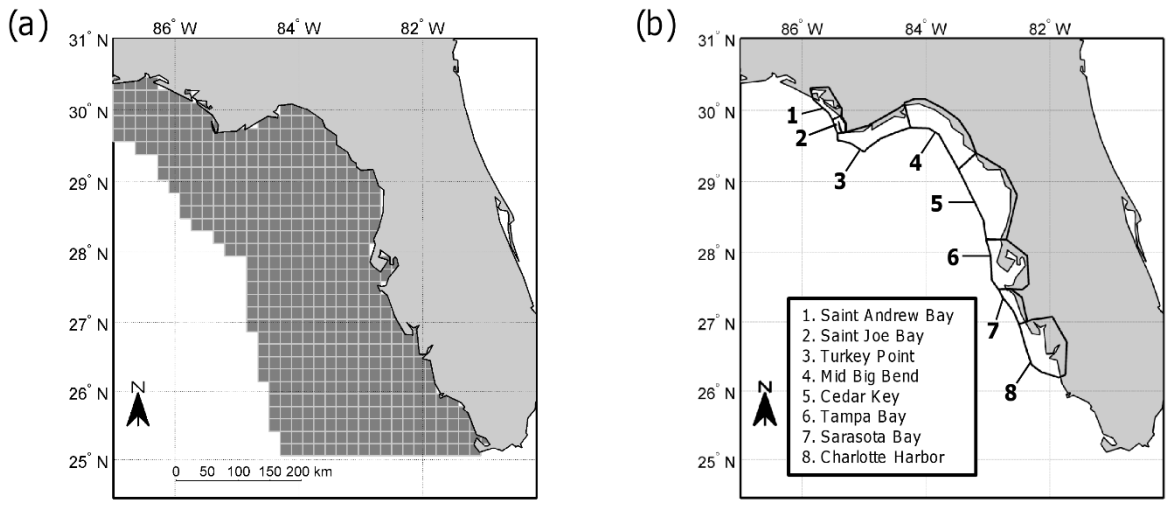


Figure 3. Succession of events within each monthly time step in the OSMOSE-WFS ecosystem model. The OSMOSE-WFS model simulates the entire life cycle of 12 high trophic level (HTL) functional groups and is forced by fields of biomass for nine low trophic level (LTL) functional groups; fields of LTL biomass only serve to provide additional food to the modelled system.

