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Evaluation of the natural mortality rates of red grouper (*Epinephelus morio*) in the West Florida Shelf ecosystem using the individual-based, multi-species model OSMOSE-WFS

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Introduction

Ecosystem-based management (EBM) of marine systems has become a central paradigm in the United States (Lubchenco and Sutley, 2010; USNOC, 2013). EBM considers interactions between exploited marine species and their biotic and abiotic environment to define management strategies. One major strength of EBM is its ability to expose indirect impacts of fisheries and tradeoffs between fisheries management objectives and conservation issues (Pikitch et al., 2004; Levin et al., 2009; McLeod and Leslie, 2009). Integrated ecosystem assessments (IEAs) are increasingly developed to organize science in order to inform decisions in EBM (Levin et al., 2009, 2013; ICES, 2010; Möllmann et al., 2013). A large IEA program has been recently initiated in the Gulf of Mexico (GOM) by the National Oceanic and Atmospheric Administration (NOAA). One of the goals of the GOM IEA program is to regularly incorporate environmental and ecosystem considerations into single-species stock assessments and deliver estimates of parameters that are highly difficult to evaluate from empirical data (http://www.noaa.gov/iea/gulfofmexico.html). In particular, the GOM IEA program is committed to informing SEDAR (SouthEast Data, Assessment, and Review) (http://www.sefsc.noaa.gov/sedar/). Several ecosystem simulation models have been used towards that goal.

The ecosystem simulation models used within the GOM IEA program include two Ecopath with Ecosim (EwE) models for the West Florida Shelf, one of the main regions of the GOM under high and increasing fishing and environmental pressures (Coleman et al., 2004; Okey et al., 2004; Steidinger, 2009; Karnauskas et al., 2013; Fig. 1). Ecopath is a widely-used trophic mass-balance model which explicitly considers major functional groups in a given ecosystem (fish, invertebrates, marine mammals, seabirds, plankton, etc.), and provides a snapshot of the trophic structure of this ecosystem (Pauly et al., 2000; Christensen and Walters, 2004). Chagaris (2013) constructed the 'WFS Reef fish Ecopath' model to analyze the trophic structure of the West Florida Shelf (WFS) over the period 2005-2009. Biomass, catch and productivity parameters of the WFS Reef fish Ecopath model were rescaled to obtain an Ecopath model for the early 1950s, from which Chagaris (2013) and Chagaris and Mahmoudi (2013) evaluated changes in biomasses, trophic interactions and mortalities in the West Florida Shelf over the period 1950-2009 using the Ecosim module (resulting in a EwE model). Gray et al. (2013) and Gray (2014) developed an EwE model similar to WFS Reef fish EwE, referred to as 'WFS Red tide EwE', in which they focused on the impacts of red tide (*Karenia brevis*) events, a type of harmful algal blooms, for gag grouper (*Mycteroperca microlepis*), over the period 1980-2009.

In addition to these EwE models, an OSMOSE model was also developed for the West Florida Shelf, referred to as 'OSMOSE-WFS' (Fig. 1; Grüss et al., 2013a, 2013b, 2014a). OSMOSE is a two-dimensional, individual-based and multispecies modeling approach explicitly representing major processes in the life cycle of high trophic level (HTL) groups of fish and invertebrate species (Shin and Cury, 2001, 2004; http://www.osmose-model.org/). OSMOSE-WFS is at present a steady-state model with a monthly time step, describing trophic interactions in the West Florida Shelf in the 2000s (Grüss et al., 2013a, 2013b, 2014a). OSMOSE-WFS and the West Florida Shelf Ecopath models share a number of characteristics, such as the spatial domain, reference period and reference biomasses. However, OSMOSE-WFS and the West Florida Shelf Ecopath models differ greatly in both their structure and assumptions. In particular, diets reconstructed from empirical data are input into Ecopath, while they emerge from size-based processes in OSMOSE. The use of the OSMOSE-WFS, WFS Reef Fish Ecopath/EwE and WFS red tide EwE models offers different perspectives on the functioning of the West Florida Shelf ecosystem, while being able to identify from where discrepancies between the different models may originate. Using a multi-model approach for the West Florida Shelf allows us to evaluate uncertainties in our knowledge of the West Florida Shelf ecosystem, and help identify avenues for reducing these uncertainties.

Grüss et al. (2014a) calibrated OSMOSE-WFS using a recently developed evolutionary algorithm that allowed simulated biomasses of HTL groups to match observed biomasses over the period 2005-2009. They also evaluated the validity of OSMOSE-WFS by comparing simulated diets to observed ones, and the simulated trophic levels (TLs) to those in WFS Reef fish Ecopath. Finally, the authors used OSMOSE-WFS to explore the trophic structure of the West Florida Shelf in the 2000s and estimate size-specific natural mortality rates for gag grouper, which were compared to gag grouper natural mortality rates predicted by WFS Reef fish Ecopath. OSMOSE-WFS outputs were in full agreement with observations as to the body size and ecological niche of prey of the different HTL groups, and to a lesser extent in agreement with the observed species composition of the diet of HTL groups. The mean TLs in output of OSMOSE-WFS and WFS Reef fish Ecopath were relatively similar, as well as the ranks of the TL values. Finally, OSMOSE-WFS and WFS Reef fish Ecopath concurred on the magnitude of the instantaneous natural mortality of the different life stages of gag grouper over the period 2005-2009, but not always on the main causes of natural mortality (Grüss et al., 2014a).

While Grüss et al. (2014a)'s OSMOSE-WFS model was validated in its steady-state configuration and behaved satisfactorily under a range of fishing mortality scenarios, it did not provide pertinent results when some HTL groups were subject to extremely high fishing mortality rates (A. Grüss, Y.-J. Shin, L. Velez and P. Verley, pers. obs.). To address this issue, we switched from the 'iterative mortality algorithm' used in Grüss et al. (2014a) to the better-performing 'stochastic mortality algorithm', which assumes that all types of mortalities are continuous processes that compete with each other, and that there is competition and stochasticity in the predation process (http://www.osmose-model.org/).

In the present paper, we introduce the new version of the OSMOSE-WFS model which employs the stochastic mortality algorithm, and use this model to estimate size-specific and age-specific natural mortality rates of red grouper (*Epinephelus morio*) in the West Florida Shelf for SEDAR 42. The new OSMOSE-WFS model presented has a monthly time step and still describes the trophic structure of the West Florida Shelf ecosystem in the 2000s. In the following, we: (1) provide a brief overview of the OSMOSE modeling approach; (2) describe the structure and assumptions of OSMOSE-WFS; (3) detail the parameterization of OSMOSE-WFS; (4) present the methodology that we implemented to calibrate OSMOSE-WFS to a reference state matching the mean observed conditions in the West Florida Shelf region over the period 2005-2009; (5) use the calibrated OSMOSE-WFS model to estimate the instantaneous natural mortality rates of different life stages and age classes of red grouper in the West Florida Shelf ecosystem over the period 2005-2009; and (6) discuss our results and describe how OSMOSE-WFS is going to be improved to provide more information to EBM in the GOM. The overview of the OSMOSE modeling approach we provide is helpful to understand the choices we made regarding the structure and assumption of OSMOSE-WFS. Our exploration of the natural mortality patterns of red grouper in the West Florida Shelf over the period 2005-2009 from OSMOSE-WFS predictions is accompanied by comparisons of OSMOSE-WFS outputs with WFS Reef fish Ecopath outputs.

Material and methods

OSMOSE (Object-oriented Simulator of Marine ecOSystem Exploitation)

OSMOSE is a two-dimensional, individual-based and multispecies model which singularity relies on both size-based interactions and explicit implementation of the whole life cycle of modeled organisms (Shin and Cury, 2001, 2004; http://www.osmose-model.org/).

OSMOSE has been used to model trophic dynamics and the impacts of fishing management strategies in a variety of ecosystems, including the Southern Benguela (e.g., Shin et al., 2004; Yemane et al., 2009; Travers et al., 2010; Travers-Trolet et al., 2014), the Humboldt (Marzloff et al., 2009), the Bamboung Bolong in Senegal (Brochier et al., 2013) and the Strait of Georgia in Canada (Fu et al., 2012, 2013).

The basic units ('super-individuals') of OSMOSE are schools, which consist in organisms belonging to the same HTL group, which have the same body length, age, food requirement and, at a given time step, the same spatial coordinates. OSMOSE includes a hierarchical structure of model classes corresponding to those in a HTL community: a 'school' belongs to a 'cohort' or age class, which itself belongs to a 'HTL group', which itself belongs to the HTL community. Such a hierarchical structure allows the assessment of output variables at different levels of aggregation (e.g., size and biomass can be evaluated at the levels of the cohort, HTL group and HTL community; Shin and Cury, 2001; Shin et al., 2004; Travers et al., 2009).

Because every super-individual is represented from the egg stage to the terminal age, thus requiring both intensive calculation capacities and integration of extensive information on whole life cycles, OSMOSE explicitly models only a limited number of HTL groups of fish and invertebrate species. However, other compartments of marine ecosystems (e.g., low trophic level (LTL) planktonic groups, top predators such as marine mammals) are implicitly taken into account in OSMOSE either through mortality parameters or prey biomass pools. Specifically, the predation on OSMOSE individuals by HTL organisms which life cycles are not represented in the model (marine mammals, seabirds, etc.) is considered through the application of a specific mortality term. Besides, the biomass of non-explicit LTL groups (plankton, benthos) constitutes a prey pool on which OSMOSE individuals can prey on, in addition to and simultaneously with other explicit preys. A major difference with other ecosystem models such as Ecopath is that, in OSMOSE, predation is opportunistic and size-based; OSMOSE individuals can potentially feed on any prey provided that: (1) the predator and potential prey co-occur spatially (i.e., overlap in the horizontal dimension); (2) there is size adequacy between them; and, (3) the vertical distribution and morphology of the potential prey makes it accessible to the predator.

In the first version of OSMOSE, HTL groups were split into piscivorous and non-piscivorous groups according to their life stage and taxonomy. The total biomass of non-piscivorous groups was constrained by a carrying capacity parameter representing the maximum biomass of LTL groups, and a minimum predator/prey size ratio was defined to restrict predation (Shin and Cury, 2004; Shin et al., 2004; Travers et al., 2006; Yemane et al., 2009). In subsequent versions of OSMOSE, the carrying capacity parameter no longer exists, and OSMOSE is either coupled to a LTL model (Travers, 2009; Travers and Shin, 2010; Travers et al., 2010; Travers-Trolet et al., 2014) or forced by LTL production or biomass (Marzloff et al., 2009; Travers et al., 2009; Brochier et al., 2013). This modification in OSMOSE structure led to the definition of a maximum predator/prey size ratio in addition to the minimum predator/prey size ratio, so as to ensure that piscivorous HTL groups do not exert an unrealistically high predation pressure on LTL organisms (Travers et al., 2009, 2010).

Accessibility coefficients are defined in OSMOSE to reflect the influence of the vertical distribution and morphology of potential prey items on their chances to be eaten. OSMOSE applications have usually focused on pelagic and demersal marine communities, and have not explicitly represented benthic HTL groups nor considered the biomass of benthic LTL organisms to force the model (but see Brochier et al. (2013)). For this reason, the accessibility coefficients of the different life stages of the HTL groups to each other have typically been set to 80%, to account for the fact that not all predator attacks are successful and that the different life stages of HTL organisms do not entirely overlap in the water column (Travers, 2009). On the other hand, the accessibility of LTL groups to HTL groups, which is affected by numerous processes (e.g., turbulence, stratification) and depends on large differences in time scales between LTL and HTL dynamics, may be much lower but is typically unknown, and has usually been estimated during the calibration process of OSMOSE (Marzloff et al., 2009; Yemane et al., 2009; Travers et al., 2010).

Biomass of LTL groups

OSMOSE-WFS is forced by the biomass of nine LTL groups, consisting of four plankton groups and five benthos groups. The selection of the nine LTL groups was based on their importance in the West Florida Shelf food web in terms of biomass, and, particularly, in the diet of the HTL groups that are explicitly considered in OSMOSE-WFS (SUSFIO, 1977; Phillips et al., 1991; Vargo and Hopkins, 1991; Okey and Mahmoudi, 2002). Biomass of LTL groups is a local input in each model cell and each month. A mechanistic Nutrient-Phytoplankton-Zooplankton-Detritus (NPZD) is currently being developed for the GOM, although results of this LTL model still need to be validated. As a consequence, and due to a lack of spatio-temporal empirical estimates of plankton and benthos biomass for the West Florida Shelf, we produced distribution maps for LTL groups based on simple assumptions.

Plankton groups include small phytoplankton, diatoms, small copepods, and large mesozooplankton, while LTL benthic groups consist of meiofauna, small infauna, small mobile epifauna, bivalves, and echinoderms and large gastropods (Table 1). Chlorophyll a concentration in the West Florida Shelf is an accepted proxy for phytoplankton biomass in this region (Boyer et al., 2009). We generated monthly maps of chlorophyll a concentration in the West Florida Shelf region from SeaWiFS (Sea-viewing Wide Field-of-view Sensor) data downloaded from http://oceancolor.gsfc.nasa.gov/SeaWiFS/ (Hooker et al., 1992; McClain et al., 2004; Fig. 2). From the monthly maps of chlorophyll a concentration and the total biomass of the phytoplankton group in the WFS Reef fish Ecopath model (Chagaris, 2013; Table 1), monthly maps of biomass for small phytoplankton and diatoms were created under the assumption that these two groups are equally abundant in biomass in each model cell and time step (month).

In the absence of detailed spatial information for all other LTL groups, a uniform distribution over the whole West Florida Shelf was assumed. The total biomass of each of these groups was taken from the WFS Reef fish Ecopath model (Chagaris, 2013; Table 1), wherein the biomass values of small copepods, large mesozooplankton and LTL benthic groups do not vary seasonally.

Life cycle of HTL groups

Twelve groups of HTL fish and invertebrate species are explicitly considered in OSMOSE-WFS. These twelve groups were selected for their contribution to total biomass and their economic value in the West Florida Shelf region during the 2000s, and/or because they are important components of the West Florida Shelf food web.

Species of a given HTL group exhibit similar life history traits, body size ranges, diets and exploitation patterns. Some individual species constitute their own group, as they are emblematic to the West Florida Shelf and of high economic importance. OSMOSE-WFS explicitly considers ten fish and two crustacean species/groups of species: (1) king mackerel (*Scomberomorus cavalla*); (2) amberjacks; (3) red grouper; (4) gag grouper; (5) red snapper (*Lutjanus campechanus*); (6) the sardine-herring-scad complex; (7) anchovies and silversides; (8) coastal omnivores; (9) reef carnivores; (10) reef omnivores; (11) shrimps; and (12) large crabs. A reference species was identified for each of the HTL groups (Table 2). Growth, reproduction, mortality and diet parameters of each group are those of the reference species of the group.

Within a monthly time step, the following succession of events occurs in OSMOSE-WFS: (1) schools are distributed on a two-dimensional grid using specific distribution maps; (2) mortalities (fishing, predation, starvation and other natural mortality) are applied to schools; (3) the growth in size and weight of schools is determined based on their predation success; and (4) reproduction occurs.

Spatial distribution of schools

The spatial distribution of a school at each time step is driven by specific maps that depend on the HTL group and cohort to which the school belongs and to the season. The great majority of these maps were produced using a delta generalized additive modeling (GAM) approach developed by Grüss et al. (2014b). Due to a lack of data, we were unable to create distribution maps for younger juveniles of red grouper and gag grouper with delta GAMs. Yearly distribution maps for these stanzas were constructed from information in the literature. The distribution maps we generated for OSMOSE-WFS are given in Fig. 3.

When the maps do not change (within a season or throughout the year), schools can move to adjacent cells within their distribution area following a random walk. Random walk movements are meant to represent small-scale foraging movements and diffusion.

Mortalities

The steady-state version of OSMOSE-WFS presented here meets the specifics of OSMOSE v3u1, where a 'stochastic mortality algorithm' rather than an 'iterative mortality algorithm' is employed to compute the mortality rates of schools (http://www.osmose-model.org). The stochastic mortality algorithm assumes that all types of mortalities are simultaneous processes, and that there is competition and stochasticity in the predation process.

