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Natural mortality rates and diet patterns of gag grouper (*Mycteroperca microlepis*) in the West Florida Shelf ecosystem in the 2000s: Insights from the individual-based, multi-species model OSMOSE-WFS

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Introduction

An Integrated Ecosystem Assessment (IEA) project has been recently initiated in the Gulf of Mexico, with the intent to deliver ecosystem considerations and parameter estimates to SEDAR on a regular basis (http://www.noaa.gov/iea/gulfofmexico.html). In particular, two ecosystem simulation models have been developed for the West Florida Shelf region, WFS Ecopath with Ecosim (WFS EwE) (Chagaris and Mahmoudi, 2013) and OSMOSE-WFS (Grüss et al., 2013). WFS EwE was used to estimate natural mortality rates for gag grouper (*Mycteroperca microlepis*) from 1950 to 2009, under alternate assumptions about compensatory survival and predation (Chagaris and Mahmoudi, 2013); while a calibration of OSMOSE-WFS was being attempted at the time of the SEDAR 33 Data Workshop (Grüss et al., 2013).

We initially tried to calibrate OSMOSE-WFS using an heuristic, derivative free method, the 'genetic algorithm' developed by Duboz et al. (2010). This attempt was useful to detect errors and inconsistencies in model code and configuration, as well as to understand the sensitivity of the dynamics of the modeled system to inputs. Unfortunately, the genetic algorithm did not converge to an optimal 'genotype' and did not help to reproduce the reference biomasses predicted by WFS Ecopath over the period 2005-2009. Consequently, we decided to attempt a calibration of OSMOSE-WFS using a more sophisticated evolutionary algorithm developed by Oliveros-Ramos et al. (in prep.). This evolutionary algorithm was successful in calibrating OSMOSE-WFS to a reference state matching the mean conditions in the West Florida Shelf region in the 2000s predicted by WFS Ecopath.

In this paper, we first briefly recall the main hypotheses of the OSMOSE-WFS model. We then describe the differences between the OSMOSE-WFS model reported in Grüss et al. (2013) and that used to provide parameter estimates to the SEDAR 33 Assessment Workshop.

Next, we provide an overview of the evolutionary algorithm utilized for model calibration. Finally, we report and discuss the natural mortality rates and diet patterns of gag grouper evaluated by OSMOSE-WFS.

Material and methods

Overview of the OSMOSE-WFS model

OSMOSE-WFS is a two-dimensional, individual-based and multispecies model explicitly representing major processes in the life cycle of a bunch of pelagic, demersal and benthic high trophic level (HTL) groups of marine species. The basic units of the OSMOSE model are schools, which consist in organisms belonging to the same HTL group, which have the same length, age, food requirement and, at a given time step, the same spatial coordinates. OSMOSE-WFS builds on WFS EwE efforts. However, OSMOSE-WFS and WFS EwE differ greatly in both their structure and assumptions. In particular, OSMOSE-WFS explicitly considers only a limited number of HTL groups. Moreover, diet compositions in OSMOSE-WFS are not determined *a priori* but rather emerge from model simulations. In OSMOSE-WFS, a HTL group can feed on any model group (i.e., low trophic level (LTL) or HTL group) provided: (1) the predator and its potential prey occur in the same geographical area; (2) there is size adequacy between them; and (3) the potential prey is accessible to the predator. Size adequacy between predators and prey in OSMOSE-WFS is dictated by minimum and maximum predator/prey size ratios, while accessibility of the prey to the predators is determined by accessibility coefficients, which primarily reflect the degree of overlap of model groups in the water column (see next subsection).

Currently, 12 HTL groups are explicitly considered in OSMOSE-WFS. Species of a given HTL group share similar life history traits, size ranges, diets and exploitation patterns.