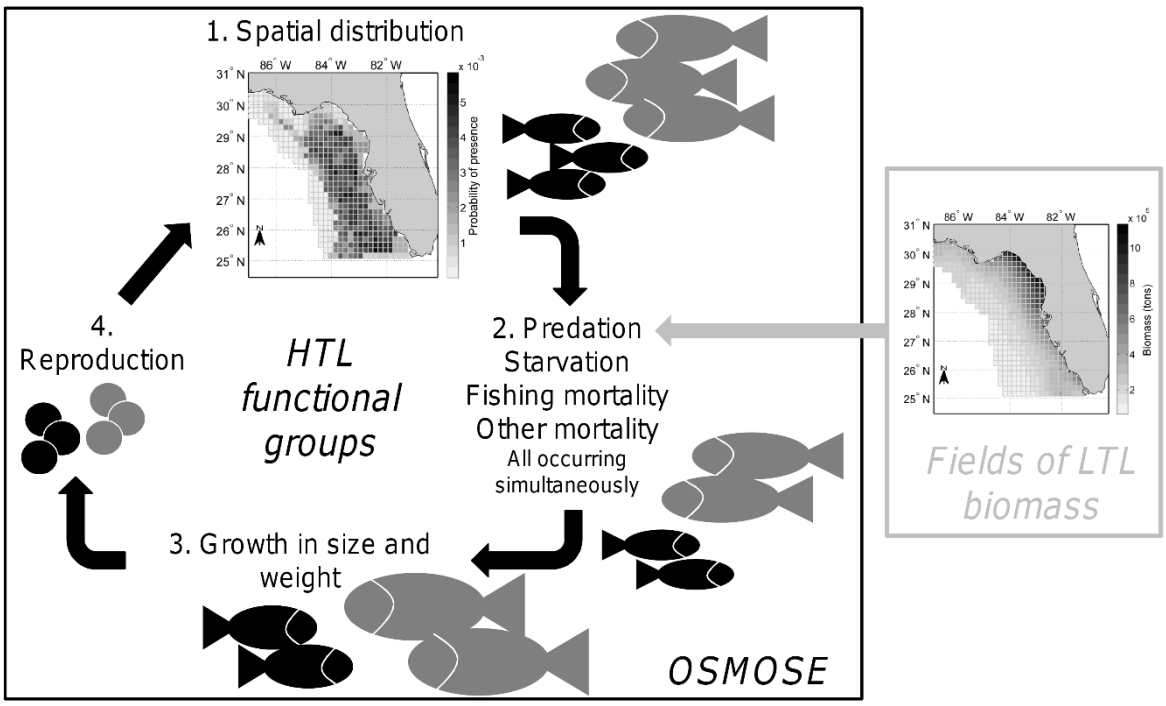


Figure 4. Spatial grids constructed for the present study. **(a)** 0.18°x0.18° spatial grid for the U.S. Gulf of Mexico. **(b-d)** Spatial prediction grids defined for **(b)** younger juvenile (ages 0-1) red snapper (*Lutjanus campechanus*); **(c)** younger juvenile (ages 0-1) red grouper (*Epinephelus morio*); and **(d)** younger juvenile (ages 0-1) gag (*Mycteroperca microlepis*). The extent of the prediction grid of a given fish life stage was defined from the spatial grid for the U.S. GOM, based on the ranges of latitude, longitude and bottom depth at which this life stage occurs according to survey data.

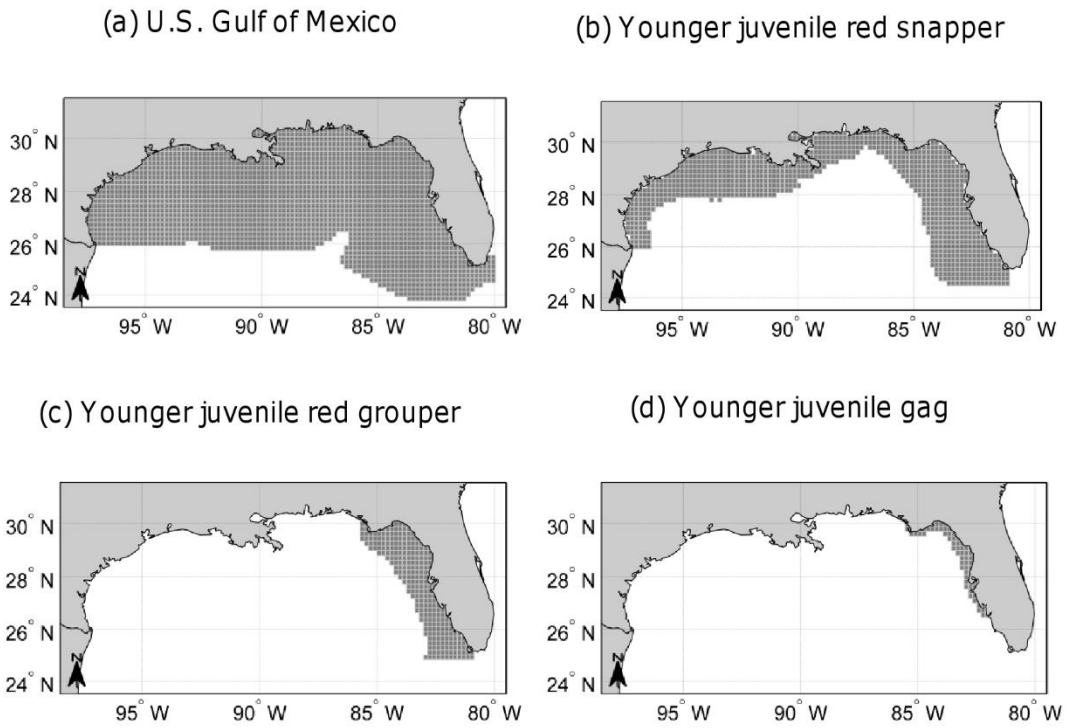


Figure 5. Distribution maps produced from the predictions of spatio-temporal generalized linear mixed models for **(a)** younger juvenile (ages 0-1) red snapper (*Lutjanus campechanus*); and **(b)** younger juvenile (ages 0-1) red grouper (*Epinephelus morio*).