Within each time step, the total mortality of a given school i is comprised of fishing mortality (F_i), starvation mortality ($M_{starvation\ i}$), predation mortality caused by various schools j ($M_{predation\ i,\ j}$), and diverse natural mortality due to causes other than starvation and predation by the HTL groups represented in the model ($M_{diverse\ i}$). In practice, OSMOSE-WFS considers each school in turn in a random order, and lets the mortality sources occur in a random order. To ensure that the random order of mortality sources does not bias the resulting instantaneous mortality rates provided in output of OSMOSE-WFS, the mortality process is iterated over 10 sub-time steps (*subdt*).

Diverse natural mortality

An additional source of natural mortality other than predation and starvation is applied to all schools older than 1 month: $M_{diverse}$, which is the mortality due to marine organisms and events (e.g., red tide events, diseases) that are not explicitly considered in OSMOSE-WFS. Moreover, an additional source of natural mortality other than predation is applied to the first age class corresponding to eggs and larvae (0-1 month old individuals): *M0*, which is due to different causes (e.g., non-fertilization of eggs, advection away from suitable habitat, sinking, mortality of first-feeding larvae). For each HTL group, the $M_{diverse}$ parameter was estimated from the predation mortality rate by marine organisms that are considered in WFS Reef fish

Ecopath but not in OSMOSE-WFS (Chagaris 2013; Table 3). *M0* is unknown for almost all the HTL groups represented in OSMOSE-WFS. Therefore, this parameter is estimated during the calibration process of OSMOSE-WFS (see below).

Fishing mortality

In the present application, fishing mortality is assumed to be uniform over space. Fishing reduces school abundance through the application of a month- and group-specific fishing mortality rate to any school whose body size is larger than the size of recruitment into the fisheries specified for each HTL group (Table 3). Monthly fishing mortality rates for each HTL group are determined from a group-specific annual fishing mortality rate F_{annual} (Table 3) and its seasonality. Discards were taken into account in the calculation of F_{annual} by the stock assessments for king mackerel (SEDAR 16, 2009), amberjacks (SEDAR, 2011), red grouper (SEDAR, 2009a), gag grouper (SEDAR, 2014) and red snapper (SEDAR, 2009b). Bycatch in the shrimp trawl fishery was also explicitly taken into account in the calculation of F_{annual} estimated in the stock assessments of king mackerel (SEDAR 16, 2009) and red snapper (SEDAR, 2009b).

In the absence of data, we assumed no fishing seasonality of F_{annual} for the sardine-herring-scad complex, anchovies/silversides and reef carnivores. The seasonality of F_{annual} of all other HTL groups – except reef omnivores that are not targeted by fishing – was estimated from the monthly total catches of their reference species over the period 2005-2009. Monthly total catches were calculated from National Marine Fisheries Service (NMFS) statistics for the commercial and recreational fisheries of the west coast of Florida (http://www.st.nmfs.noaa.gov/index; http://www.st.nmfs.noaa.gov/recreational-fisheries/index; Fig. 4).

Predation mortalities

Each school *i* has a maximum food ration in biomass at each sub-time step *subdt*, $Y^*_{i,subdt}$, determined from the maximum annual ingestion rate of the HTL group to which its belongs; due to a lack of species-specific information, we set the maximum ingestion rate of all HTL groups to 3.5 g of food per g of individual and per year (Shin and Cury, 2011, 2004). Any model organism *j* present in the same model cell as school *i* (*j* belonging either to a HTL group or to a LTL group) could be preyed upon by *i* provided that model organism *j* (1) falls in the feeding size range of *i*, as determined by predator/prey size ratios (Table 5); and (2) is accessible to *i*, as determined by accessibility coefficients. Therefore, if the total biomass of prey accessible to school *i* at sub-time step *subdt* is greater than $Y^*_{i,subdt}$, then, provided that model organism *j* falls in the feeding size range of school *i*, the biomass of *j* consumed by *i* at *subdt* ($B^{\Pr eyed}_{j,i,subdt}$) is equal to:

$$B^{\Pr eyed}_{j,i,subdt} = \frac{B^{Access}_{j,i,subdt}}{\sum_j B^{Access}_{j,i,subdt}} Y^*_{i,subdt} \qquad (1)$$

where $B^{Access}_{j,i,subdt}$ is the biomass of *j* accessible to school *i* at sub-time step *subdt*. Otherwise, $B^{\Pr eyed}_{j,i,subdt}$ is equal to $B^{Access}_{j,i,subdt}$, which is given by:

$$B^{Access}_{j,i,subdt} = \delta_{j,i} B_{j,subdt} \qquad (2)$$

where $\delta_{j,i}$ is the accessibility of model organism *j* to school *i*; and $B_{j,subdt}$ is the biomass of model organism *j* at sub-time step *subdt*. The accessibility coefficients of the different life stages of the HTL groups ('life-stage groups') to each other were taken from Grüss et al.

(2015) (Tables 6 and 7), while the accessibility of a given LTL group *j* to school *i* (in %) is evaluated as:

$$\delta_{j,i} = \rho_{j,i}.\alpha_j \tag{3}$$

where $\rho_{j,i}$ is the theoretical accessibility coefficient of LTL group *j* to the HTL group and life stage to which school *i* belongs, which was taken from Grüss et al. (2015) (Tables 8 and 9); and α_j the availability coefficient of LTL group *j* to all HTL groups, which is estimated from the calibration process of OSMOSE-WFS (see below).

Then, the food ration in biomass of school *i* at sub-time step *subdt* is obtained as:

$$Y_{i,subt} = \sum_j B^{\Pr eyed}_{j,i,subdt} \tag{4}$$

When the mortality event is completed, i.e., when the 10 sub-time steps are completed, the predation mortality rate of model organism *j* by school *i* at time step *t* is calculated as:

$$M_{predation\ j,i,t} = Z_{j,t} \frac{\sum_{subdt} B^{\Pr eyed}_{j,i,subdt} \big/ W_j}{N^{Dead}_{j,t}} \tag{5}$$

where $N^{Dead}_{j,t}$ is the total number of dead individuals of model organism *j* when sub-time steps are completed; W_j is the average weight of individuals of model organism *j*; and $Z_{j,t}$ is the total mortality rate of model organism *j*, which is calculated as:

$$Z_{j,t} = \ln\left(\frac{N_{j,t}}{N_{j,t} - N^{Dead}_{j,t}}\right) \tag{6}$$

where $N_{j,t}$ is the abundance of model organism *j* at the beginning of the time step t.

Starvation mortality

The starvation mortality applied to school *i* at sub-time step *subdt*, $M_{starvation\ i,subdt}$, depends on the predation efficiency of this school at time step *t-1*, $\xi_{i,t-1}$. Specifically, if $\xi_{i,t-1}$ is less than the critical predation efficiency ensuring body maintenance of the HTL group to which school *i* belongs, ξ_i^{crit}, then school *i* undergoes a starvation mortality at sub-time step *subdt* increasing linearly with the decrease of $\xi_{i,t-1}$ (Shin and Cury, 2001, 2004):

$$M_{starvation\ i,subdt} = \frac{M_{starvation\ i}^{\max} - \dfrac{M_{starvation\ i}^{\max}}{\xi_i^{crit}} \xi_{i,t-1}}{nsubdt} \tag{7}$$

where $M_{starvation\ i}^{\max}$ is the maximum starvation mortality rate of school *i* at any monthly time step, determined for the HTL group to which school *i* belongs; and *nsubdt* is the number of sub-time steps considered during the mortality event (*nsubdt* = 10). The predation efficiency of school *i* at *t*, $\xi_{i,t}$, is given by :

$$\xi_{i,t} = \frac{\sum_{subdt} Y_{i,subdt}}{Y_i^*} \tag{8}$$

Due to a lack of species-specific information, for all HTL groups, we set critical predation efficiency to 0.57 and maximum starvation mortality to 0.3 year^{-1} (Shin and Cury, 2001, 2004).

Growth

When the predation efficiency of school i at time t is greater than ζ_i^{crit}, its growth in length at time t ($\Delta L_{i,t}$) varies between 0 and twice the mean length increase ΔL calculated from a von Bertalanffy model, depending on $\xi_{i,t}$ (Shin and Cury, 2001, 2004):

$$\Delta L_{i,t} = \frac{2\Delta L}{1-\zeta_i^{crit}}\left(\xi_{i,t} - \zeta_i^{crit}\right) \tag{9}$$

A von Bertalanffy model is used to calculate mean length increase above a threshold age A_{thres} determined for each HTL group from the literature. Below A_{thres}, a simple linear model is used. The rationale behind this is that von Bertalanffy parameters are usually estimated from data excluding youngs of the year or including only very few of them. Assuming a linear growth between age 0 day and A_{thres} ensures a more realistic calculation of mean length increases for early ages of HTL groups (Travers, 2009). The weight of school i at time t is evaluated from the allometric relationship:

$$W_{i,t} = cL_{i,t}{}^{b} \tag{10}$$

where b and c are allometric parameters for the HTL group to which school i belongs.

Reproduction

Any school whose length is greater than the length at sexual maturity L_{mat} reproduces at the end of each time step, allowing for the generation of new schools at the eggs stage for the next time step. At the scale of the HTL group, the number of eggs produced at time t ($N_{0,t}$) is calculated as:

$$N_{0,t} = SR.\Phi^{Month}\Theta SSB_t \quad if\ t = Month \tag{11}$$

where SR is the female: male sex ratio of the HTL group; Θ the relative annual fecundity of the group (number of eggs spawned per gram of mature female per year); Φ^{Month} the probability for the HTL group to spawn a given month relatively to the other months of the year; SSB_t the spawning stock biomass of the HTL group at time t. In the absence of information, we assumed no seasonality of reproduction for reef omnivores. The Φ^{Month} parameters of all other HTL groups were estimated from the literature (Fig. 5 and Table 4). The eggs of all HTL groups are allocated a size of 1 mm, which appears to be a representative average estimate for marine fish species regardless of the body size of the adults (Cury and Pauly, 2000), and a weight of 0.0005386 g, considering eggs as spheres with water density.

It can be noted that, since the growth of schools is evaluated in relation to their predation efficiency, the number of eggs produced at each time step, which depends on biomass (Eq. 9), also depends implicitly on the food intake of schools (Shin and Cury, 2001, 2004).

Parameterization of OSMOSE-WFS

The spatial domain of OSMOSE-WFS corresponds to that considered implicitly in the non-spatial WFS Reef fish Ecopath model (Chagaris, 2013); it extends from approximately 25.2° N to 31°N in latitude and from approximately 80.2°W to 87°W in longitude and comprises 465 square cells in a grid with closed boundaries (Fig. 1).

The growth and reproduction parameters of the HTL groups and their mortality parameters other than those related to predation and starvation processes are detailed in Table 3, along with their sources. It is worth noting that two HTL groups considered in OSMOSE-WFS, red grouper and gag, are protogynous, i.e., these species mature first as females and then change sex to males (Coleman et al., 1996; Koenig et al., 1996). Explicitly considering sex change in OSMOSE would necessitate differentiating between female and male fish schools. Furthermore, egg fertilization of protogynous species may decrease when fishing increases female: male sex ratio above a certain threshold, although solid empirical evidence of this phenomenon is lacking (Coleman et al., 1996; Koenig et al., 1996; Fitzhugh et al., 2006). For sake of simplicity, we chose to not represent sex change in OSMOSE-WFS, though we accounted for sex ratios biased towards females in red grouper and gag (Table 3). Moreover, the inverse estimation of the mortality of eggs and larvae, *M0*, through model calibration compensates for not explicitly representing the numerous processes affecting the survival of the first life stage including egg fertilization.

Calibration of OSMOSE-WFS

OSMOSE-WFS was calibrated so that the biomasses of the HTL groups represented in the model match values of biomasses observed over the period 2005-2009, hereafter referred to as ‘reference biomasses’. Mean reference biomasses are associated with valid intervals, i.e., minimum and maximum possible values, accounting for variability and uncertainty of mean biomass estimates over the period 2005-2009 (Table 10). While ensuring that the mean biomasses predicted by OSMOSE-WFS when the model reaches a steady-state are on average within valid intervals, the calibration process allows to estimate unknown parameters, i.e., the mortality rates of the eggs and larvae (0-1 month old individuals) of HTL groups (referred to as ‘larval mortality rates’; *M0* parameters) and availability coefficients of LTL groups to all HTL groups (α parameters). OSMOSE-WFS is a stochastic model due to the distribution of limited numbers of schools over space using density maps and the implementation of random walk movements when the distribution of schools remains static. Because OSMOSE-WFS is an individual-based and stochastic model, classical derivative-based optimization methods cannot be used for its calibration. Therefore, we used an evolutionary algorithm (EA) recently developed by Oliveros-Ramos and Shin (in prep.) for the calibration of complex stochastic models, based on a previous simpler version (Duboz et al., 2010).

The EA assumes that biomass errors are log-normally distributed and uses likelihood objective functions. It was applied to estimate a set of 21 unknown parameters, comprising the *M0* parameters of the twelve HTL species represented in OSMOSE-WFS and the α parameters of the nine LTL groups considered in the model. The 21-dimensional search space corresponded to search intervals of [0; 18 month^{-1}] for *M0* parameters and [0; 1] for α parameters.

The calibration process of OSMOSE models is an iterative rather than a one-shot process. In addition to estimating the values of unknown parameters, the process is useful to detect inconsistencies in model configuration, leading to adjustments. Thus, the L_{pred}/L_{prey}'s of some HTL groups needed to be altered during the calibration process of OSMOSE-WFS so as to constrain diets, essentially to prevent a biomass outburst for some HTL groups.

Systems modeled in OSMOSE generally stabilize after a period equal to approximately twice the maximum age of the longest-lived HTL group being explicitly considered. Red snapper is the longest-lived HTL group currently represented in OSMOSE-WFS and lives up to 57 years (SEDAR 7, 2005). Therefore, OSMOSE-WFS was run for 134 years to make sure that the model reaches a steady state and only the last twenty years of simulation (years 114 to 134) were averaged and analyzed in the EA.

Analyses conducted with OSMOSE-WFS

Once OSMOSE-WFS was calibrated, the model was used to evaluate the trophic structure of the West Florida Shelf in the 2000s, with a focus on the natural mortality rates of red grouper. The following outcomes from OSMOSE-WFS were compared to empirical data or outcomes from WFS Reef fish Ecopath (Chagaris, 2013): (1) the diet composition of HTL groups, expressed in percentage of mass of prey groups; (2) the trophic level (TL) of HTL groups and that of the HTL community; and (3) the annual instantaneous natural mortality rates of different life stages and age classes of red grouper.

Since OSMOSE is a stochastic model, 10 simulation replicates were considered for analyzing the outcomes of the last 20 years of simulation (i.e., years 114 to 134) conducted with OSMOSE-WFS. The maximum number of schools per annual cohort was set to 240, so as to ensure long-term system stability while allowing for reasonable computation time.

Diet compositions

In order to evaluate the validity of our model, we compared the diets predicted by OSMOSE-WFS to diets reconstructed from empirical data (‘observed diets’) as well as the TLs obtained with OSMOSE-WFS to those in WFS Reef fish Ecopath. Observed diets were reconstructed from stomach contents data collected by the Florida Fish and Wildlife Research Institute (FWRI) and information available in published studies.

For purpose of comparison with WFS Reef Fish Ecopath, only individuals older than 1 month were included in the calculation of the diet composition of HTL groups, except for shrimps for which only juveniles were included (i.e., individuals smaller than 8 cm; Hart and Nance, 2010). For all HTL groups, individuals younger than 1 month were assumed to belong to ichthyoplankton, and shrimps older than 1 month and smaller than 8 cm were considered to belong to the small mobile epifauna group. For king mackerel, red grouper, gag grouper and red snapper which are represented by multi-stanza populations in WFS Reef fish Ecopath (Chagaris, 2013), diet output from OSMOSE-WFS were detailed by stanzas (Table 11).