HTL groups include 10 fish species/groups of fish species and two crustacean groups: (1) king mackerel (*Scomberomorus cavalla*); (2) amberjacks; (3) red grouper (*Epinephelus morio*); (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. These 12 groups were selected for their contribution to total biomass and economic value in the West Florida Shelf region during the 2000s, and/or because they are key to the West Florida Shelf food web and, particularly, to the diet of gag grouper and red grouper. A reference species was identified for each of the HTL groups (Table 1). Growth, reproduction, mortality and diet parameters of each group are those of the reference species of the group. OSMOSE-WFS is currently forced by the biomass of 9 LTL groups, consisting of 2 phytoplankton groups (phytoplankton and diatoms), 2 zooplankton groups (small copepods and large mesozooplankton) and 5 benthos groups (meiofauna, small infauna, small mobile epifauna, bivalves, and echinoderms and large gastropods). Biomass of LTL groups is a local input in each model cell and each month.

The following succession of events occurs in OSMOSE-WFS within a time step: (1) schools are distributed on a two-dimensional grid; (2) mortalities (fishing mortality, predation and starvation mortalities, and natural mortality from other sources) are applied to schools; (3) the growth in size and weight of schools is evaluated based on their predation success; and, finally, (4) reproduction takes place. For more details, the reader is referred to Grüss et al. (2013). The current inputs of OSMOSE-WFS are those described in Tables 2, 4 and 5 and in Boxes 1, 2, 3 and 4 of Grüss et al. (2013) unless stated otherwise in next subsection.

Recent changes in OSMOSE-WFS

To be able to properly calibrate OSMOSE-WFS, we had to make some changes in the hypotheses and parameters reported in Grüss et al. (2013).

The major change that was made in OSMOSE-WFS was the introduction of availability coefficients for LTL benthos groups. In the OSMOSE-WFS model reported in Grüss et al. (2013), availability coefficients were estimated during the calibration process for plankton groups only. Currently, the accessibility of a given HTL group *i* to a given LTL group *j* ($\delta_{j,i}$, in %), *j* being a plankton group or a benthos group, is evaluated as:

$$\delta_{j,i} = \rho_{j,i} . \alpha_j \qquad (1)$$

where $\rho_{j,i}$ is the theoretical accessibility coefficient of HTL group *i* to a LTL group *j* (in %); and α_j the availability coefficient of LTL group *j* to all HTL groups. The ρ parameters were determined from the literature and from expert opinion (J. Simons) (Box 1), while the α parameters were estimated during the calibration process of OSMOSE-WFS (see below). The values attributed to the theoretical accessibility coefficients of HTL groups to LTL benthos groups are meant to reflect the degree of overlap of model groups in the water column and, to a lesser extent, strong diet preferences. Intentionally, these values differ from the default value of 80% only if it is completely unrealistic to assume something else than low (10% or 40%) or no accessibility (0%), so as to let the diet compositions of the HTL groups emerge primarily from spatial co-occurrence and size adequacy between predators and prey. Theoretical accessibility coefficients to plankton groups are set to either 0% or 100% (Appendix A6).

The rationale behind the estimation of availability coefficient is to account for 'ecotrophic efficiency', i.e., for the fact that only a small fraction of the production of LTL groups is effectively utilized by HTL groups (Ricker, 1969; Polovina, 1984). The introduction of α parameters for LTL benthos groups prevents the system from being overproductive and, therefore, an explosion in the biomass of some HTL groups belonging to high trophic levels accompanied by the collapse of HTL groups belonging to low trophic levels.

Some of the parameters influencing predation in OSMOSE-WFS, i.e., some predator/prey size ratios and accessibility coefficients, were also modified. Our intent here was to constrain diets so as to prevent an explosion in the biomass of some HTL groups, but also to ensure that the diet compositions emerging from model simulations are relevant. We tried to modify accessibility coefficients as little as possible, so as to let the diet compositions of HTL groups essentially emerge from size adequacy between prey and predators and spatial co-occurrence. All changes in predator/prey size ratios and accessibility coefficients are given in Table 2 and Box 2, respectively. For example, we set the accessibility of anchovies and silversides to most HTL groups to 10% to account for the fact that anchovies and silversides are found primarily in very coastal areas (estuaries and bays), whereas most of other HTL groups (e.g., king mackerel and amberjacks) occur in more offshore waters (Robinette, 1983; SEDAR 9, 2006; SEDAR 16, 2009). We also increased the minimum predator/prey size ratio of anchovies and silversides so as to prevent this HTL group to feed on the early stages of HTL groups belonging to high trophic levels, which is unrealistic according to the literature (Odum and Heald, 1972; Carr and Adams, 1973; Sheridan, 1978; Din, 1981; Peebles and Hopkins, 1993). All these different changes in model parameterization allowed the biomass of anchovies and silversides to be within its valid interval at the end of simulations (i.e., after 30 to 50 years of simulations; see below).