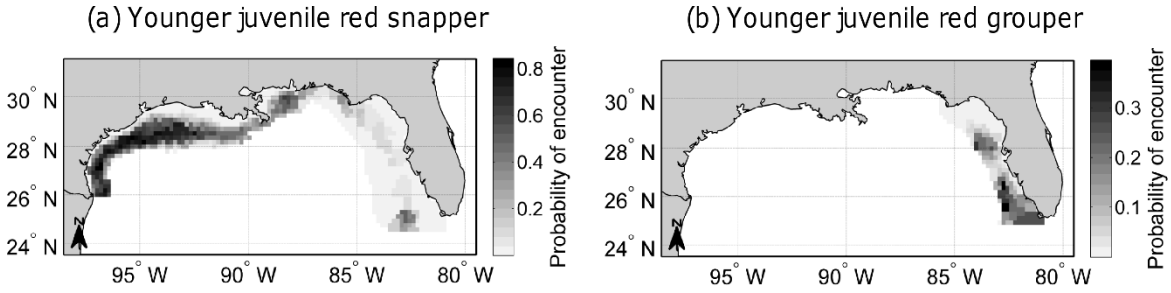


Figure 6. Distribution maps produced from the predictions of a spatio-temporal generalized linear mixed model for younger juvenile (ages 0-1) gag (*Mycteroperca microlepis*). **(a)** is a probability of encounter map for the entire U.S. Gulf of Mexico. **(b)** shows the average probability of encounter of younger juvenile gag in the eight regions of the West Florida Shelf where the life stage has been consistently found over the recent years (Ingram *et al.*, 2013).