TLs

TLs provided by Ecopath rely on predetermined dietary linkages and relative biomasses of prey in the diet of predators. By contrast, the TLs predicted by OSMOSE emerge from size-based trophic interactions. Under the assumption that the turnover rate of tissues is 2 months, the trophic level of each school *i* at time *t*, $TL_{i,t}$, is calculated in OSMOSE-WFS as (Travers et al., 2010):

$$TL_{i,t} = \frac{\sum_{t=t-2}^{t=t-1} \Delta W_{i,t} \left(1 + \sum_{j} TL_{j,t} DC_{j,i,t}\right)}{\sum_{t=t-2}^{t=t-1} \Delta W_{i,t}} \tag{12}$$

where $DC_{j,i,t}$ is the proportion of prey *j* in the diet of school *i* at time *t*; and $\Delta W_{i,t}$ is the weight increase of school *i* at time *t*. The mean TL of each HTL group at time *t* is then calculated as the average of the TLs of all the schools of the HTL group at *t* weighted by the schools biomass at *t*. Following Travers (2009), we assume that the TL of eggs is identical to that of first-feeding larvae (TL = 3), and that individuals that have not fed enough to fulfill maintenance in the previous two months keep their previous TL. We also consider that the TL of LTL groups is constant through time. TL of LTL groups varies from 1 (small phytoplankton, and diatoms) to 2.5 (echinoderms/large gastropods) (Table 1). The mean TL of the HTL community at time *t* is calculated as the average of the TLs of all HTL groups at *t* weighted by the HTL groups' biomass at *t*.

Red grouper natural mortality rates

The annual natural mortality rates we evaluated for red grouper from simulations of OSMOSE-WFS consist of: (1) the total instantaneous natural mortality rate (M); (2) the total instantaneous predation mortality rate ($M_{predation}$); and (3) the instantaneous natural mortality rate M_{others}, which is the sum of the mortality due to marine organisms and events (e.g., red tide blooms, diseases) that are not considered in OSMOSE-WFS (D) and the instantaneous starvation mortality rate ($M_{starvation}$).

These natural mortality rates were evaluated for: (1) younger juvenile, older juvenile and adult red groupers so as to allow for comparisons with natural mortality rates predicted by WFS Reef fish Ecopath; and (2) different age classes of red grouper (younger juveniles, 1-2 year old individuals, 2-3 years old individuals, …, 8-9 years old individuals, 9+ years old individuals). Note that, in WFS Reef fish Ecopath, M is the sum of $M_{predation}$ and unexplained mortality, which is equivalent to M_{others} evaluated with OSMOSE-WFS (Chagaris, 2013).

Results

Calibration of OSMOSE-WFS

Using the EA, we obtained a fully calibrated OSMOSE-WFS model such that the biomasses of all HTL groups fell on average within valid intervals over the last 20 years of simulation, i.e., after 115 to 134 years of simulation (Fig. 6). Among the different simulation replicates, the biomasses of all HTL groups except amberjacks, red snapper and shrimps were always within valid intervals from year 114 to year 134. However, the biomasses of amberjacks, red snapper and shrimps were rarely outside valid intervals from year 114 to year 134. The system modeled in OSMOSE-WFS reached a steady state after approximately 70 years of simulation. The biomasses of the sardine-herring-scad complex, anchovies and silversides, coastal omnivores and reef omnivores showed a strong oscillatory behavior. This oscillatory behavior is at times irregular due to the stochasticity of the model (Figs. 7a).

Availability coefficients of LTL groups to all HTL groups (α parameters) can be divided into three categories. The first category consists of small phytoplankton and large mesozooplankton, whose α is high (Table 1). Meiofauna, small copepods, small infauna, small mobile epifauna and echinoderms/large gastropods constitute the second category, characterized by a low α. The third category includes diatoms and bivalves whose α is very low.

Monthly larval mortality rates (i.e., *M0* parameters) could be divided into three categories (Table 6). The first category is made of king mackerel, amberjacks, red grouper, gag grouper, red snapper, shrimps and large crabs, whose *M0* is extremely high (greater than 14 month^{-1}). The second category consists of reef carnivores, which have a very high *M0* (12.70 month^{-1}). Finally, the third category includes all the other HTL groups represented in OSMOSE-WFS, i.e., the sardine-herring-scad complex, anchovies/silversides, coastal omnivores and reef omnivores. The *M0* of these HTL groups varies between 4.85 and 9.45 month^{-1}. The strong oscillatory behavior of the biomasses of the sardine-herring-scad complex, anchovies and silversides, coastal omnivores and reef omnivores observed in Figs. 7a is most likely due to their small *M0*.

Diets and TLs

We used the comparison of the diets predicted by OSMOSE-WFS to observed diets and of the TLs provided by OSMOSE-WFS to TLs in WFS Reef fish Ecopath as a means to validate OSMOSE-WFS structure and parameterization.

OSMOSE-WFS and observations agree more or less as to the specific composition of the diet of HTL groups and stanzas, due to taxonomic resolution captured by OSMOSE-WFS. Nonetheless, OSMOSE-WFS is in full agreement with observations as to the body size and ecological niche of prey of the different HTL groups (results not shown here).

The mean TLs in output of OSMOSE-WFS and WFS Reef fish Ecopath were relatively similar, as well as the ranks of the TL values (Fig. 8). However, we can note a noticeable difference between the mean TL of large crabs predicted by OSMOSE-WFS and that predicted by WFS Reef fish Ecopath (Fig. 8).

Red grouper natural mortality rates

The annual total instantaneous natural mortality rate *M* of younger juvenile red grouper is very high in both OSMOSE-WFS and WFS Reef fish Ecopath, yet significantly higher in OSMOSE-WFS (2.71±0.54 year^{-1} in OSMOSE-WFS vs. 2 year^{-1} in WFS Reef fish Ecopath; Fig. 9a). This mortality rate essentially results from predation in OSMOSE-WFS vs. 'unexplained' causes in WFS Reef fish Ecopath (Fig. 9a). The main predators of younger juvenile red grouper in OSMOSE-WFS are, in order of importance: adult red grouper (responsible for 39% of the predation mortality of younger juvenile red grouper), adult king mackerel (17%), adult gag grouper (17%), amberjacks (10%), reef carnivores (7%) and adult red snapper (4%) (Fig. 10a). In WFS Reef fish Ecopath, older juvenile red grouper, adult king mackerel and amberjacks are responsible for, respectively, 37%, 33% and 3% of the total predation mortality of younger juvenile gag grouper (Fig. 10b). 27% of the total predation mortality of younger juvenile red grouper in WFS Reef fish Ecopath is caused by HTL groups that are not represented in OSMOSE-WFS, of which mainly 'other shallow water groupers' (*Epinephelus* sp. and *Mycteroperca* sp.) and yellowedge grouper (*Epinephelus flavolimbatus*).

The annual total instantaneous natural mortality rate M of older juvenile red grouper is relatively high and results mainly from causes other than predation in both OSMOSE-WFS and WFS Reef fish Ecopath (Fig. 9b). However, this mortality rate is more than three times higher in WFS Reef fish Ecopath than in OSMOSE-WFS (0.8 year^{-1} vs. 0.24 ± 0.05 year^{-1}). Major predators of older juvenile red grouper include adult gag grouper, amberjacks and adult king mackerel in both OSMOSE-WFS and WFS Reef fish Ecopath (responsible for, respectively, 43%, 30% and 22% of the predation mortality of older juvenile red grouper in OSMOSE-WFS; Figs. 10 c and d). Adult red grouper is another major predator of younger juvenile red grouper in OSMOSE-WFS (responsible for 5% of the predation mortality of the stanza; Fig. 10 c). 22% of the total predation mortality of younger juvenile red grouper in WFS Reef fish Ecopath is caused by HTL groups that are not represented in OSMOSE-WFS, of which mainly 'other shallow water groupers' and black grouper (*Mycteroperca bonaci*) (Fig. 10d).

The annual total instantaneous natural mortality rate M of adult red grouper is relatively low and almost entirely due to causes other than predation in both OSMOSE-WFS and WFS Reef fish Ecopath (0.11 ± 0.01 year^{-1} in OSMOSE-WFS vs. 0.16 year^{-1} in WFS Reef fish Ecopath; Fig. 9c). In OSMOSE-WFS, the M of adult red grouper is mainly due to starvation plus organisms and events (e.g., red tides) not represented in OSMOSE-WFS, i.e., M_{others}. In WFS Reef fish Ecopath, adult red grouper is preyed upon by the billfish and tunas' group only, and its predation mortality rate is negligible compared to its mortality rate due to 'unexplained' causes (Fig. 9c and 10f). The M of adult red grouper due to organisms and events not represented in OSMOSE-WFS was estimated from the predation mortality rate of adult red grouper by animals that are considered in WFS Reef fish Ecopath but not in OSMOSE-WFS. Therefore, the bulk of the M of red grouper in OSMOSE-WFS is caused by starvation. Only three HTL groups and stanzas feed on adult red grouper in this model: adult gag grouper, amberjacks and adult king mackerel, which contribute, respectively, to 80%, 15% and 5% of the total predation mortality of the stanza (Fig. 10e).

We also estimated instantaneous natural mortality rates for different age classes of red grouper (younger juveniles, 1-2 year old individuals, 2-3 years old individuals, …, 8-9 years old individuals, 9+ years old individuals), which are provided in Fig. 11 and Table 12. The annual total instantaneous natural mortality rate M of red grouper decreases with age. The mean M of red grouper is very high for younger juveniles (2.71 year^{-1}), relatively high for 1-2 years old individuals (0.47 year^{-1}) and becomes low at age 2 years ($\leq$ 0.18 year^{-1}) (Figs. 11a and b and Table 12). Predation is the major source of mortality of younger juvenile and 1-2 years old red groupers, while the bulk of the mortality of 2+ years old red groupers is due to causes other than predation (Figs. 11c-f). The mean predation mortality rate (mean $M_{predation}$) of younger juveniles and 1-2 years old individuals is, respectively, very high and relatively high (2.64 year^{-1}and 0.31 year^{-1}, respectively; Fig. 11c). The mean $M_{predation}$ of red grouper becomes very low at age 2 years ($\leq$ 0.01 year^{-1}) (Fig. 11d). The mean mortality rate due causes other than predation (mean M_{others}) of red grouper is 0.06 year^{-1} for younger juveniles, is almost three times higher for 1-5 years old individuals (0.15-0.16 year^{-1}), and decreases with age starting at age 5 years (0.13 year^{-1} for 5-6 years old individuals and 0.05 year^{-1} for 9+ years old individuals) (Figs. 11e and f).

Discussion

In the present study, we introduced a new steady state version of the OSMOSE-WFS model, describing trophic interactions in the West Florida Shelf ecosystem in the 2000s. We detailed the parameterization of this model as well as its calibration, which proved to be challenging. We then validated the model by comparing the predicted diets to observed diets, and the predicted TLs to TLs from the WFS Reef fish Ecopath model. Finally, we used

OSMOSE-WFS to evaluate natural mortality rates of different life stages and age classes of red grouper for SEDAR 42.

Calibration of OSMOSE-WFS

The calibration of the OSMOSE-WFS model allowed us to estimate unknown parameters, which were here the availability coefficients of LTL groups to all HTL groups and the mortality rates of eggs and larvae of HTL groups (also referred to as 'larval mortality rates').

The availability coefficients of LTL groups determined during calibration are all very low except those of small phytoplankton and large mesozooplankton.

Mortality rates of eggs and larvae in OSMOSE-WFS represent mortality sources other than predation by OSMOSE-WFS predators. These parameters are meaningful ecologically and quantitatively in the case where the fecundity parameters and the target reference biomass are reliable. Otherwise, they just act as calibration parameters ensuring (among other parameters involved in the calibration process) that biomass levels in OSMOSE-WFS match observed biomass levels. The relatively low larval mortality rates obtained for the sardine-herring-scad complex, anchovies/silversides, coastal omnivores and reef omnivores reflect the fact that explicit predation and events not explicitly considered in OSMOSE-WFS (e.g., predation by organisms not represented in the model, red tide blooms) were the main sources of mortality in OSMOSE-WFS.

Moreover, the calibration process of OSMOSE-WFS showed that outputs of the model were very sensitive to the minimum and maximum predator/prey size ratios, which needed to be adjusted cautiously (1) due to the fact that we switched from the 'iterative mortality algorithm' to the 'stochastic mortality algorithm' in OSMOSE-WFS (http://www.osmose-model.org/); and (2) so as to ensure that presence/absence of a given prey item in the diet of HTL groups was correct (Table 5). Accessibility coefficients and theoretical accessibility coefficients are other uncertain OSMOSE parameters that can be adjusted at the time of model calibration to constrain the diets of HTL groups.

Validation of OSMOSE-WFS

The outputs of the new steady-state version of the OSMOSE-WFS model are in full agreement with observations as to the body size and ecological niche of prey of the different HTL groups, and to a lesser extent in agreement with the observed species composition of the diet of HTL groups. Moreover, the mean TLs predicted by OSMOSE-WFS and those predicted by WFS Reef fish Ecopath are relatively similar, as well as the ranks of the TL values. These results validate the new steady-state version of the OSMOSE-WFS model.

One major discrepancy that we noted between the OSMOSE-WFS and WFS Reef fish Ecopath models is the mean TL of large crabs, which is significantly higher in OSMOSE-WFS due to the greater proportion of HTL prey in the diet of large crabs in that model (results not shown here).

Natural mortality rates of red grouper

OSMOSE-WFS and WFS Reef fish Ecopath are often in disagreement on the magnitude of the instantaneous natural mortality M of the different stanzas of red grouper. In both OSMOSE-WFS and WFS Reef fish Ecopath, the M of younger juvenile red grouper and older juvenile red grouper is, respectively, very high and relatively high. However, the M of younger juvenile red grouper is significantly higher in OSMOSE-WFS than in WFS Reef fish Ecopath, while the *M* of older juvenile red grouper estimated by WFS Reef fish Ecopath is almost three times higher than that estimated by OSMOSE-WFS. On the other hand, both OSMOSE-WFS and WFS Reef fish Ecopath predict the *M* of adult red grouper to be relatively low.

By contrast, OSMOSE-WFS and WFS Reef fish Ecopath often agree on the main causes of the *M* of the different stanzas of red grouper. Causes other than predation are responsible for the majority of the natural mortality of all life stages of red grouper in WFS Reef fish Ecopath. In OSMOSE-WFS, this is also the case for all stanzas of red grouper but younger juveniles, which are under very high predation pressure. Predation mortality in OSMOSE-WFS is not conditioned by a diet matrix, but rather constrained by predator/prey size ratios, spatial co-occurrence and, to a lesser extent, accessibility coefficients primarily reflecting degrees of overlap between model groups in the vertical dimension. Thus, due to their relatively small body size, younger juveniles of red grouper are potential prey of different life stages of various small and large predators in OSMOSE-WFS.

The *M* of adult red grouper in both OSMOSE-WFS and WFS Reef fish Ecopath is very low and almost entirely due to causes other than predation (starvation in OSMOSE-WFS and ‘unexplained’ causes in WFS Reef fish Ecopath). Adult red grouper has three predators in OSMOSE-WFS, which are adult gag grouper, amberjacks and adult king mackerel. Only the billfish and tunas’ group feeds on adult red grouper in WFS Reef fish Ecopath. This is because a limited number of diet studies on large offshore predators are available, and encounters with fish large enough to consume an adult red grouper are rare during most research surveys (Chagaris and Mahmoudi, 2013). However, on the West Florida Shelf, goliath grouper (*Epinephelus itajara*), a species sharing the ecological niche of red grouper and gag grouper, was observed feeding on adult gag grouper (D. C. Parkyn, School of Forest Resources and Conservation, University of Florida, pers. comm.).

The WFS Red tide EwE model (Gray et al., 2013; Gray, 2014) is going to be updated and used to inform the SEDAR 42 Assessment Workshop (Sagarese et al., in prep.). WFS Red tide EwE will provide estimates of predation mortality, mortality due to red tide and 'unexplained mortality' for juvenile and adult red groupers over the period 2005-2009. We will then be able to compare the natural mortality rates of the life stages of red grouper predicted by three different modeling platforms (i.e., WFS Reef fish Ecopath/EwE, WFS Red tide EwE and OSMOSE-WFS) to further inform SEDAR 42.

We produced estimates of instantaneous natural mortality for different age classes of red grouper over the recent period (summarized in Table 12), which could be used in the Stock Synthesis assessment model employed for SEDAR 42. Several methods have been proposed for incorporating estimates of instantaneous natural mortality into a single-species stock assessment model, each with advantages and disadvantages. The best method depends on the specifics of the assessment model being used, and which is most appropriate for Gulf of Mexico red grouper is beyond the scope of this paper and will be discussed elsewhere. In any case, the definition of age classes of red grouper presented in this paper (i.e., younger juveniles, 1-2 year old individuals, 2-3 years old individuals, …, 8-9 years old individuals, 9+ years old individuals) can be altered if necessary

Ongoing work with OSMOSE-WFS

OSMOSE-WFS, like any other ecosystem simulation model, is a simplified representation of a much more complex system. To be able to build a consistent multi-model approach for the West Florida Shelf in the long term, we decided to develop a new steady-state version of the OSMOSE-WFS model as parsimonious as possible in the first place. This model will benefit from many short-term and long-term improvements.