Calibration of OSMOSE-WFS

OSMOSE-WFS was calibrated using a sophisticated evolutionary algorithm (EA) developed by Oliveros-Ramos et al. (in prep.). The main goal of the EA was to ensure that the biomasses of HTL groups predicted by OSMOSE-WFS after 30 to 50 years of simulation match the mean values of biomasses predicted by WFS Ecopath for the period 2005-2009 (hereafter referred to as 'reference biomasses'; Table 3; Chagaris and Mahmoudi, 2013). The EA was preferred to the genetic algorithm designed by Duboz et al. (2010), essentially because it converges faster to a solution, is more reliable to find a global optimum, and is more intuitive.

The EA was applied to a set of 21 unknown parameters, comprising the larval mortalities (*M0* parameters) of the 12 HTL groups considered in OSMOSE-WFS and the availability coefficient of the 9 LTL groups to all HTL groups (α parameters). Reference biomasses were associated with coefficients of variation and, therefore, valid intervals (i.e., minimum and maximum possible values). These coefficients of variation were defined to reflect the uncertainty of WFS Ecopath biomass estimates, according to the criteria specified in Okey and Mahmoudi (2002) (Table 3). So as to justify comparisons between OSMOSE-WFS and WFS Ecopath, we considered similar individuals to those modeled by means of functional groups in WFS Ecopath for evaluating biomasses in OSMOSE-WFS during the calibration process. Thus, to calculate biomasses in OSMOSE-WFS during calibration, we only took into account individuals older than 1 month for all HTL groups, except for the shrimps group for which we only took into account individuals older than 4 months. For all HTL groups except the shrimps group, individuals younger than 1 month belong to the 'ichthyoplankton' group in WFS Ecopath. Shrimps younger than 4 months, i.e., juvenile shrimps (Hart and Nance, 2010), belong to the 'small mobile epifauna' group in WFS Ecopath.

The EA method aims at selecting the best set of unknown parameters based on the Darwinian theory of evolution, which makes the assumption that only the best-adapted genotypes survive and reproduce. The calibration process begins with 63 sets of unknown parameters, constituting the 'genotype', set randomly inside their search space ([0; 20 month^{-1}] for larval mortalities and [0; 1] for availability coefficients). These genotypes are evaluated by running OSMOSE simulations for 50 years: the closer the biomasses of the HTL groups produced by OSMOSE-WFS to reference biomasses, the lower the error of the genotypes tested. This error estimate results from a combination of 12 pre-error functions (one per HTL group), each of which increases with increasing distance between the biomass simulated by OSMOSE-WFS and the reference biomass. Only the best 21 genotypes are selected and cross-combined to determine a Gaussian distribution law for the different parameters. These distribution laws are employed to produce 63 new genotypes, to be evaluated at the next generation. Using distribution laws allows the introduction of new values of parameters called 'mutations', which have been shown to improve the convergence of EAs. Technical details about the EA will soon be available in a dedicated paper.