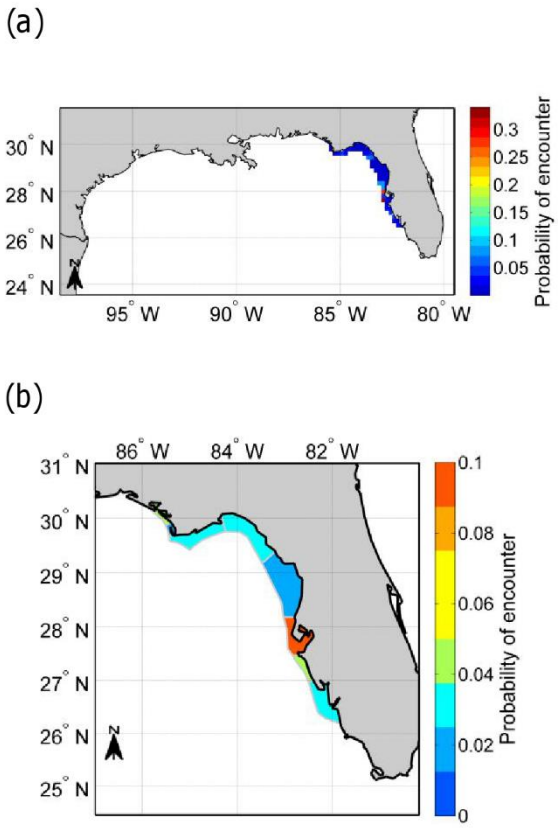
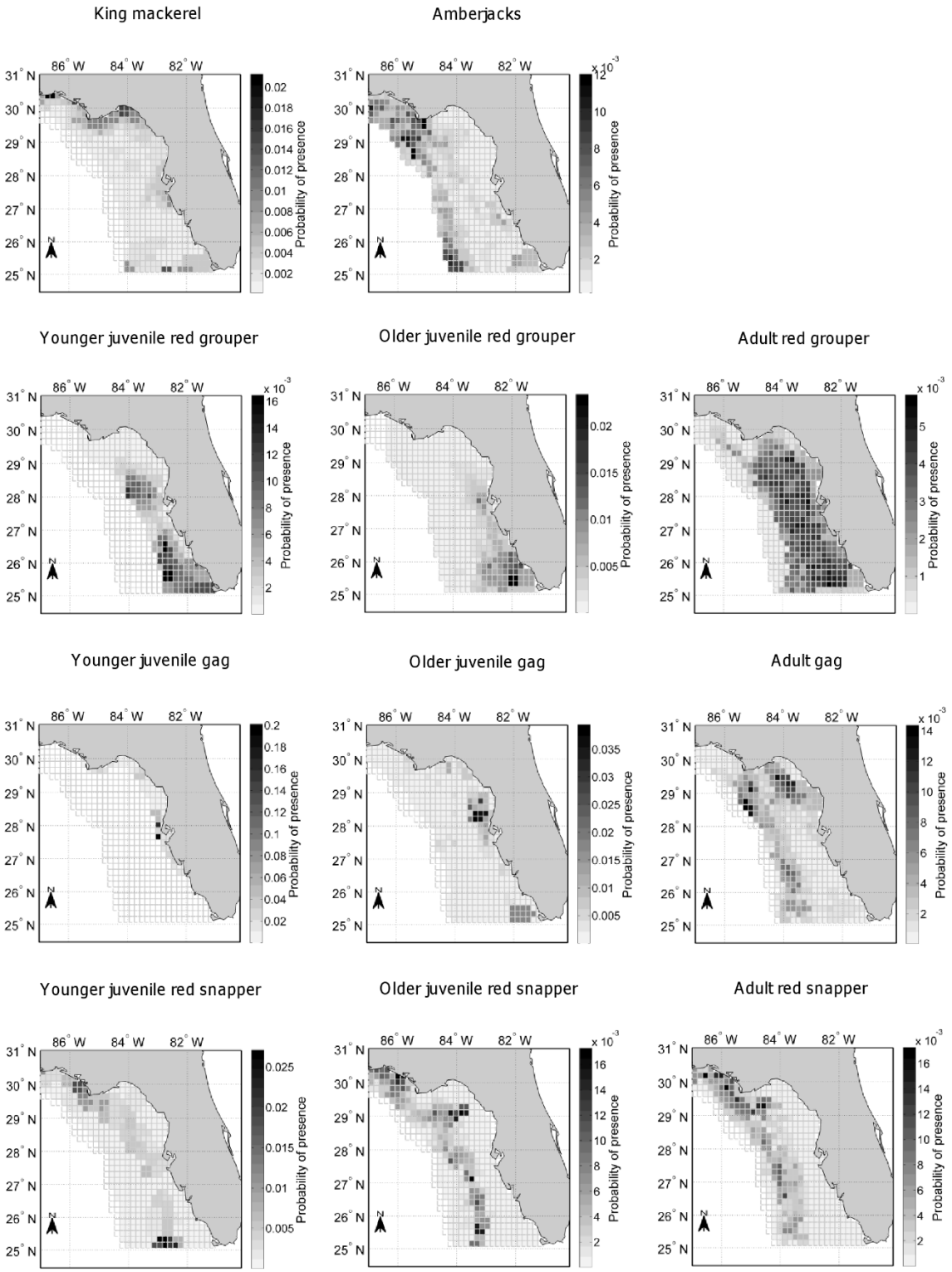
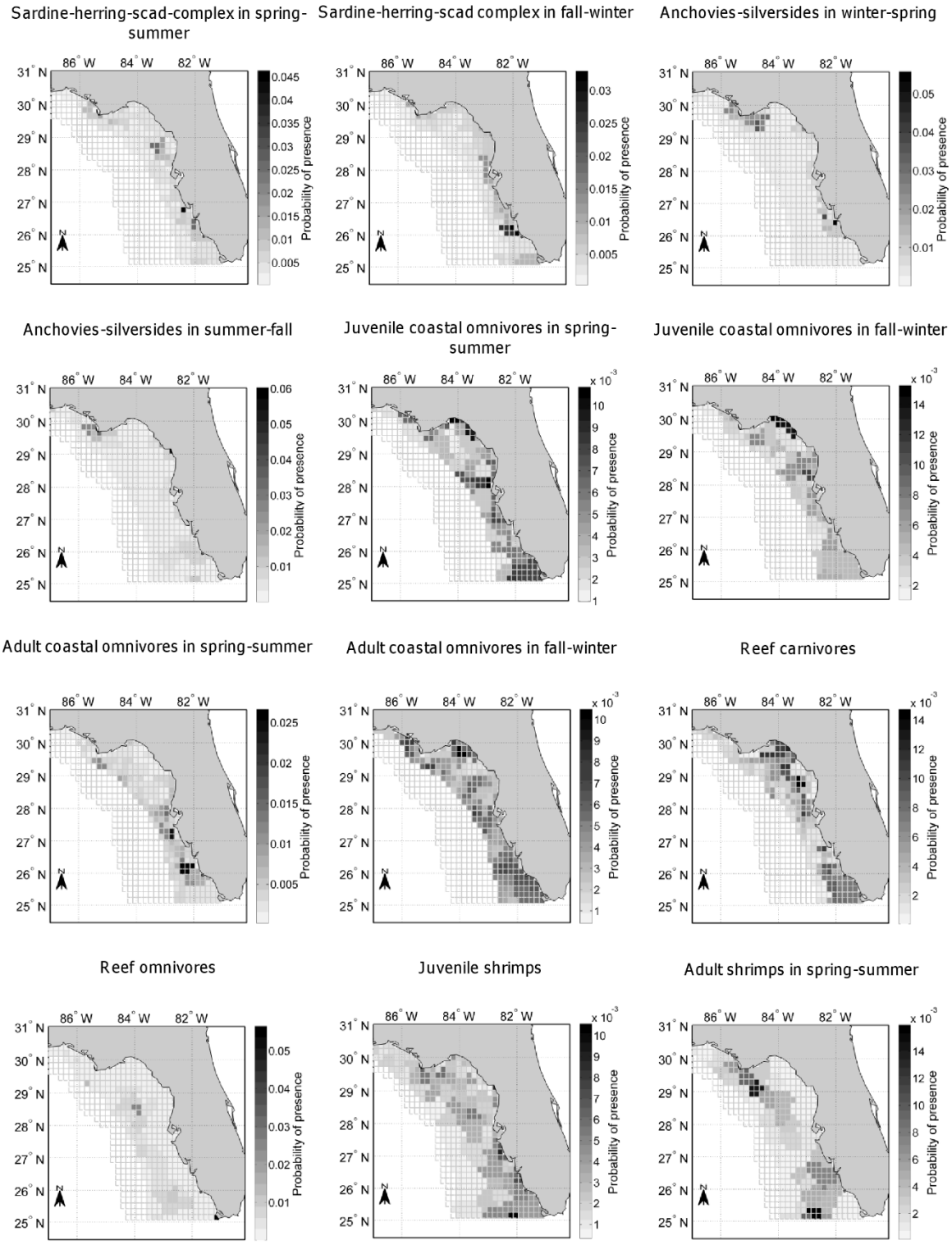