Short-term improvements include: (1) the adjustment of the minimum and maximum predator/prey size ratios of some HTL groups so as to obtain entirely satisfactory diet patterns for all the HTL groups represented in OSMOSE-WFS; (2) the introduction of fishing selectivity patterns in the model; and (3) the introduction of fisheries catch data in the calibration process of the model.

Long-term improvements include, but are not limited to: (1) the introduction of a few additional HTL and LTL groups in OSMOSE-WFS; (2) the forcing of the model by plankton fields predicted by the LTL model COSINE-13 applied to the Gulf of Mexico (deRada et al., 2009) so as to increase spatio-temporal variability in LTL biomass in OSMOSE-WFS; (3) the explicit consideration of red tide blooms in OSMOSE-WFS; and (4) the expansion of the current steady-state OSMOSE-WFS model to a dynamic model so as to be able to provide time-specific estimates of natural mortality rates to SEDAR.

Last but not least, during the coming months, the new version of the OSMOSE-WFS model will be used to explore simple fishing mortality scenarios and to evaluate harvest control rules (HCRs) implemented for GOM red grouper. An evaluation of the performance of HCRs implemented for GOM red grouper under alternate natural mortality scenarios is critical given the severe red tide event that occurred in the northeast GOM during the summer 2014, which led to the death of a large and uncertain number of red grouper (http://myfwc.com/research/redtide/statewide/).

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Tables

Table 1. Parameters of the low trophic level (LTL) groups considered in OSMOSE-WFS, their mean biomass in the West Florida Shelf over the period 2005-2009 according to WFS Reef fish Ecopath (Chagaris, 2013), and their availability coefficients to all high trophic level (HTL) groups (α) estimated through the calibration of OSMOSE-WFS.

LTL group	Size range (mm)	Trophic level	Biomass in WFS Reef fish Ecopath (tons)	α parameter
Small phytoplankton	0.002-0.02	1 *	2 309 400	0.4182
Diatoms	0.02-0.2	1 *	2 309 400	2.10^{-4}
Small copepods	0.2-1.3 [a,b,c]	2.09 *	1 550 700	$9.42.10^{-2}$
Large mesozooplankton	1-3 [d]	2.28 *	1 148 400	0.3155
Meiofauna	0.065-0.5 [e]	2.13 *	2 315 800	$4.9.10^{-3}$
Small infauna	0.5-20 [e]	2.25 *	3 283 800	3.10^{-3}
Small mobile epifauna	0.5-20 [f]	2.25 *	1 979 600	3.10^{-3}
Bivalves	0.2-95 [f,g]	2 *	8 508 800	2.10^{-4}
Echinoderms and large gastropods	20-450 [f,h]	2.5 *	3 085 908	5.10^{-3}

[a] Grice (1960) - [b] Ferrari (1975) - [c] Turner (2004) - [d] Kimmel et al. (2010) - [e] SUSFIO (1977) – [f] Okey and Mahmoudi (2002) - [g] Rosenberg (2009) - [h] Miller and Pawson (1984) - * Arbitrarily set

Table 2. High trophic level (HTL) groups explicitly considered in OSMOSE-WFS. The reference species of each group is indicated in bold.

HTL group	Species
King mackerel	**King mackerel (*Scomberomorus cavalla*)**
Amberjacks	**Greater amberjack (*Seriola dumerili*)** , banded rudderfish (*Seriola zonata*), lesser amberjack (*Seriola fasciata*)
Red grouper	**Red grouper (*Epinephelus morio*)**
Gag grouper	**Gag grouper (*Mycteroperca microlepis*)**
Red snapper	**Red snapper (*Lutjanus campechanus*)**
Sardine-herring-scad complex	**Scaled sardine (*Harengula jaguana*)**, Spanish sardine (*Sardinella aurita*), Atlantic thread herring (*Opisthonema oglinum*), round scad (*Decapterus punctatus*)
Anchovies and silversides	**Bay anchovy (*Anchoa mitchilli*)**, striped anchovy (*Anchoa hepsetus*), silversides (Atherinidae spp.), alewife (*Alosa* sp.)
Coastal omnivores	**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	**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*), scopian 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	**Doctorfish (*Acanthurus chirurgus*)**, other surgeons (Acanthuridae spp.), blue angelfish (*Holacanthus bermudensis*), gray angelfish (*Pomacanthus arcuatus*), cherubfish (*Cantropyge 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*), bibled goby (*Coryphopterus glaucofraenum*), Bermuda chub (*Kyphossus sectarix*)
Shrimps	**Pink shrimp (*Farfantepenaeus duorarum*)**, brown shrimp (*Farfantepenaeus aztecus*), white shrimp (*Litopenaeus setiferus*), other shrimp species
Large crabs	**Blue crab (*Callinectes sapidus*)**, stone crabs (*Menippe mercenaria* and *Menippe adina*), horseshoe crab (*Limulus polyphemus*), hermits crab (e.g., *Pylopagurus operculatus* and *Clibanaris vittatus*), spider crabs (e.g., *Stenocionops furcatus*), arrow crabs (e.g., *Stenorynchus seticornis*)

Table 3. (a) Growth, reproduction and mortality parameters of the 12 high trophic level groups explicitly considered in OSMOSE-WFS, and (b) sources used to estimate these parameters. L_{∞}: maximum size – K: instantaneous growth rate at small size- t_0: theoretical age of zero length - A_{max}: threshold age below which a linear growth model is used to calculate mean length increase – c: constant of proportionality of the allometric length-weight relationship - b: exponent of the allometric length-weight relationship - Θ: annual number of eggs per gram of mature female – SR: female:male sex ratio – L_{mat}: size at sexual maturity – A_{max}: longevity – D: mortality rate due to marine organisms and events (e.g., red tide blooms, diseases) not represented in OSMOSE-WFS – L_{rec}: size of recruitment into fisheries – F_{annual}: annual fishing mortality rate - N/A: not applicable. All the parameters related to body size in this table are for sizes in cm TL unless otherwise specified. TL: total length – FL: fork length – CW: carapace width. We highlighted in grey parameter estimates imported from studies conducted on species related to the reference species of the HTL group elsewhere than in Southeastern US.

a) Parameter values	Growth						Reproduction				Mortality		
	L_∞ *(cm)*	***K*** *(yr^{-1})*	***t_0*** *(yr)*	***A_{thres} (yrs)***	***c*** *($g.cm^{-3}$)*	***b***	***Θ*** *($eggs.g^{-1}$)*	***SR***	***L_{mat} (cm)***	***A_{max}*** *(yrs)*	***D*** *(yr^{-1})*	***L_{rec} (cm)***	***F_{annual} (yr^{-1})***
King mackerel	152.2	0.17	-1.83	1	$8.5.10^{-3}$ (FL)	2.98	1904	0.5	73.4	27	0.28	32.5	0.16
Amberjacks	164.5	0.14	-2.53	1	$3.25.10^{-2}$ (FL)	2.87	1208	0.55	90.3	15	0.01	14.8	0.61
Red grouper	85.4	0.16	-0.19	1	$8.3.10^{-3}$	3.14	1419	0.78	34.1	29	0.02	25.2	0.22
Gag grouper	130	0.14	-0.19	1	$1.07.10^{-2}$	3.03	1068	0.92	46.8	31	0.01	34.3	0.53
Red snapper	94.1	0.18	-0.55	1	$1.67.10^{-2}$	3.06	3477	0.5	34.6	57	0.19	22.9	0.55
Sardine-herring-scad complex	19.4	0.6	-0.25	0.5	$1.06.10^{-2}$ (FL)	3.25	2640	0.5	9.3	3	1.43	8.5	0.2
Anchovies and silversides	11.1	0.36	-0.81	0.5	$1.71.10^{-2}$	2.81	3313	0.5	4.6	3	2.29	2.4	0.17
Coastal omnivores	25.7	0.33	-1.1	0.5	$1.04.10^{-2}$ (FL)	3.25	1234	0.5	15.3	7	1.1	16.5	0.12
Reef carnivores	32.7	0.19	-4.21	2	$7.8.10^{-2}$	2.75	1925	0.5	17.4	18	0.35	19	0.28
Reef omnivores	33.4	0.086	-5.76	2	$4.1.10^{-3}$ (FL)	3.53	17739	0.5	15.5	17	0.55	N/A	0
Shrimps	19.9	2.87	0	0	$7.5.10^{-3}$	3.06	83161	0.5	8	2	1.58	7.6	0.36
Large crabs	17.6	1.45	0.13	0.5	0.2275 (CW)	2.44	17802	0.5	13.1	3	0.74	12.7	0.57

b) Sources	Growth	Reproduction	Mortality
King mackerel	Godcharles and Murphy, 1986; Devries and Grimes, 1997	SEDAR 5, 2004; Fitzhugh et al., 2008	Trent et al., 1983; SEDAR 16, 2009; WFS Reef fish Ecopath
Amberjacks	Murie and Parkyn, 2008; Froese and Pauly, 2010	Harris, 2004; SEDAR 9, 2006	Diaz et al., 2005; SEDAR, 2011; WFS Reef fish Ecopath
Red grouper	SEDAR 12, 2006; SEDAR, 2009a	Coleman et al., 1996; Fitzhugh et al., 2006b; SEDAR, 2009a	Rothschild et al., 1997; SEDAR, 2009b; WFS Reef fish Ecopath
Gag grouper	SEDAR, 2009b	Fitzhugh et al., 2006a; SEDAR, 2009b	SEDAR 10, 2006; SEDAR, 2009b; SEDAR 33, in prep.; WFS Reef fish Ecopath
Red snapper	Schirripa and Legault, 1999; Wilson and Nieland, 2001	Woods et al., 2003; Fitzhugh et al., 2004; White and Palmer, 2004; SEDAR 7, 2005	Allman et al., 2002; SEDAR, 2009c; WFS Reef fish Ecopath
Sardine-herring-scad complex	Froese and Pauly, 2010	Martinez and Houde, 1975; Houde, 1977; Carpenter, 2002; B. Mahmoudi, FMRI St. Petersburg, pers. comm.	B. Mahmoudi, FMRI St. Petersburg, pers. comm.; WFS Reef fish Ecopath
Anchovies and silversides	Froese and Pauly, 2010	Robinette, 1983; Wang and Houde, 1995; Froese and Pauly, 2010	Acosta, 2000; B. Mahmoudi, FMRI St. Petersburg, pers. comm., WFS Reef fish Ecopath
Coastal omnivores	Nelson, 2002; Froese and Pauly, 2010	Caldwell, 1957; Nelson, 2002	Nelson, 2002; WFS Ecopath
Reef carnivores	Potts and Manooch III, 2001; Murie and Parkyn, 2005	de Silva and Murphy, 2001; Murie and Parkyn, 2005; Palazón-Fernández, 2007; Froese and Pauly, 2010	de Silva and Murphy, 2001; WFS Reef fish Ecopath
Reef omnivores	Kishore and Chin, 2001; Froese and Pauly, 2010	Bushnell et al., 2010; Froese and Pauly, 2010	WFS Reef fish Ecopath
Shrimps	Bielsa et al., 1983; Palomares and Pauly, 2010	Eldred et al., 1961; Martosubroto, 1974; Palacios and Racotta, 2003	Nance, 2009; Hart and Nance, 2010; WFS Reef fish Ecopath
Large crabs	Smith, 1997; Guillory et al., 2001	Tagatz, 1968; Millikin and Williams, 1984; Guillory et al., 2001	Murphy et al., 2007; WFS Reef fish Ecopath

Table 4. Sources used to estimate the seasonality of reproduction of the high trophic level (HTL) groups represented in OSMOSE-WFS. The reference species of each HTL group is indicated.

HTL group	**Reference species**	**Source**
King mackerel	King mackerel (*Scomberomorus cavalla*)	Fitzhugh et al. (2008)
Amberjacks	Greater amberjack (*Seriola dumerili*)	Harris (2004)
Red grouper	Red grouper (*Epinephelus morio*)	Fitzhugh et al. (2006b)
Gag grouper	Gag grouper (*Mycteroperca microlepis*)	Fitzhugh et al. (2006a)
Red snapper	Red snapper (*Lutjanus campechanus*)	Fitzhugh et al. (2004)
Sardine-herring-scad complex	Scaled sardine (*Harengula jaguana*)	Carpenter (2002)
Anchovies and silversides	Bay anchovy (*Anchoa mitchilli*)	Robinette (1983)
Coastal omnivores	Pinfish (*Lagodon rhomboides*)	Nelson (2002)
Reef carnivores	White grunt (*Haemulon plumieri*)	Murie and Parkyn (1999)
Shrimps	Pink shrimp (*Farfantepenaeus duorarum*)	Bielsa et al. (1983)
Large crabs	Blue crab (*Callinectes sapidus*)	Millikin and Williams (1984)

Table 5. Feeding size ranges of the high trophic level (HTL) groups explicitly considered in OSMOSE-WFS expressed as predator/prey size ratios, taken from Grüss et al. (2014a). L_{thres} is here the body size threshold that separates two sets of predator/prey size ratios for some HTL groups, one set for the juvenile individuals and one set for adult individuals - $(L_{pred}/L_{prey})_{min}$: minimum predator to prey body size ratio - $(L_{pred}/L_{prey})_{max}$: maximum predator to prey body size ratio. The values of some of the $(L_{pred}/L_{prey})_{min}$ and $(L_{pred}/L_{prey})_{max}$ reported here result from adjustments operated during the calibration process of OSMOSE-WFS. The values of $(L_{pred}/L_{prey})_{min}$ and $(L_{pred}/L_{prey})_{max}$ taken from Grüss et al. (2014a) that were altered during the calibration process are given between brackets.

	L_{thres} *(cm TL)*	$(L_{pred}/L_{prey})_{min}$		$(L_{pred}/L_{prey})_{max}$	
		Juveniles	***Adults***	***Juveniles***	***Adults***
King mackerel	73.4	6.5 (2.9)	6.5 (4.5)	11 (18)	11 (30)
Amberjacks	90.3	6.5 (4.5)	6.5 (4.5)	12	12
Red grouper	34.1	6.5 (4.5)	6.5 (4.5)	30 (40)	30
Gag grouper	46.8	5.5 (1.8)	5.5 (3.9)	23 (100)	23
Red snapper	34.6	3.5	9	30 (100)	30
Sardine-herring-scad complex	9.3	10	100	150	10000
Anchovies and silversides	4.6	20	20	500	500
Coastal omnivores	15.3	50	50	80	80
Reef carnivores	17.4	4.5	4.5	50	50
Reef omnivores	15.5	100	100	1000	1000
Shrimps	8	4.5	7.5	10000	242
Large crabs	13.1	1.1	1.1	50	50

Table 6. Accessibility of the different life stages of the HTL groups (in rows) to each other (in columns), determined from the literature and expert opinion (J. Simons, Center for Coastal Studies, Texas A&M University-Corpus Christi).

	Juvenile king mackerel	**Adult king mackerel**	**Amberjacks**	**Red grouper**	**Juvenile gag grouper**	**Adult gag grouper**	**Juvenile red snapper**	**Adult red snapper**	**Sardine-herring-scad complex**
Juvenile king mackerel	80%	80%	0%	0%	0%	0%	80%	80%	80%
Adult king mackerel	80%	80%	0%	0%	0%	0%	80%	80%	80%
Amberjacks	80%	80%	0%	0%	0%	0%	80%	80%	80%
Red grouper	80%	80%	80%	80%	80%	80%	80%	80%	40%
Juvenile gag grouper	80%	80%	80%	80%	80%	80%	80%	80%	40%
Adult gag grouper	80%	80%	80%	80%	80%	80%	80%	80%	40%
Juvenile red snapper	80%	80%	80%	80%	80%	80%	80%	80%	40%
Adult red snapper	80%	80%	80%	80%	80%	80%	80%	80%	40%
Sardine-herring-scad complex	80%	80%	80%	80%	80%	80%	80%	80%	80%
Anchovies and silversides	80%	80%	80%	80%	80%	80%	80%	80%	10%
Coastal omnivores	80%	80%	80%	80%	80%	80%	80%	80%	40%
Reef carnivores	80%	80%	80%	80%	80%	80%	80%	80%	40%
Reef omnivores	80%	80%	80%	80%	80%	80%	80%	80%	40%
Shrimps	40%	40%	40%	80%	80%	40%	80%	80%	10%
Large crabs	0%	0%	10%	80%	80%	40%	80%	40%	10%

Table 6. (continued).