Evaluation of natural mortality rates and diet patterns of gag grouper

Once calibrated, we used the OSMOSE-WFS to evaluate the natural mortality rates and diet patterns of gag grouper in the West Florida Shelf ecosystem in the reference situation, i.e., in the 2000s. The following patterns were analyzed from the outcomes of the OSMOSE-WFS, and compared to the outcomes of simulations of WFS EwE under the 'baseline' scenario (Chagaris and Mahmoudi, 2013): (1) the diet composition of gag grouper, expressed as percentage of prey groups in mass; (2) their trophic level (TL); (3) their relative degree of omnivory; and (4) their annual natural mortality rates. OSMOSE-WFS was run for

50 years, and the outputs of the model were saved for the last 20 years of simulation. Since OSMOSE is a stochastic model, 10 simulations were considered for analyzing the outcomes of the reference scenario. The maximum number of schools per annual annum was set to 240, so as to ensure long-term system stability while allowing for reasonable computation time.

The diet composition of the HTL groups in WFS Ecopath was defined *a priori*, primarily from data of stomach contents collated by the Florida Fish and Wildlife Research Institute (FWRI) and information in FishBase (Froese and Pauly, 2010). By contrast, the diet composition of each HTL group in OSMOSE-WFS emerges from encounters at the different time steps with prey of suitable size that are accessible. To calculate the diet composition of HTL groups represented in OSMOSE-WFS, we only took into account individuals older than 1 month, except for the shrimps group for which we only took into account individuals older than 4 months. For all HTL groups except the shrimps group, individuals younger than 1 month were assumed to belong to the ichthyoplankton, while for shrimps individuals younger than 4 months were considered to belong to small mobile epifauna. The rationale behind that is to allow for rigorous comparisons between the outcomes of the OSMOSE-WFS and those of WFS Ecopath. Still with the aim to make rigorous comparisons between the outcomes of OSMOSE-WFS and WFS Ecopath, we did not evaluate the diet composition of the HTL group as a whole for king mackerel, red grouper, gag grouper and red snapper. Rather, we calculated the diet composition of juveniles and adults of king mackerel and red snapper, and that of 0-1, 1-3 and 3+ years old red grouper and gag grouper.

TLs provided by Ecopath rely on predetermined dietary linkages and the relative abundance of each of the functional groups. By contrast, the TLs predicted by OSMOSE are estimated from the diet compositions of the HTL groups emerging from model simulations.

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 as (Travers et al., 2010):

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

where $DC_{j,i,t}$ is the proportion of prey *j* in the diet of school *i*; and $\Delta W_{i,t}$ the weight increase of school *i* at time *t*. The mean TL of each HTL group at time *t* is then evaluated as the sum 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 and large gastropods) (Grüss et al., 2013). The mean TL of the HTL community at time *t* is assessed as the sum of the TLs of all HTL group at *t* weighted by the HTL groups biomass at *t*.

In OSMOSE-WFS, the degree of omnivory of a given HTL group is the variance of the TL of that HTL group. Then, the relative degree of omnivory of the HTL group, *OD*, is obtained by dividing the degree of omnivory of the HTL group by the mean degree of omnivory of the HTL community. In Ecopath, an omnivory index, *OI*, is calculated for each functional group as the variance of the TL of the functional group (Pauly et al., 1993). The relative degree of omnivory of HTL group *g* predicted by WFS Ecopath is calculated as:

$$OD_g = \frac{OI_g^{\max}}{\overline{OI_g^{\max}}} \tag{3}$$

where $OI_g^{\max}$ is the maximum OI across all the stanzas of HTL group *g*; and $\overline{OI_g^{\max}}$ the mean value of $OI_g^{\max}$ of the HTL community.

The natural mortality rates we evaluated for gag grouper from simulations of OSMOSE-WFS comprise: (1) the total instantaneous natural mortality rate (*M*); (2) the total instantaneous predation mortality rate (P_{total}); and (3) the instantaneous natural mortality rate due to all other causes (M_{others}), which is the sum of $M_{diverse}$ and the instantaneous starvation mortality rate, *S*. These natural mortality rates were evaluated for 0-1, 1-3 and 3+ years old gag groupers so as to allow for comparisons with natural mortality rates predicted by WFS Ecopath. In WFS Ecopath, *M* is the sum of P_{total} and unexplained mortality, which is the equivalent of the M_{others} variable evaluated with OSMOSE-WFS (Chagaris and Mahmoudi, 2013).