Figure 7. Distribution maps produced for the functional groups and life stages represented in the OSMOSE-WFS ecosystem model.

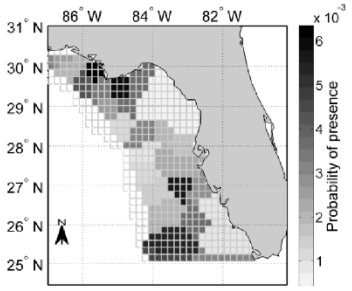


938

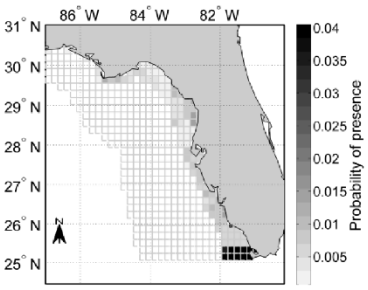

Sardine-herring-scad-complex in spring-summer
Sardine-herring-scad complex in fall-winter
Anchovies-silversides in winter-spring
Anchovies-silversides in summer-fall
Juvenile coastal omnivores in spring-summer
Juvenile coastal omnivores in fall-winter
Adult coastal omnivores in spring-summer
Adult coastal omnivores in fall-winter
Reef carnivores
Reef omnivores
Juvenile shrimps
Adult shrimps in spring-summer
86° W
84° W
82° W
31° N
30° N
29° N
28° N
27° N
26° N
25° N
Probability of presence
x 10-3