	Anchovies and silversides	Costal omnivores	Reef carnivores	Reef omnivores	Shrimps	Large crabs
Juvenile king mackerel	80%	40%	80%	80%	0%	0%
Adult king mackerel	80%	40%	80%	80%	0%	0%
Amberjacks	80%	40%	80%	80%	0%	0%
Red grouper	40%	80%	80%	80%	0%	0%
Juvenile gag grouper	40%	80%	80%	80%	0%	0%
Adult gag grouper	40%	80%	80%	80%	0%	0%
Juvenile red snapper	40%	80%	80%	80%	0%	0%
Adult red snapper	40%	80%	80%	80%	0%	0%
Sardine-herring-scad complex	80%	40%	80%	80%	0%	10%
Anchovies and silversides	10%	40%	80%	80%	0%	10%
Coastal omnivores	40%	80%	80%	80%	0%	10%
Reef carnivores	40%	80%	80%	80%	0%	0%
Reef omnivores	40%	80%	80%	80%	0%	0%
Shrimps	10%	40%	80%	80%	0%	80%
Large crabs	10%	0%	80%	80%	0%	80%

Table 7. Comments on the value of some accessibility coefficients.

	Comments
Juvenile king mackerel	Accessibility of shrimps to juvenile king mackerel set to 40% to account for little overlap in the vertical dimension. Accessibility of large crabs set to 0% to account for very little overlap in the vertical dimension and a very weak preference for large crabs; according to FWRI (unpub. data), juvenile king mackerel feeds on zoeae and megalopae of large crabs, though in little quantities.
Adult king mackerel	Accessibility of shrimps to adult king mackerel set to 40% to account for little overlap in the vertical dimension. Accessibility of large crabs set to 0% to account for very little overlap in the vertical dimension and a very weak preference for large crabs; according to FWRI (unpub. data), adult king mackerel feeds on zoeae and megalopae of large crabs, though in little quantities.
Amberjacks	Accessibility of shrimps to amberjacks set to 40% to account for little overlap in the vertical dimension. Accessibility of large crabs set to 10% to account for very little overlap in the vertical dimension. Accessibility of amberjacks set to 0% to account for the fact that amberjacks are not cannibalistic according to available evidence (Froese and Pauly, 2010; FWRI, unpub. data). Accessibility of juvenile and adult king mackerels set to 0% to account for the fact that amberjacks cannot predate on king mackerels which have high swimming capabilities.
Red grouper	Accessibility of juvenile and adult king mackerels and of amberjacks to red grouper set to 0%, to account for the fact that red grouper is primarily a benthic dweller around hard bottoms and reefs, while king mackerel and amberjacks are pelagic and also fleet swimmers.
Juvenile gag grouper	Accessibility of juvenile and adult king mackerels and of amberjacks to juvenile gag grouper set to 0%, to account for the fact that gag grouper is primarily a benthic dweller around hard bottoms and reefs, while king mackerel and amberjacks are pelagic and also fleet swimmers.
Adult gag grouper	Accessibility of shrimps and large crabs to adult gag grouper set to 40% to account for little overlap in the vertical dimension. Accessibility of juvenile and adult king mackerels and of amberjacks set to 0%, to account for the fact that gag grouper is primarily a benthic dweller around hard bottoms and reefs, while king mackerel and amberjacks are pelagic and also fleet swimmers.
Adult red snapper	Accessibility of large crabs to red snapper set to 40% to account for little overlap in the vertical dimension.
Sardine-herring-scad complex	Accessibility of red grouper, gag grouper, red snapper, coastal omnivores, reef carnivores and reef omnivores to the sardine-herring-scad complex set to 40% to account for little overlap in the vertical dimension. Accessibility of anchovies/silversides set to 10% to account for weak preference. Accessibility of shrimps and large crabs set to 10% to account for very little overlap in the vertical dimension.
Anchovies and silversides	Accessibility of red grouper, gag grouper, red snapper, coastal omnivores, reef carnivores and reef omnivores to anchovies/silversides set to 40% to account for little overlap in the vertical dimension. Accessibility of anchovies/silversides set to 10%, because predation on post-larval stages of anchovies and silversides (i.e., individuals older than 1 month) is unlikely; anchovies/silversides only feed on very small prey items belonging to low trophic levels (Froese and Pauly, 2010). Accessibility of shrimps and large crabs set to 10% to account for very little overlap in the vertical dimension.
Coastal omnivores	Accessibility of king mackerel, amberjacks, the sardine-herring-scad complex, anchovies /silversides and shrimps to coastal omnivores set to 40% to account for little overlap in the vertical dimension. Accessibility of large crabs set to 0% to account for little overlap in the vertical dimension and for the fact that the morphology of coastal omnivores is not well suited to feed on large crabs.
Shrimps	Accessibility of all HTL groups to shrimps set to 0% to account for the fact that shrimps only feed on very small items, mostly very small benthic organisms, detritus and benthic algae (Eldred et al., 1961; Odum and Heald, 1972).
Large crabs	Accessibility of the sardine-herring-scad complex, anchovies/silversides and coastal omnivores to large crabs set to 10% to account for very

	little overlap in the vertical dimension. Accessibility of all other HTL fish groups set to 0% to account for the fact that large crabs can certainly capture small fish on occasion along with many other small invertebrates, and detritus, but not large fish (Darnell, 1958; Tagatz, 1968; Laughlin, 1982; Alexander, 1986; Stoner and Buchanan, 1990).

Table 8. Theoretical accessibility of LTL groups (in rows) to the different life stages of the HTL groups (in columns), determined from the literature and expert opinion (J. Simons, Center for Coastal Studies, Texas A&M University-Corpus Christi).

	Juvenile king mackerel	Adult king mackerel	Juvenile amberjacks	Adult amberjacks	Juvenile red grouper	Adult red grouper	Juvenile gag grouper	Adult gag grouper	Juvenile red snapper	Adult red snapper	Sardine-herring-scad complex	Juveniles of anchovies and silversides
Small phytoplankton	100%	0%	100%	0%	100%	0%	100%	0%	100%	0%	100%	100%
Diatoms	100%	0%	100%	0%	100%	0%	100%	0%	100%	0%	100%	100%
Small copepods	100%	0%	100%	0%	100%	0%	100%	0%	100%	0%	100%	100%
Large mesozooplankton	100%	0%	100%	0%	100%	0%	100%	0%	100%	0%	100%	100%
Meiofauna	40%	10%	10%	10%	80%	80%	80%	40%	40%	40%	10%	40%
Small infauna	40%	10%	10%	10%	80%	80%	80%	40%	40%	40%	10%	40%
Small mobile epifauna	40%	10%	10%	10%	80%	80%	80%	40%	40%	40%	10%	40%
Bivalves	40%	10%	10%	10%	10%	0%	80%	40%	10%	10%	10%	10%
Echinoderms and large gastropods	40%	10%	10%	10%	10%	0%	80%	40%	10%	10%	10%	10%

Table 8. (continued).

	Adults of anchovies and silversides	Juveniles of costal omnivores	Adults of costal omnivores	Juveniles of reef carnivores	Adults of reef carnivores	Juveniles of reef omnivores	Adults of reef omnivores	Juvenile shrimps	Adult shrimps	Juvenile large crabs	Adult large crabs
Small phytoplankton	0%	0%	0%	0%	0%	100%	0%	100%	0%	100%	0%
Diatoms	0%	0%	0%	0%	0%	100%	0%	100%	0%	100%	0%
Small copepods	100%	100%	0%	100%	0%	100%	0%	100%	0%	100%	0%
Large mesozooplankton	100%	100%	0%	100%	0%	100%	0%	100%	0%	100%	0%
Meiofauna	40%	80%	80%	80%	80%	80%	80%	80%	80%	80%	80%
Small infauna	40%	80%	80%	80%	80%	80%	80%	80%	80%	80%	80%
Small mobile epifauna	40%	80%	80%	80%	80%	80%	80%	80%	80%	80%	80%
Bivalves	10%	80%	80%	80%	80%	80%	80%	80%	80%	80%	80%
Echinoderms and large gastropods	10%	80%	80%	80%	80%	80%	80%	80%	80%	80%	80%

Table 9. Comments on the value of some theoretical accessibility coefficients.

	Comments
Juvenile king mackerel	Accessibility of the different LTL benthos groups to juvenile king mackerel set to 40% to account for little overlap in the vertical dimension.
Adult king mackerel	Accessibility of the different LTL benthos groups to adult king mackerel set to 10% to account for very little overlap in the vertical dimension.
Amberjacks	Accessibility of the different LTL benthos groups to amberjacks set to 10% to account for very little overlap in the vertical dimension.
Juvenile red grouper	Accessibility of bivalves and of echinoderms/large gastropods to juvenile red grouper set to 10% to account for very small overlap in the vertical dimension and for the fact that the morphology of red grouper is not well suited to feed on the two aforementioned LTL benthos groups.
Adult red grouper	Accessibility of bivalves and of echinoderms/ large gastropods to adult red grouper set to 0% to account for very small overlap in the vertical dimension and for the fact that the morphology of red grouper is not well suited to feed on the two aforementioned LTL benthos groups.
Adult gag grouper	Accessibility of the different LTL benthic groups to adult gag grouper set to 40% to account for little overlap in the vertical dimension.
Juvenile red snapper	Accessibility of meiofauna, small infauna and small mobile epifauna to juvenile red snapper set to 40% to account for little overlap in the vertical dimension. Accessibility of bivalves and of echinoderms/ large gastropods set to 10% to account for very small overlap in the vertical dimension and for the fact that the morphology of red snapper is not well suited to feed on the two aforementioned LTL benthos groups.
Adult red snapper	Accessibility of meiofauna, small infauna and small mobile epifauna to adult red snapper set to 40% to account for little overlap in the vertical dimension. Accessibility of bivalves and of echinoderms/ large gastropods set to 10% to account for very small overlap in the vertical dimension and for the fact that the morphology of red snapper is not well suited to feed on the two aforementioned LTL benthos groups.
Sardine-herring-scad complex	Accessibility of the different LTL benthos groups to the sardine-herring-scad complex set to 10% to account for very little overlap in the vertical dimension.
Anchovies and silversides	Accessibility of meiofauna, small infauna and small mobile epifauna to anchovies/silversides set to 40% to account for little overlap in the vertical dimension. Accessibility of bivalves, and echinoderms/large gastropods set to 10% to account for very little overlap in the vertical dimension.

Table 10. Target biomass of the 12 high trophic level (HTL) groups considered in OSMOSE-WFS, associated valid intervals (defined by minimum and maximum possible biomasses), and larval mortality rates of the different HTL groups estimated through the calibration of OSMOSE-WFS.

HTL group	Target biomass (tons)	Minimum possible biomass (tons)	Maximum possible biomass (tons)	Source of biomass estimates	Larval mortality rates ($month^{-1}$)
King mackerel	9 703	4 852	14 555	SEDAR 16 (2009)	14.15
Amberjacks	1 328	663	1 991	SEDAR (2011)	17.11
Red grouper	19 759	9 880	29 639	SEDAR (2009a)	16.99
Gag grouper	9 189	4 594	13 783	SEDAR (2009c)	17.02
Red snapper	8 786	4 393	13 179	SEDAR (2009b)	16.14
Sardine-herring-scad complex	289 000	57 800	520 200	WFS Reef fish Ecopath	9.45
Anchovies and silversides	162 120	32 424	291 816	WFS Reef fish Ecopath	4.85
Coastal omnivores	303 450	60 690	446 210	WFS Reef fish Ecopath	8.23
Reef carnivores	276 980	55 396	498 564	WFS Reef fish Ecopath	12.70
Reef omnivores	78 862	15 774	141 970	WFS Reef fish Ecopath	7.51
Shrimps	154 710	77 355	232 065	Nance (2009)	15.43
Large crabs	109 640	21 928	197 352	WFS Reef fish Ecopath	15.89

Table 11. Model groups considered when evaluating the diet composition of high trophic level groups and stanzas predicted by OSMOSE-WFS.

Model group	Nature of the model group
Juvenile king mackerel	Stanza: Individuals older than 1 month and smaller than 73.4 cm TL
Adult king mackerel	Stanza: Individuals larger than 73.4 cm TL
Amberjacks	High trophic level (HTL) group
Younger juvenile red grouper	Stanza: Individuals older than 1 month and smaller than 14.8 cmTL
Older juvenile red grouper	Stanza: Individuals larger than 14.8 cm TL and smaller than 34.1 cm TL
Adult red grouper	Stanza: Individuals larger than 34.1 cm TL
Younger juvenile gag grouper	Stanza: older than 1 month and smaller than 20 cm TL
Older juvenile gag grouper	Stanza: Individuals larger than 20 cm TL and smaller than 46.8 cm TL
Adult gag grouper	Stanza: Individuals larger than 46.8 cm TL
Juvenile red snapper	Stanza: Individuals older than 1 month and smaller than 34.6 cm TL
Adult red snapper	Stanza: Individuals larger than 34.6 cm TL
Sardine-herring-scad complex	HTL group
Anchovies and silversides	HTL group
Coastal omnivores	HTL group
Reef carnivores	HTL group
Reef omnivores	HTL group
Adult shrimps	Stanza: Individuals larger than 8 cm TL
Large crabs	HTL group
Ichthyoplankton	Low trophic level (LTL) group, made of the 0-1 month individuals of all the HTL groups represented in OSMOSE-WFS
Phytoplankton	Aggregation of two LTL groups, small phytoplankton and diatoms
Zooplankton	Aggregation of two LTL groups, small copepods and large mesozooplankton
Meiofauna	LTL group
Small infauna	LTL group
Small mobile epifauna	LTL group and juvenile shrimps, i.e., shrimps older than 1 month and smaller than 8 cm TL
Bivalves	LTL group
Echinoderms and large gastropods	LTL group

Table 12. Annual instantaneous natural mortality rates of different age classes of red grouper predicted by OSMOSE-WFS. Note that 0-1 year old individuals exclude 0-1 month individuals, which belong to the ichthyoplankton (Table 11). 10 replicates and only the last 20 years of simulations (i.e., years 114 to 134) were considered to produce the estimates reported here. M: total instantaneous natural mortality rate - $M_{predation}$: total instantaneous predation mortality rate - M_{others}: instantaneous natural mortality rate due to all other causes.

Age (years)	M **(year^{-1})**	**CV of** M	$M_{predation}$ **(year^{-1})**	**CV of** $M_{predation}$	M_{others} **(year^{-1})**	**CV of** M_{others}
0-1	2.71	0.20	2.64	0.20	0.06	0.28
1-2	0.47	0.01	0.31	0.17	0.16	0.01
2-3	0.19	0.43	0.01	0.64	0.15	0.11
3-4	0.17	0.01	0.008	0.17	0.16	0.01
4-5	0.16	0.43	0.009	0.64	0.15	0.11
5-6	0.13	0.34	0.003	1.43	0.13	0.17
6-7	0.12	0.01	0.001	0.17	0.12	0.01
7-8	0.11	0.43	0.001	0.64	0.11	0.11
8-9	0.10	0.34	4.10^{-4}	1.43	0.10	0.17
9+	0.05	0.27	9.10^{-5}	2.64	0.05	0.24

Figures

Fig. 1. Map of the West Florida Shelf in the Gulf of Mexico showing the spatial cells of OSMOSE-WFS (filled in dark grey).