Results

Calibration of OSMOSE-WFS

The calibration process of OSMOSE-WFS was useful to estimate the value of unknown parameters, i.e., larval mortality rates of HTL groups and availability coefficients of LTL groups, but also, as mentioned earlier, to detect errors in model code and inconsistencies in model configuration and make necessary adjustments. The EA revealed incoherence in model configuration when it found no solution to fit the biomasses of HTL groups to reference biomasses. After 19 attempts of calibration with the EA, we obtained a calibrated OSMOSE-WFS model such as the biomasses of all HTL groups but shrimps were on average within valid intervals after 30 to 50 years of simulation (Fig. 1). The biomass of shrimps is on average 1.15 higher after 30 to 50 years of simulation than its maximum biomass reported in

Table 3. The system modeled in OSMOSE-WFS reaches a steady state after around 20 years of simulation (Fig. 2).

Availability coefficients to be used for evaluating the natural mortality rates and diet patters of gag grouper usually are very low, and estimated to be: (1) $5.8.10^{-3}$ for small phytoplankton; (2) 3.10^{-4} for diatoms; (3) $1.46.10^{-2}$ for small copepods; (4) 0.2058 for large mesozooplankton; (5) 1.10^{-4} for meiofauna; (6) 3.10^{-4} for small infauna; (7) 2.10^{-4} for small mobile epifauna; (8) 1.10^{-4} for bivalves; and (9) $4.23.10^{-2}$ for echinoderms and large gastropods.

Monthly larval mortality rates to be used for the reference scenario for the different HTL groups are split into four groups (Table 3). The first group comprises king mackerel and amberjacks, whose larval mortality rates are extremely high (greater than 15 month^{-1}). The second group includes red grouper, gag grouper and red grouper, which have very high larval mortality rates (over the range of 11 to 13 month^{-1}). Reef carnivores, shrimps and large crabs constitute the third group, characterized by high larval mortality rates (over the range of 9 to 11 month^{-1}). Finally, the fourth group comprises all the other HTL groups that are explicitly considered in OSMOSE-WFS, i.e., the sardine-herring-scad complex, anchovies and silversides, coastal omnivores and reef omnivores. The monthly larval mortality rates of these HTL groups are low and vary between 0.63 and 6.14 month^{-1}. The larval mortality rate of gag grouper is estimated to be 11.94 month^{-1} by the EA.

Natural mortality rates of gag grouper

The instantaneous natural mortality rates of 0-1 year old, 1-3 years old and 3+ years old gag grouper in the West Florida Shelf ecosystem in the 2000s estimated by OSMOSE-WFS are displayed in Fig. 3.

The total annual instantaneous natural mortality rate, *M*, of 0-1 year old gag evaluated by OSMOSE-WFS is very high (2.99 ± 0.38 year^{-1}), and essentially results from predation by HTL groups that are explicitly considered in the model, P_{total} (Fig. 3a). Reef carnivores (46%), king mackerel (20%), amberjacks (10%), gag grouper (10%) and red grouper (9%) are the main contributors of P_{total} for 0-1 year old gag (Fig. 4a). The mean *M* estimated for 0-1 year old gag grouper over the period 2005-2009 with WFS EwE is significantly smaller than that predicted by OSMOSE-WFS (1.65 vs. 2.99 year^{-1}; Chagaris and Mahmoudi, 2013). Reef carnivores and gag grouper do not predate on 0-1 year old gag in WFS Ecopath. King mackerel, red grouper and amberjacks are the only HTL groups explicitly represented in OSMOSE-WFS that feed on 0-1 year old gag grouper in WFS EwE. The aforementioned species contribute, respectively, to 30.5%, 23.1% and 7% of the P_{total} of 0-1 year old gag in WFS EwE (i.e., to 60.6% of the P_{total} of 0-1 year old gag in WFS EwE in total ; Chagaris and Mahmoudi, 2013).