939

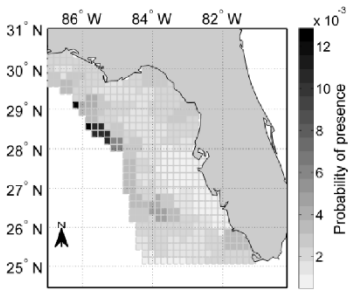
Adult shrimps in fall-winter



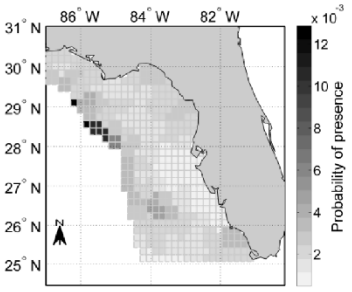
Large crabs



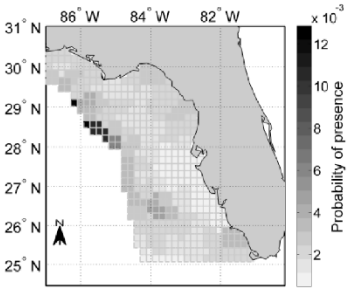
Meiofauna



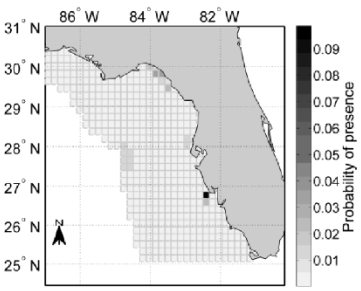
Small infauna



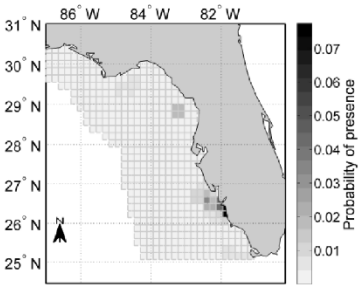
Small mobile epifauna



Bivalves



Echinoderms and gastropods



940

Boxes

Box 1. Discussion of the spatial distribution patterns of younger juveniles of red snapper, red grouper and gag predicted in the present study.

The comprehensive survey database for the Gulf of Mexico (GOM) provided a large amount of encounter data for younger juvenile red snapper. In the case of younger juvenile red snapper, data collected over the entire U.S. GOM shelf (by OBSSHRIMP, SMALLPEL and TRAWL) and over the Texas continental shelf (by TXTRAWL) were retained in the comprehensive survey database. The great majority of younger juvenile red snappers collected by these surveys were encountered in the western U.S. GOM (Table 3) and, therefore, the spatio-temporal binomial generalized linear mixed model (GLMM) of younger juvenile red snapper predicted the probability of encounter of the fish life stage to be much higher in the western U.S. GOM than in the eastern U.S. GOM (i.e., than on the West Florida Shelf) (Figure 5a). The literature on the spatial distribution of younger juvenile red snapper is limited, due to the cryptic nature of the fish life stage (Szedlmayer and Mudrak, 2014). However, the rare studies on the spatial distribution of younger juvenile red snapper also report that the bulk of younger juvenile red snappers are found from the Florida-Alabama border to the Texas-Mexico border (Gallaway *et al.*, 1999, 2009; Monk *et al.*, 2015).