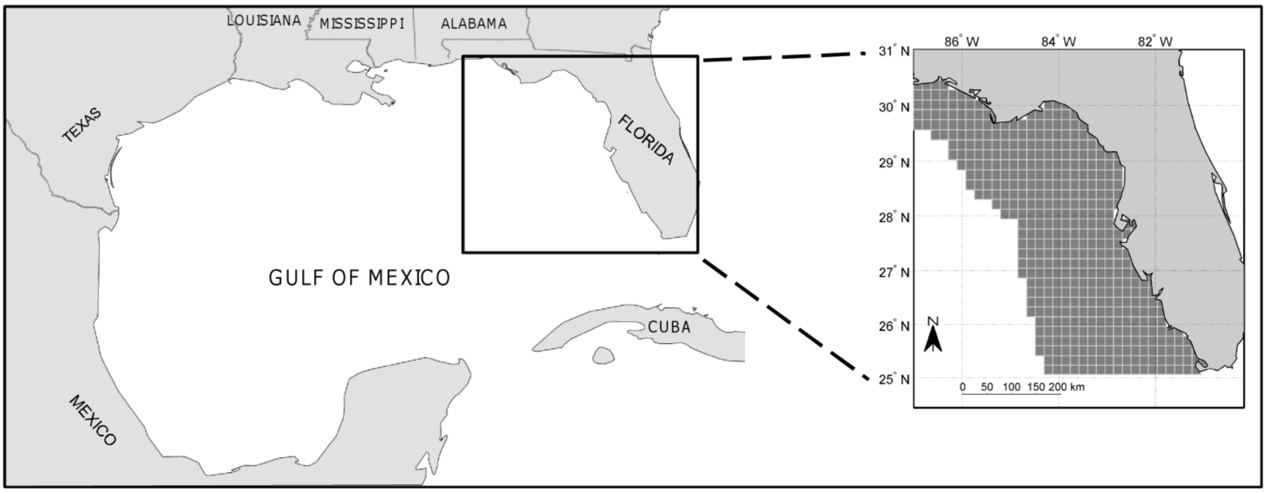


Fig. 2. Monthly maps of total phytoplankton biomass in the West Florida Shelf (in tons), produced from chlorophyll a SeaWiFS (Sea-viewing Wide Field-of-view Sensor) data downloaded from http://oceancolor.gsfc.nasa.gov/SeaWiFS/.

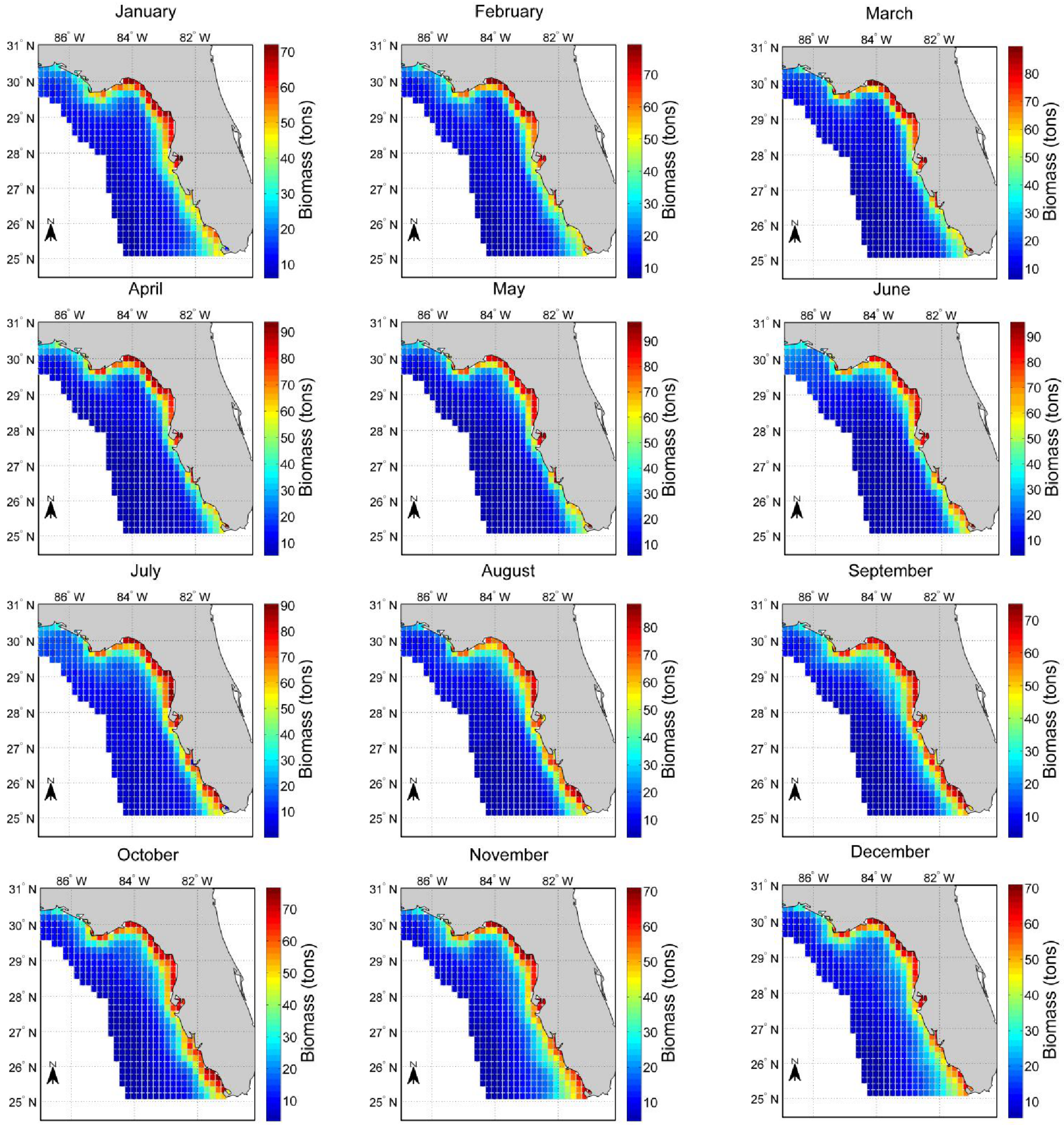
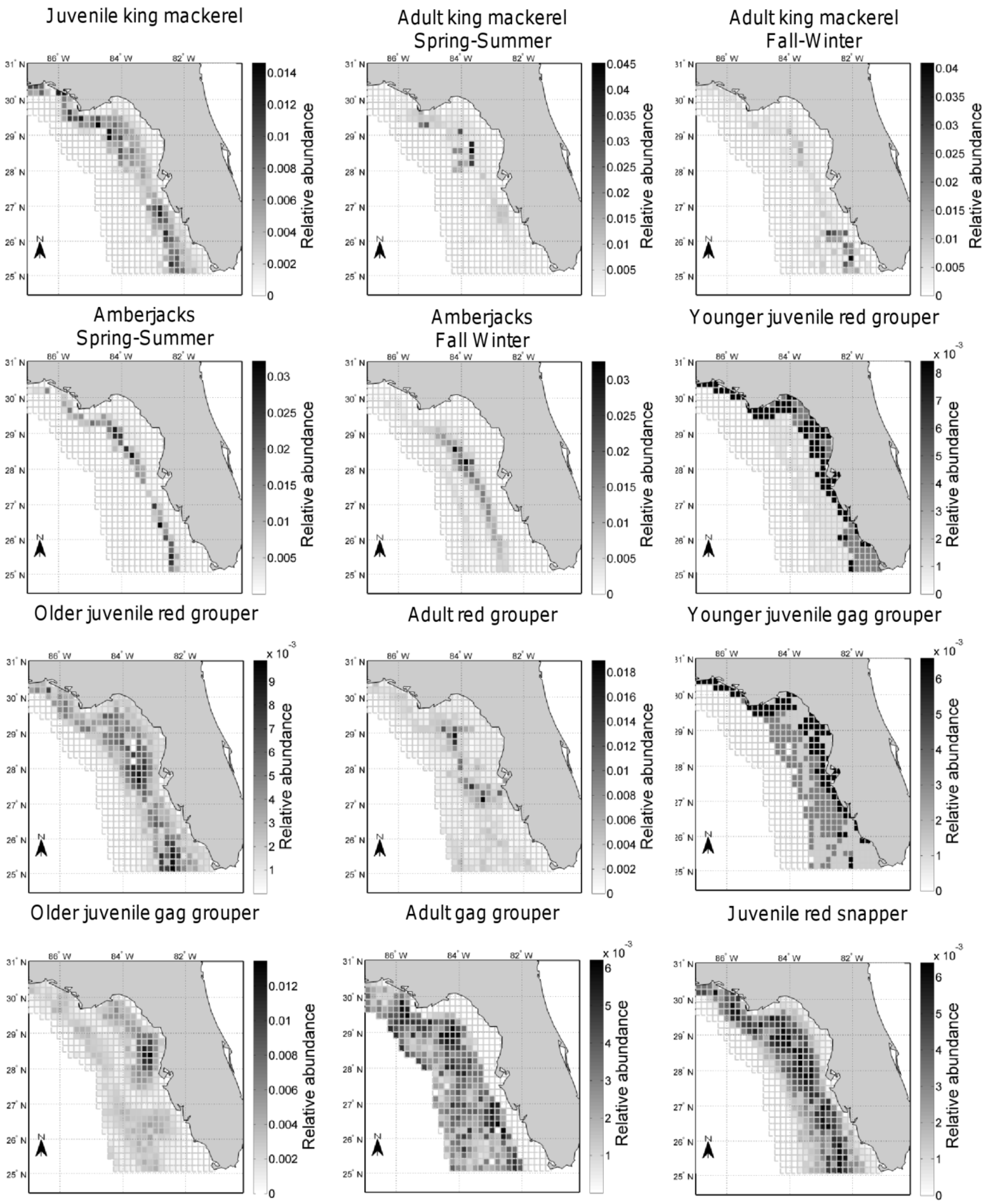
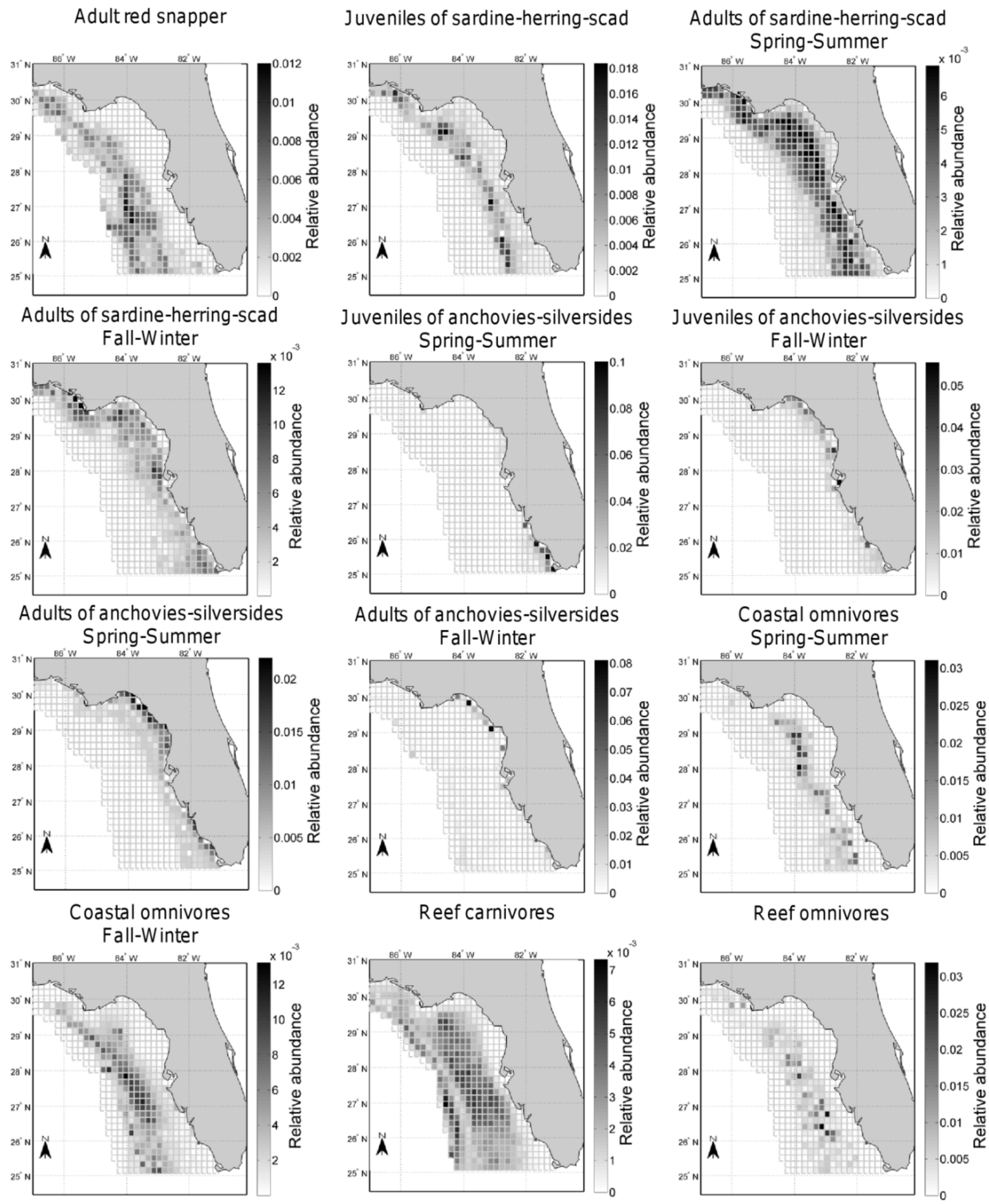


Fig. 3. Distribution maps used in input of OSMOSE-WFS. Maps were produced for different life stages of the high trophic level groups explicitly considered in OSMOSE-WFS ('life-stage groups'), using a delta generalized modeling approach (all life-stage groups except younger juveniles of red grouper and gag grouper; Grüss et al., 2014b) or from information in the literature (younger juveniles of red grouper and gag grouper).




Adult red snapper
Juveniles of sardine-herring-scad
Adults of sardine-herring-scad Spring-Summer
Adults of sardine-herring-scad Fall-Winter
Juveniles of anchovies-silversides Spring-Summer
Juveniles of anchovies-silversides Fall-Winter
Adults of anchovies-silversides Spring-Summer
Adults of anchovies-silversides Fall-Winter
Coastal omnivores Spring-Summer
Coastal omnivores Fall-Winter
Reef carnivores
Reef omnivores
Relative abundance
86° W
84° W
82° W
31° N
30° N
29° N
28° N
27° N
26° N
25° N
N

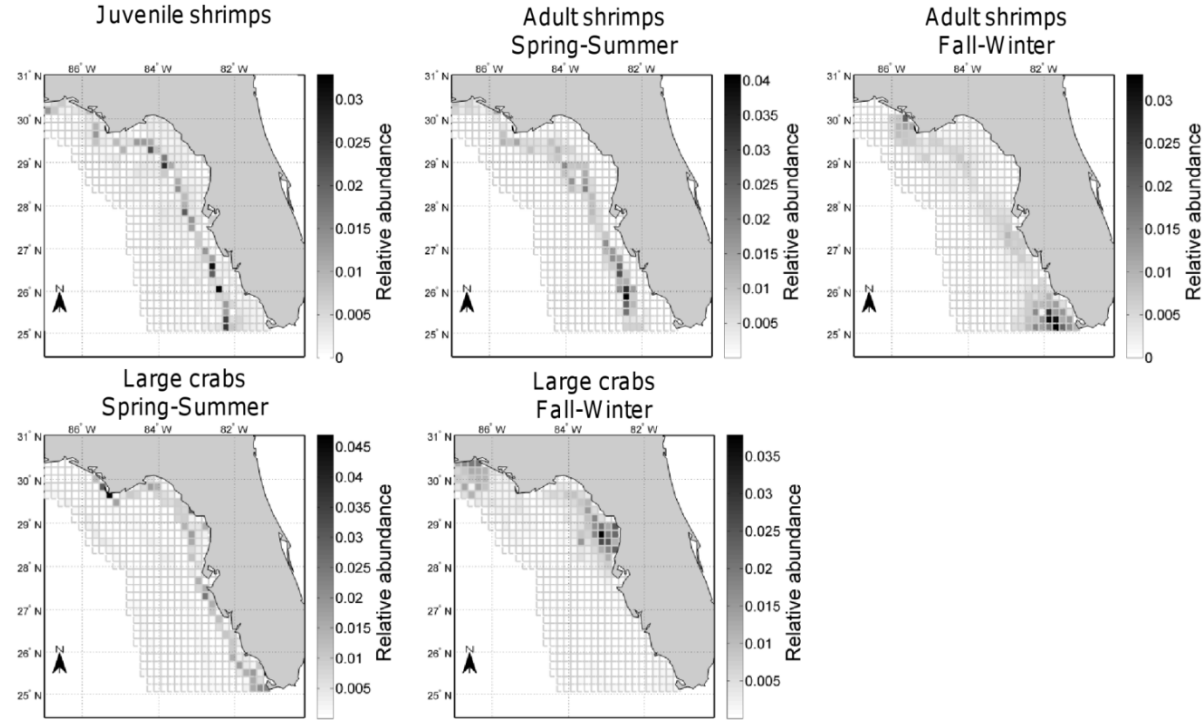

Juvenile shrimps
Adult shrimps
Spring-Summer
Adult shrimps
Fall-Winter
Large crabs
Spring-Summer
Large crabs
Fall-Winter
86° W
84° W
82° W
31° N
30° N
29° N
28° N
27° N
26° N
25° N
N
Relative abundance
0
0.005
0.01
0.015
0.02
0.025
0.03
0.035
0.04
0.045

Fig. 4. Fishing seasonality of some high trophic level groups represented in OSMOSE-WFS, estimated from National Marine Fisheries statistics (NMFS statistics). Annual F: Annual fishing mortality rate.