The *M* of 1-3 years old gag grouper in OSMOSE-WFS is high (0.41 ± 0.16 year^{-1}), and also mainly results from P_{total} (Fig. 3b). King mackerel (51%) and, to a lesser extent, gag grouper (20%) and amberjacks (18%) are responsible for the bulk of the P_{total} of 1-3 years old gag (Fig. 4b). The mean *M* estimated for 1-3 years old gag grouper over the period 2005-2009 with WFS EwE is greater than that estimated with OSMOSE-WFS (0.65 vs. 0.41 year^{-1}; Chagaris and Mahmoudi, 2013). Among the HTL groups explicitly considered in OSMOSE-WFS, only king mackerel and amberjacks predate on 1-3 years old gag in WFS EwE. The two groups account for, respectively, 48.7% and 11.1% of P_{total} of this age group in WFS EwE (i.e., for 59.8% of the P_{total} of this age group in WFS EwE in total; Chagaris and Mahmoudi, 2013).

Finally, the *M* of 3+ years old gag grouper evaluated by OSMOSE-WFS is very low (0.05 ± 0.01 year^{-1}) and is mainly caused by starvation plus predation by organisms that are explicitly represented in WFS Ecopath but not in OSMOSE-WFS, i.e., M_{others} (Fig. 3c). In WFS EwE, 3+ years old gag is predated by the billfish/tuna group only, and its predation mortality rate is negligible ($3.64.10^{-5}$ year^{-1}; Chagaris and Mahmoudi, 2013). Therefore, in OSMOSE-WFS, the bulk of *M* for 3+ years old gag grouper is caused by starvation. Only 3 HTL groups feed upon 3+ years old gag in this model: king mackerel, amberjacks and gag grouper, which contribute, respectively, to 51%, 33% and 16% of the P_{total} of this age group (Fig. 4c). The mean *M* evaluated for 3+ years old gag grouper over the period 2005-2009 with WFS EwE is higher than that with OSMOSE-WFS, and is quasi-entirely due to ‘unexplained’ causes (0.13 vs. 0.05 year^{-1}; Chagaris and Mahmoudi, 2013).

Diet patterns of gag grouper

The major prey of 0-1 year old gag grouper in OSMOSE-WFS comprise zooplankton (21% of the diet), anchovies and silversides (17%), reef omnivores (15%), the sardine-herring-scad complex (13%) and adult shrimps (13%) (Fig. 5a). The major prey of this age group in WFS Ecopath are slightly different, and include anchovies and silversides (20%), adult shrimps (20%), coastal omnivores (13%) and small mobile epifauna (11%) (Fig. 5b).

Both in OSMOSE-WFS and WFS EwE, 1-3 years old gag grouper feeds mainly on the same prey, which are adult shrimps (20% of the diet in OSMOSE-WFS), coastal omnivores (19% in OSMOSE-WFS), the sardine-herring-scad complex (12% in OSMOSE-WFS) and anchovies and silversides (11% in OSMOSE-WFS) (Figs. 5c and d).

Finally, the sardine-herring-scad complex represents only 10% of the diet of 3+ years old gag grouper in OSMOSE-WFS vs. 50% in WFS Ecopath (Figs. 5e and f). The major prey of 3+ years old gag in OSMOSE-WFS are relatively different from those in WFS Ecopath and comprise coastal omnivores (28% of the diet), adult shrimps (16%), and echinoderms and large gastropods (11%) (Fig. 5e).

The examination of diet compositions of gag grouper reveals that the species feeds upon many different prey items in OSMOSE-WFS (Fig. 5 and Table 4). In particular, 0-1 year old gag grouper and, to a lesser extent, 1-3 years old gag grouper consume a very large spectrum of prey sizes (Figs 5a, c and e and Table 4). As a result, the biomass of the gag population distributes largely across TLs (Figs. 6 and 7), which indicates a high degree of omnivory for the species. The mean TL of gag grouper in OSMOSE-WFS is 4.44 ± 0.54 (vs. 4.12 in WFS Ecopath), and is 1.11 times greater than the mean TL of the HTL community (3.70) (Fig. 6). The degree of omnivory of gag grouper in OSMOSE-WFS is 1.36 times greater than the mean degree of omnivory of the HTL community, suggesting that gag is one of the most opportunist HTL groups being explicitly considered in the model (Fig. 8a). In fact, gag grouper is the second most opportunistic HTL group in OSMOSE-WFS after amberjacks. The degree of omnivory of gag grouper in WFS Ecopath is 2 times greater than the mean degree of omnivory of the HTL community, though the species is far from being the most opportunistic functional group in this model (Fig. 8b).