The spatial distribution patterns of younger juvenile red snapper predicted in the present study concur with the limited literature on the topic. Firstly, we found that hotspots of probability of encounter for younger juvenile red snapper are located in those areas of the GOM where bottom depth ranges from 20 to 60 m, while Johnson *et al.* (2013) reported that high-value red snapper larval settlement habitat occurs between 15 and 64 m of water depth. Gallaway *et al.* (1999) estimated that younger juvenile red snapper habitat lies in areas of the GOM where bottom depth ranges from 18 and 64 m and the authors

found peak abundance for the life stage at 37 m of water depth, while we predicted younger juvenile red snapper to be encountered at 43 m of water depth on average. Secondly, consistent with Szedlmayer and Conti (1999) and Gallaway *et al.* (1999), we found that the greatest probabilities of encounter of younger juvenile red snapper in the western U.S. GOM are located in the mid-shelf area offshore Alabama and on the Texas continental shelf. Finally, the spatio-temporal binomial GLMM of younger juvenile red snapper predicted the probability of encounter of the life stage in the eastern U.S. GOM to be highest near the Florida Keys and Dry Tortugas, which concurs with Karnauskas *et al.* (2013a); Karnauskas *et al.* (2013a) carried out simulations with the Connectivity Modelling System (CMS) biophysical model, which revealed that red snapper larval settlement on the West Florida Shelf is poor and primarily occurs in the southern extent of the Shelf. Our results could be used to improve understanding of where younger juvenile red snappers are likely to be caught as bycatch in shrimp trawls (Monk *et al.*, 2015).

Despite the compilation of a comprehensive survey database for the GOM, we had limited encounter data for younger juvenile red grouper (Table 3). This result is due to the cryptic nature of red grouper, which has not allowed previous studies to determine the dominant habitat of the younger juveniles of the species (Moe, 1969; Koenig and Coleman, 1999; Coleman *et al.*, 2010). In the case of younger juvenile red grouper, fisheries-independent data collected in West Florida waters (by FLTRAWL and FLHAUL) and over the entire U.S. GOM shelf (by TRAWL) suggest that the life stage is distributed on the West Florida Shelf only. The spatio-temporal binomial model of younger juvenile red grouper predicts the life stage to be distributed mainly from Sarasota to the southern West Florida Shelf, at 24 m water depth on average.

More encounter data were available for younger juvenile gag than for younger juvenile red grouper (Table 3). In the case of younger juvenile gag, only fisheries-

991 independent datasets for Florida (the FLHAUL, FLTRAWL and FLBAY datasets) were
992 retained in the comprehensive survey database for the GOM. However, younger juvenile
993 gag does not occur solely in West Florida waters. When we contacted the Texas Parks and
994 Wildlife Department to request their survey data, the state agency provided us with the
995 Texas Marine Sport-Harvest Monitoring Program Survey (TXFD) dataset, which reports
996 catches per unit effort (CPUEs) at fixed locations. We extracted encounter/non-encounter
997 data from the TXFD dataset, and found that younger juvenile gag was encountered in
998 Texas coastal waters in 2000. Moreover, since older juveniles and adults of gag are
999 encountered in the western U.S. GOM, we suspect that the younger juveniles of the species
1000 can also be encountered there. Currently, besides the TXFD survey, no research survey in
1001 the western U.S. GOM (conducted using a random or a fixed-station sampling scheme) has
1002 collected data for younger juvenile gag. Therefore, it would be interesting to initiate new
1003 research surveys or to expand existing ones so as to elucidate where younger juvenile gag
1004 is distributed in the western U.S. GOM.

1005 Besides the FLHAUL, FLTRAWL and FLBAY datasets, we received two datasets
1006 that provide a reasonable amount of CPUE data for younger juvenile gag for the West
1007 Florida Shelf: (1) the NMFS Panama City Laboratory St. Andrew Bay Juvenile Reef Fish
1008 Survey (PCJUV), which collects data for gag and a few other species in St. Andrew Bay, at
1009 fixed seagrass locations pre-determined to be settlement areas; and (2) the Florida State
1010 University Estuarine Gag Survey (FSUEST), which collects data for gag at fixed locations,
1011 primarily in seagrass habitat, in the eight regions of the West Florida Shelf where Ingram
1012 *et al.* (2013) reported younger juvenile gag to be consistently found. However, we were
1013 unable to include PCJUV and FSUEST data in the comprehensive survey database for the
1014 GOM, due to the fact that these data were collected using a fixed-station sampling scheme.
1015 Yet, using FLHAUL, FLTRAWL and FLBAY data only, the spatio-temporal binomial