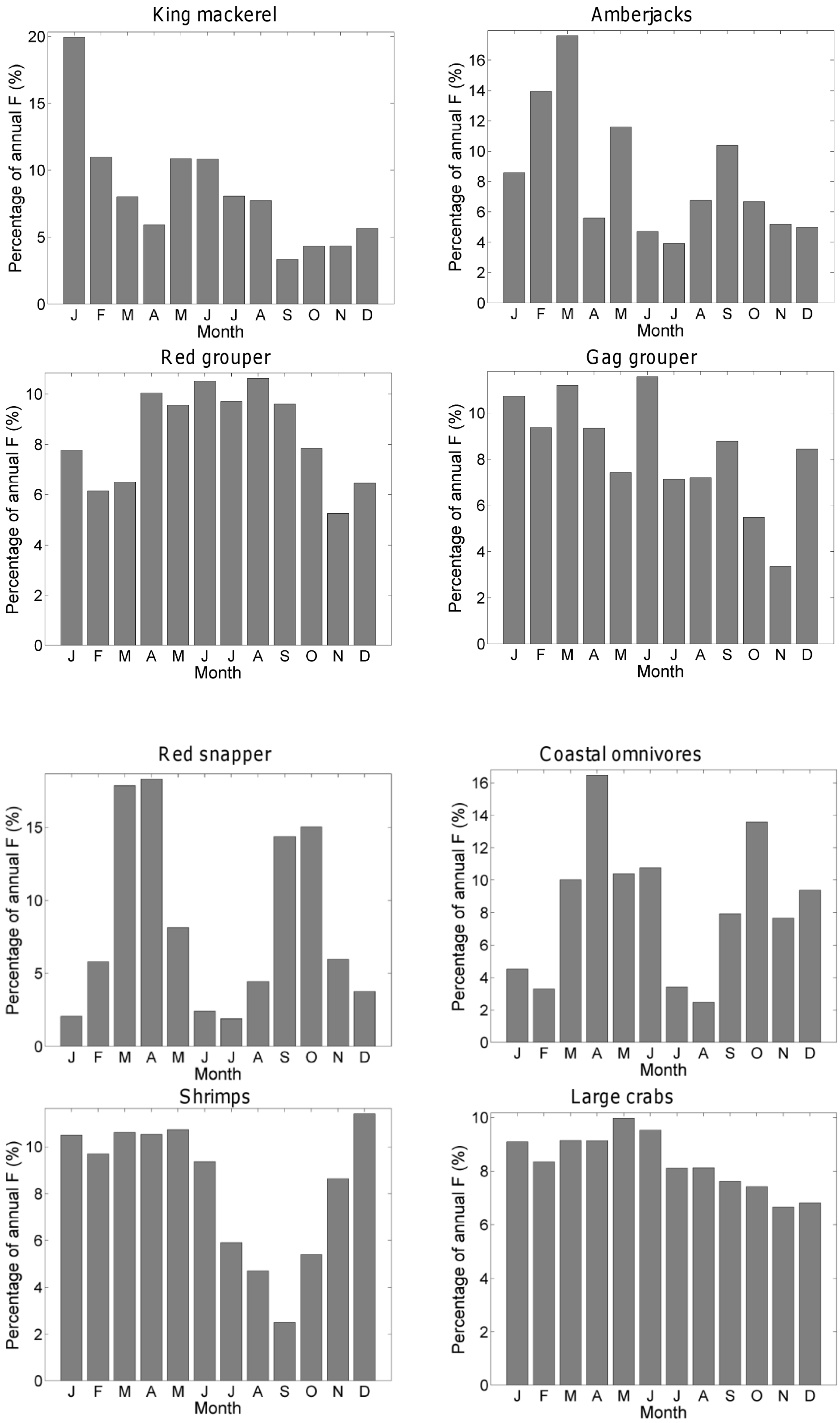
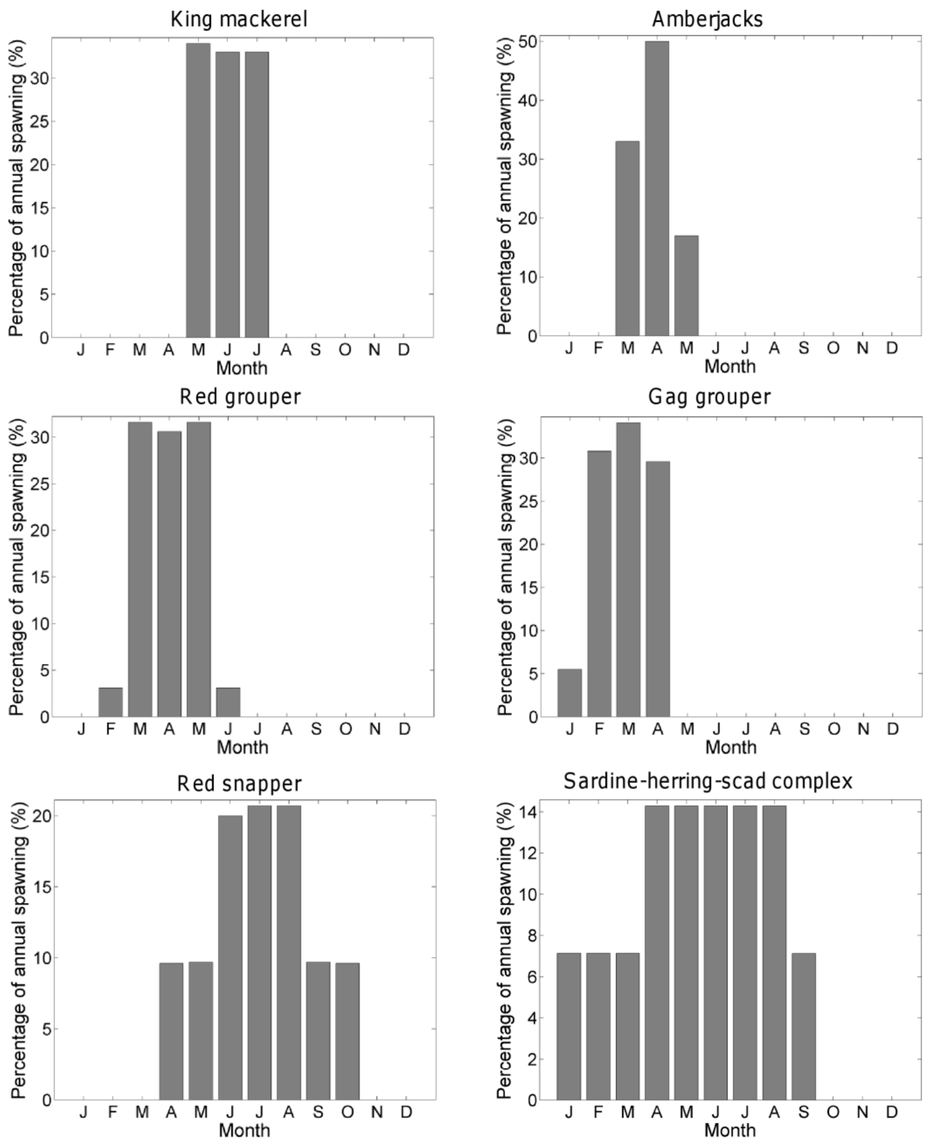
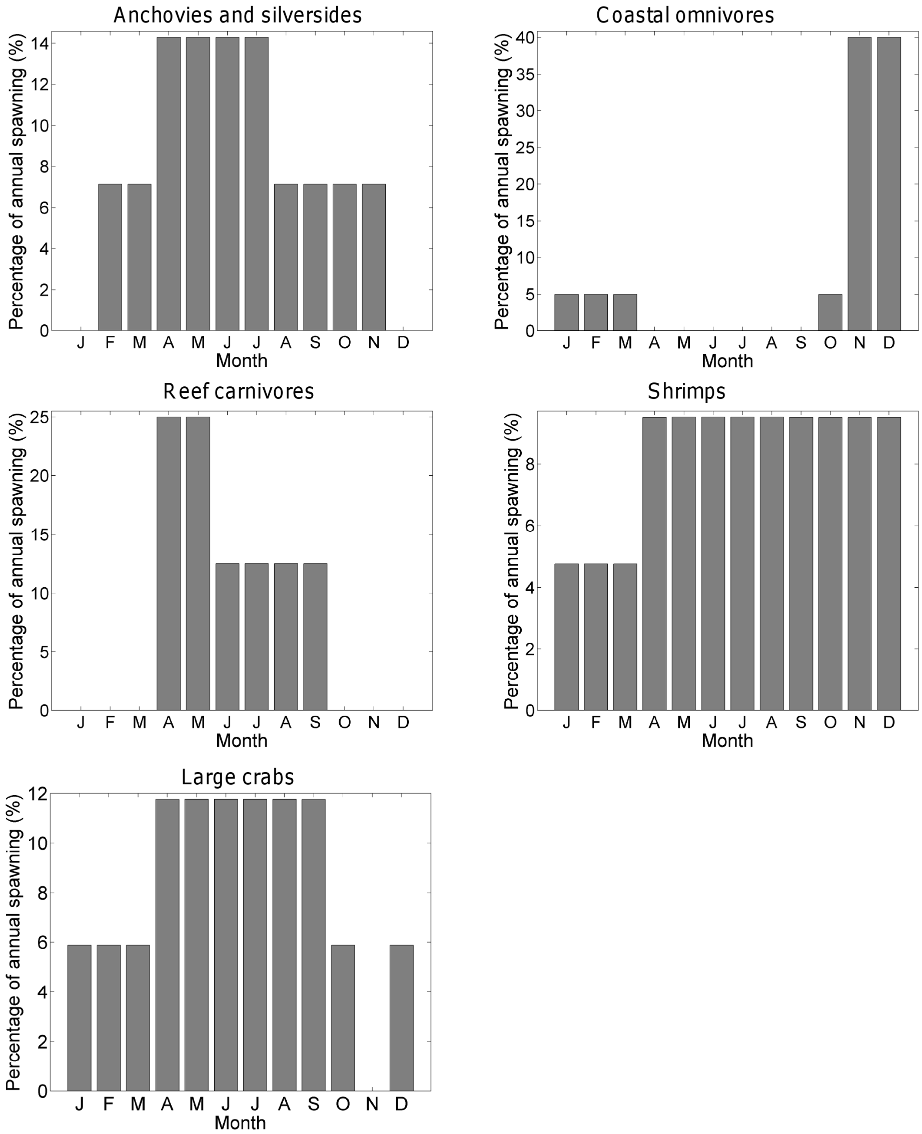


Fig. 5. Seasonality of reproduction of some of the high trophic level groups represented in OSMOSE-WFS estimated from the literature.





Anchovies and silversides
Coastal omnivores
Reef carnivores
Shrimps
Large crabs
Percentage of annual spawning (%)
Month
J F M A M J J A S O N D

Fig. 6. Biomasses observed over the period 2005-2009 (gray boxplots) and predicted by OSMOSE-WFS (black boxplots) for the 12 high trophic level (HTL) groups explicitly considered in OSMOSE-WFS. Mean observed biomasses (gray dots) are associated with valid intervals, i.e., minimum and maximum possible values, accounting for variability and uncertainty of mean biomass estimates over the period 2005-2009. Biomasses simulated with OSMOSE-WFS correspond to mean biomasses (black dots) +/- standard deviations for 10 replicates after 114 to 134 years of simulation. Note the change of scale of the y-axis between the left and right panels. **(a)** km: king mackerel – am: amberjacks – rg: red grouper – gg: gag grouper – rs: red snapper; **(b)** shs: sardine-herring-scad complex – as: anchovies and silversides – co: coastal omnivores – rc: reef carnivores – ro: reef omnivores – shr: shrimps – lc: large crabs.

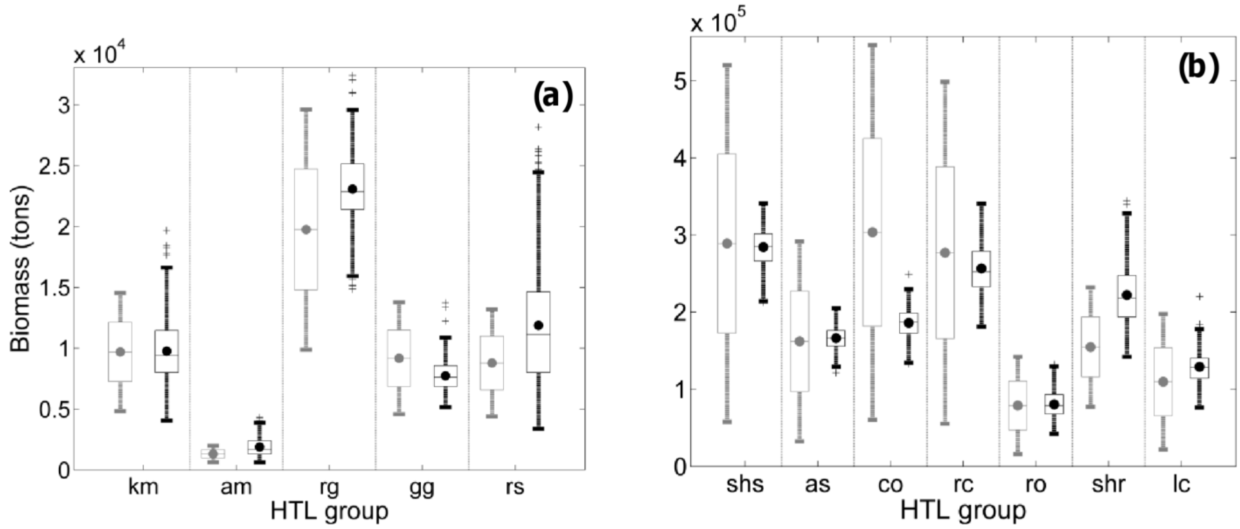


Fig. 7. Mean trajectories of biomasses in OSMOSE-WFS (a) after 114 to 134 years of simulation for all HTL groups; and (b) after 114 to 134 years of simulation for king mackerel, amberjacks, red grouper, gag grouper and red snapper. 10 simulation replicates were run to produce these plots.

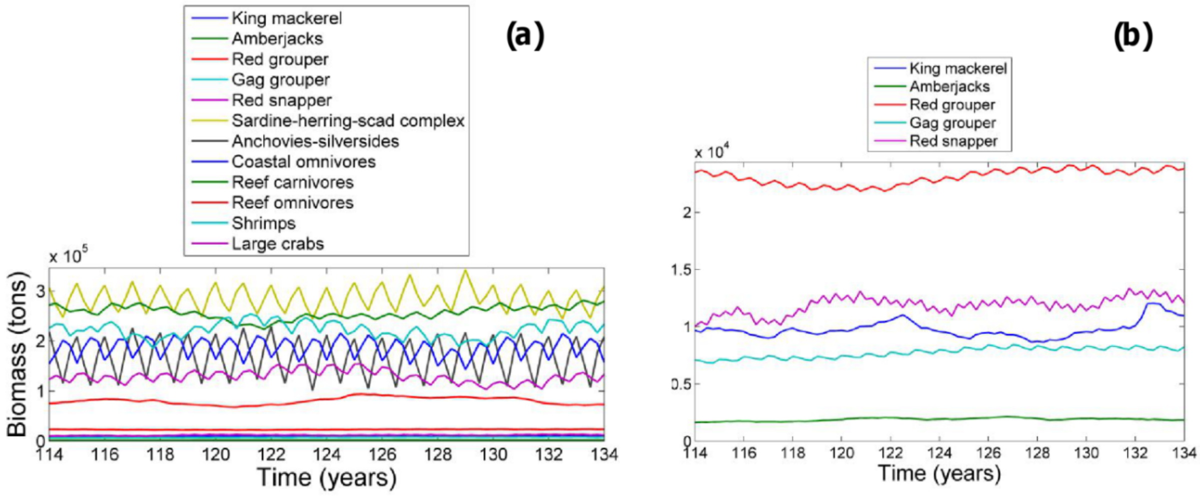


Fig. 8. Mean trophic level (TL) of OSMOSE-WFS species groups predicted by OSMOSE-WFS (black diamonds) and by WFS Reef fish Ecopath (grey circles). For OSMOSE-WFS, 10 replicates and only the last 20 years of simulations (i.e., years 114 to 134) were considered to estimate TLs. km: king mackerel – am: amberjacks – rg: red grouper – gg: gag grouper – rs: red snapper - shs: sardine-herring-scad complex – as: anchovies and silversides – co: coastal omnivores – rc: reef carnivores – ro: reef omnivores – shr: shrimps – lc: large crabs.