Discussion

In this paper, we detailed the calibration process of OSMOSE-WFS and reported the natural mortality rates and diet patterns of gag grouper evaluated by the model.

Switching from the genetic algorithm developed by Duboz et al. (2010) to a more sophisticated evolutionary algorithm (EA) designed by Oliveros-Ramos (in prep.) allowed us to fully calibrate a first OSMOSE model for the West Florida Shelf ecosystem. The biomasses of HTL groups predicted by OSMOSE-WFS are on average within valid intervals after 30 to

50 years of simulation, except for shrimps. However, the biomass of shrimps after 30 to 50 years of simulation was on average only 1.15 higher than its maximum possible biomass in the 2000s (according to WFS Ecopath), which is greatly acceptable.

The calibration of OSMOSE-WFS using the EA also provided estimates for parameters that were unknown, and that are highly difficult to estimate from empirical studies: availability coefficients for LTL groups and larval mortality rates for HTL groups. The availability coefficients that were evaluated by the EA globally were very low, confirming the idea that only a very small fraction of the production of LTL groups must be effectively utilized by HTL groups to prevent the modeled system from being overproductive (Ricker, 1969; Polovina, 1984). The monthly larval mortality rate of gag grouper was estimated to be 11.94 month^{-1} by the EA. This value may not be very reliable since it strongly depends on the value specified for gag relative annual fecundity. However, the larval mortality rates evaluated by OSMOSE-WFS may be the best available estimates given that the quasi-totality of them has never been assessed and that they are very difficult or impossible to obtain.

The instantaneous natural mortality rates predicted by OSMOSE-WFS and by WFS Ecopath from 2005 to 2009 under the 'baseline scenario' are relatively different, though the two models globally are in agreement regarding patterns of natural mortality for gag grouper. Both in OSMOSE-WFS and WFS Ecopath, 0-1 year old and 1-3 years old gag suffer, respectively, very high and high natural mortality, essentially due to predation pressure, and in great part because of the predation of king mackerel and amberjacks. On the other hand, reef carnivores and gag grouper exert a high predation pressure on juvenile gag in OSMOSE-WFS, whereas they do not feed on 0-1 year old and 1-3 years old gag in WFS Ecopath. In OSMOSE-WFS, reef carnivores are responsible for 46% of the predation mortality of 0-1 year old gag, while gag grouper contribute to, respectively, 10% and 20% of the predation mortality of 1-3 years old gag.

By contrast, 3+ years old gag suffer low natural mortality, primarily due to starvation in OSMOSE-WFS, and quasi-entirely to ‘unexplained’ causes in WFS Ecopath. Predation pressure on 3+ years old gag in OSMOSE-WFS is very low and comes from king mackerel and, to a lesser extent, amberjacks and gag grouper. Predation pressure on 3+ years old gag in WFS Ecopath is negligible, and comes only from the tuna/billfish group, which is contentious for some of the authors of the present paper. One could reasonably assume that ‘unexplained’ causes of natural mortality in WFS Ecopath are essentially red tide blooms. Gray et al. (2013) used another EwE model for the West Florida Shelf ecosystem to estimate the natural mortality on adult gag grouper (2+ years old individuals in their model) caused by red tide blooms. The authors found red tide mortality on adult gag to be on the order of 0.03 to 0.15 year^{-1} over the period 2005-2009, while the natural mortality due to causes other than the predation of HTL groups represented in OSMOSE-WFS was found to be 0.05 year^{-1} in OSMOSE-WFS and 0.13 year^{-1} in WFS Ecopath.