GLMM of younger juvenile gag was able to predict that the life stage is encountered in the eight regions identified by Ingram *et al.* (2013), namely Saint Andrew Bay, Saint Joe Bay, Turkey Point, the Mid Big Bend, Cedar Key, Tampa Bay, Sarasota Bay, and Charlotte Harbor (Figure 6). The spatio-temporal binomial GLMM of younger juvenile gag did not predict the life stage to occur in the Marco Island region, which is located just south of Charlotte Harbor (Figure 6b). Ingram *et al.* (2013) excluded the Marco Island region from their analyses, because, over the period 1991-2012, only a few younger juvenile gags were caught in the region in 2005, 2006 and 2007. Fitzhugh *et al.* (2005) reported that sampling to collect younger juvenile gags are usually not conducted in the Marco Island region, because the great majority of the seagrass beds in that region, which provide suitable settlement habitat for gag larvae, have been severely reduced since the late 1980s. Experts report that most of the younger juvenile gags are caught between 0 and 2 m of water depth (Ingram *et al.*, 2013), while the spatio-temporal binomial GLMM that we fit for younger juvenile gag predicts the life stage to be encountered at a mean bottom depth of 8 m.

The probabilities of encounter of younger juvenile gag predicted for the eight regions identified in Ingram *et al.* (2013) are usually consistent with the findings of previous studies (Switzer *et al.*, 2012, 2015). In accordance with Switzer *et al.* (2012), we found the probability of encounter of younger juvenile gag to be low in Cedar Key. Switzer *et al.* (2012) advanced several possible explanations for this. One of these possible explanations is that discharge from a nearby river (the Suwannee River) is highly variable and that it diminishes the quality of younger juvenile gag habitat. Another possible explanation is that gags settling in Cedar Key may be diluted by the large amount of seagrass habitat in that region, or they may settle at the edge of seagrass habitat in waters deeper than those at which the FLHAUL, FLTRAWL and FLBAY surveys take place. Finally, the specific hydrographic conditions in Cedar Key, which is an open coastal

1041 system and not a semi-enclosed estuary (like Tampa Bay, for example), may limit gag
1042 larval settlement in the Cedar Key region (Switzer *et al.*, 2012). Moreover, both the present
1043 study and Switzer *et al.* (2015) found that the probability of encounter of younger juvenile
1044 gag is low in the Mid Big Bend. According to Switzer *et al.* (2015), this may be due in part
1045 to the fact that seagrass habitat is found in deeper waters in the Mid Big Bend than
1046 elsewhere on the West Florida Shelf, and to the fact that drift algae, which reduce the
1047 catchability of younger juvenile gag, are abundant in the Mid Big Bend region. Both this
1048 study and Switzer *et al.* (2015) also found that younger juvenile gag has a high probability
1049 of encounter in Tampa Bay, presumably due to the large quantity of fragmented seagrass
1050 habitat in that region. By contrast, the spatio-temporal binomial GLMM of younger
1051 juvenile gag predicted the probability of encounter of the life stage to be almost as low in
1052 Turkey Point and Charlotte Harbor as in Cedar Key (Figure 6b), which does not concur
1053 with Switzer *et al.* (2015). The low probability of encounter of younger juvenile gag in
1054 Turkey Point predicted by the spatio-temporal binomial GLMM may be explained by the
1055 large winter leaf dieback of seagrasses that occurs earlier in winter in northern West
1056 Florida and results in higher mortality rates in younger juvenile gag in northern West
1057 Florida than in southern West Florida (Fitzhugh *et al.*, 2005; Casey *et al.*, 2007; Switzer *et*
1058 *al.*, 2012). Then, the low probability of encounter of younger juvenile gag in Charlotte
1059 Harbor predicted by its spatio-temporal binomial GLMM may be explained by the smaller
1060 quantity of seagrass habitat in Charlotte Harbor compared to Tampa Bay and Sarasota Bay
1061 (Casey *et al.*, 2007; Switzer *et al.*, 2012). Although younger juvenile gags also inhabit
1062 mangroves, oyster reefs, jetties and seawalls (Hastings, 1979; Bullock and Smith, 1991;
1063 Casey *et al.*, 2007), Casey *et al.* (2007) found that younger juvenile gag CPUE is
1064 significantly correlated with the amount of seagrass habitat.