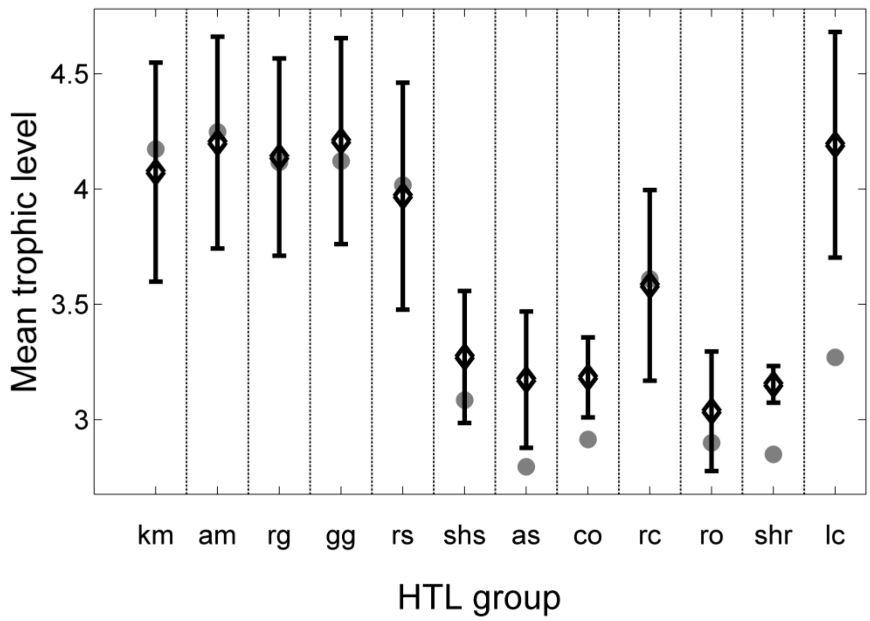


Fig. 8. Annual instantaneous natural mortality rates of (a) younger juvenile red grouper, (b) older juvenile red grouper and (c) adult red grouper predicted by OSMOSE-WFS (black boxplots) and WFS Reef fish Ecopath (large gray dots). Mean instantaneous mortality rates predicted by OSMOSE-WFS are indicated by small black dots. For OSMOSE-WFS, 10 replicates and only the last 20 years of simulations (i.e., years 114 to 134) were considered. *M*: total instantaneous natural mortality rate - $M_{predation}$: total instantaneous predation mortality rate - M_{others}: instantaneous natural mortality rate due to all other causes.

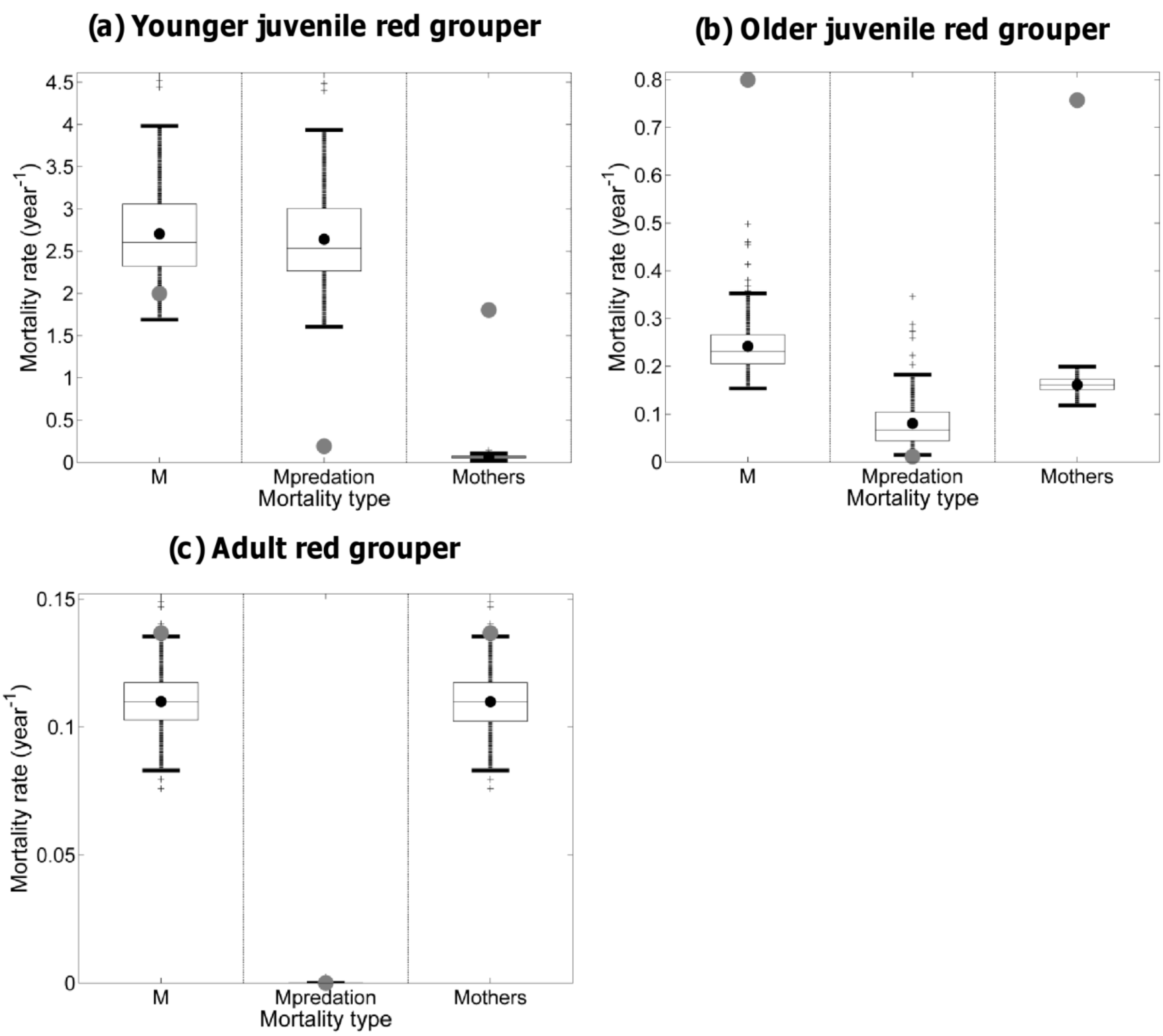


Fig. 10. Contributors to the predation mortality of (a,b) younger juvenile red grouper, (c,d) older juvenile red grouper and (e,f) adult red grouper predicted by (a,c,e) OSMOSE-WFS and (b,d,f) WFS Reef fish Ecopath. For OSMOSE-WFS, 10 replicates and only the last 20 years of simulations (i.e., years 114 to 134) were considered.

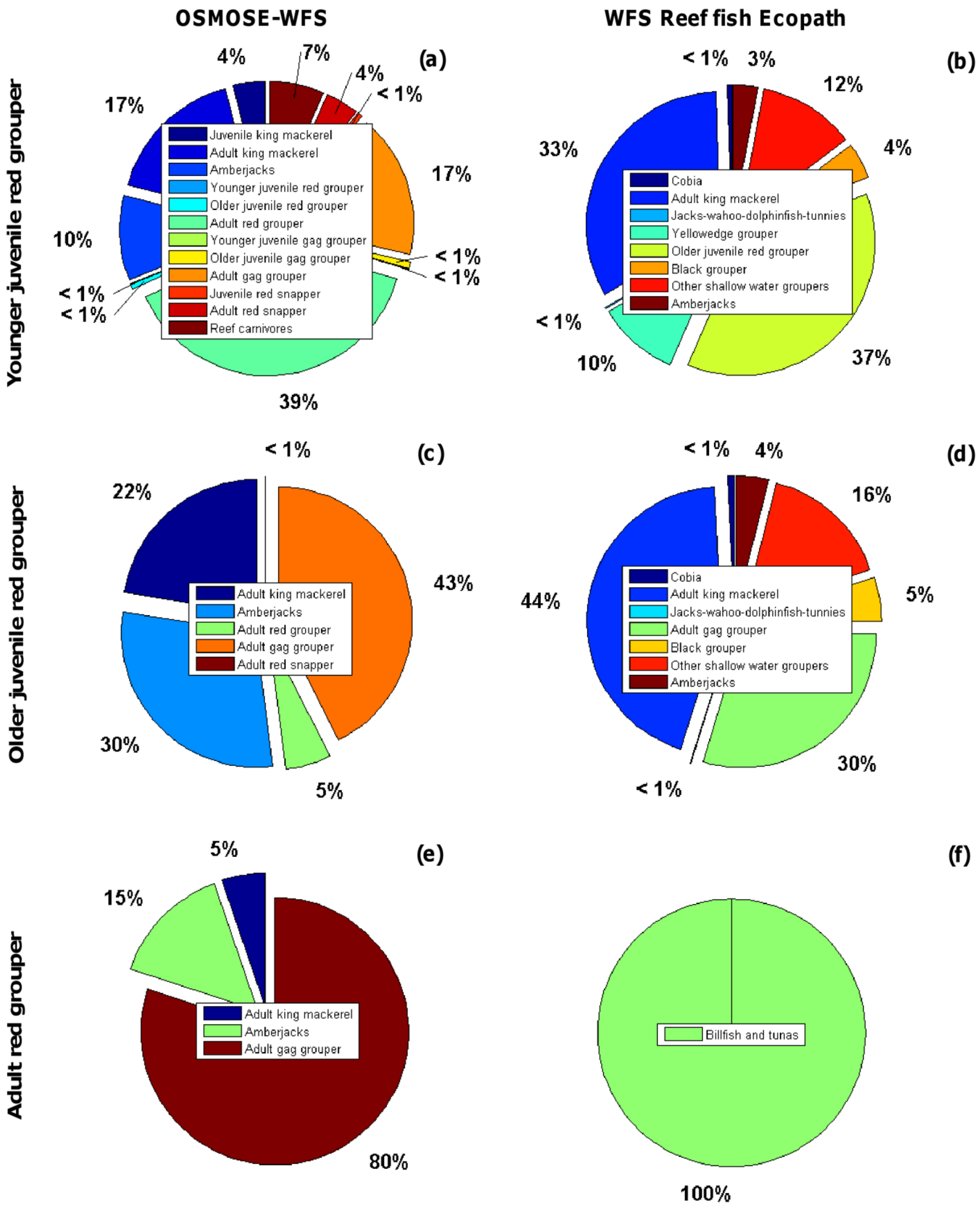
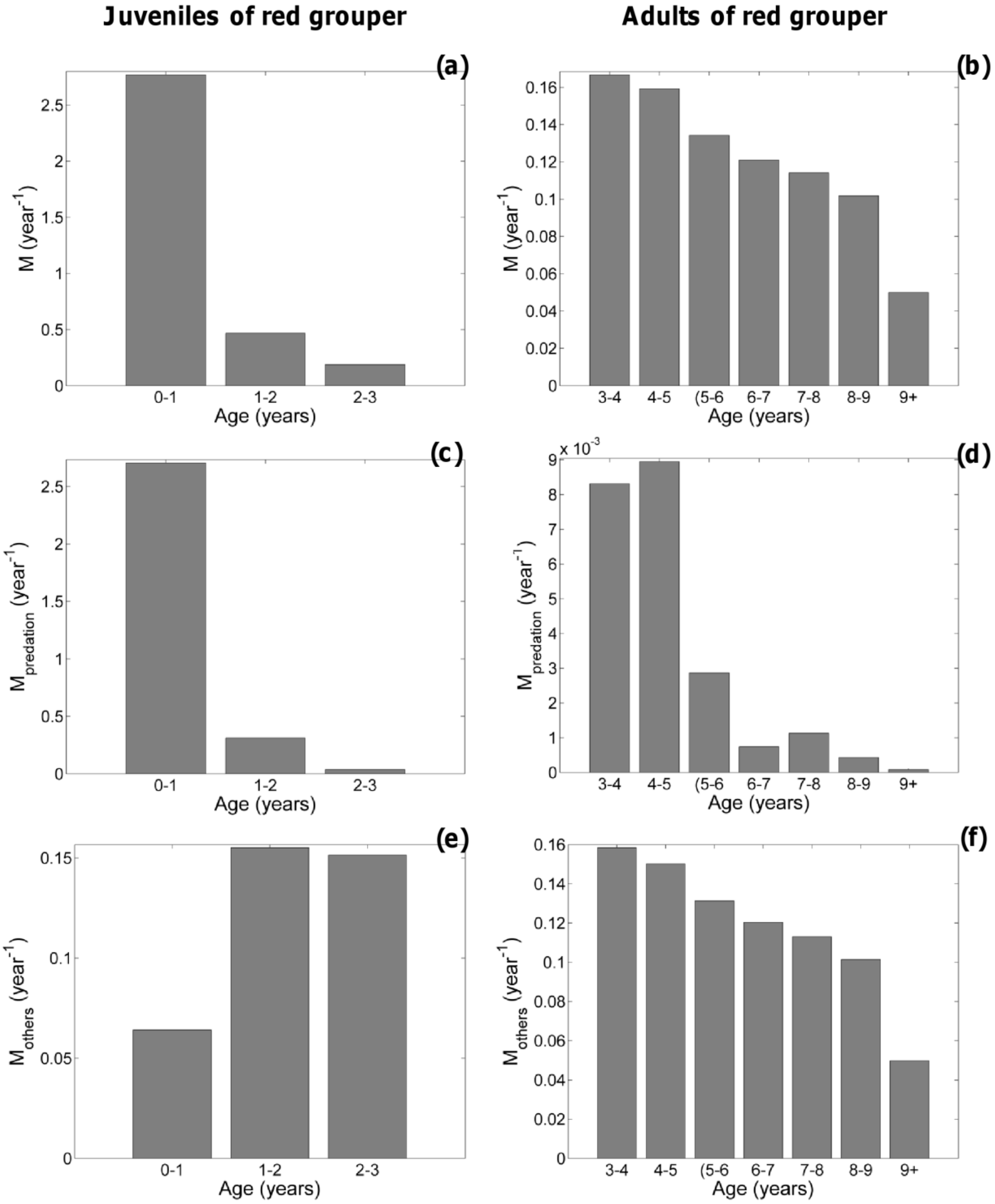


Fig. 11. Annual instantaneous natural mortality rates of different age classes of red grouper predicted by OSMOSE-WFS. (a,b,c) are for juveniles (i.e., 0-1 year old, 1-2 years old and 2-3 years old individuals), while **(d,e,f)** are for adults (i.e., 3-4 years old, …, 8-9 years old and 9+ years old individuals). Note that 0-1 year old individuals exclude 0-1 month individuals, which belong to the ichthyoplankton (Table 11). **(a,d)** give total instantaneous natural mortality rates (M), **(b,e)** give total instantaneous predation mortality rates ($M_{predation}$) and **(c,f)** give instantaneous natural mortality rate due to all other causes (M_{others}). 10 replicates and only the last 20 years of simulations (i.e., years 114 to 134) were considered to produce the bar plots.



Juveniles of red grouper
Adults of red grouper
(a)
(b)
(c)
(d)
(e)
(f)
M (year^{-1})
$M_{predation}$ (year^{-1})
M_{others} (year^{-1})
x 10^{-3}
Age (years)
0-1
1-2
2-3
3-4
4-5
(5-6
6-7
7-8
8-9
9+