The diet compositions estimated from OSMOSE simulations indicate that adult shrimps are major prey of all age classes of gag grouper, while the sardine-herring-scad complex and anchovies and silversides have an important contribution to the diet of juvenile gag (0-1 year old and 1-3 years old individuals), and coastal omnivores to the diet of 1-3 and 3+ years old gags. Zooplankton and reef omnivores also largely contribute to the diet of 0-1 year old gag, and echinoderms and large gastropods to that of 3+ years old gag. These diet patterns emerged from model simulations but were highly influenced by the minimum ($(L_{pred}/L_{prey})_{min}$) and maximum predator/prey size ratios ($(L_{pred}/L_{prey})_{max}$) specified for gags. All age classes of gag grouper feed on various prey items in OSMOSE-WFS, but juvenile individuals consume a larger spectrum of prey sizes than 3+ years old individuals (adults) because of the predator/prey size ratios that were defined for them ($(L_{pred}/L_{prey})_{min}$) = 1.5 for juveniles vs. 3.9 for adults and $(L_{pred}/L_{prey})_{max}$) = 200 for juveniles vs. 23 for adults; Table 2). As a result, gag grouper has a high degree of omnivory in OSMOSE-WFS. Unsurprisingly, the trophic level of gag in OSMOSE-WFS is greater than 4, and higher than the mean trophic level of the HTL community explicitly considered in the model.

OSMOSE-WFS and WFS Ecopath are more or less in agreement regarding the diet compositions of gag grouper. The diets of 0-1 year old gag in WFS Ecopath and OSMOSE-WFS are pretty similar. On the other hand, the diet compositions of 1-3 and 3+ years old gag in WFS Ecopath and OSMOSE-WFS are relatively different. Diets in Ecopath are defined *a priori*, while those in OSMOSE emerge from model simulations and, as noted earlier, are highly influenced by predator/prey size ratios defined by model users. Predation in OSMOSE is therefore highly opportunistic, and any HTL group explicitly considered in the model will feed upon any prey item, provided the prey item is of suitable size and accessible. Thus, OSMOSE allows for a high degree of opportunism in feeding behavior and cannibalism, both of which are typically reported for fish populations in the literature (e.g., Bond, 1979; Laevastu and Larkins, 1981; Crawford, 1987). We can note, that in WFS Ecopath the degree of omnivory of the HTL groups represented in OSMOSE-WFS is generally high (Fig. 8b; Chagaris and Mahmoudi, 2013). This stems from the fact that many more functional groups are explicitly considered in WFS Ecopath than in OSMOSE-WFS when calculating diet compositions (70 vs. 26), but also from the fact that it is generally necessary to distribute the predation pressure of certain functional groups over a wide range of model groups to balance Ecopath models properly (Okey and Mahmoudi, 2002; Christensen et al., 2005).

Based on comparisons with WFS EwE and on insights from the literature, the predictions of OSMOSE-WFS reported in the present paper and those not presented here (e.g., the diet compositions of model groups other than gag grouper) can be deemed relevant.

We believe that the outcomes of OSMOSE-WFS reported here could be used for SEDAR 33, provided it is clearly stated that they were obtained under specific assumptions. The total annual instantaneous natural mortality rates of gag grouper we estimated could be used as priors in the Stock Synthesis (SS) model employed for SEDAR 33 Assessment (Schirripa et al., 2013). Moreover, the diet compositions and predation rates emerging from OSMOSE-WFS simulations could be used to parameterize diets in the Ecopath models developed for the West Florida Shelf ecosystem. In particular, these outcomes of OSMOSE-WFS would be useful to define predation pressure on functional groups such as 3+ years old gag in WFS Ecopath. This idea was already mentioned in Chagaris and Mahmoudi (2013).

Short-term and long-term perspectives for OSMOSE-WFS are numerous. Most of them are detailed in Grüss et al. (2013). One very interesting perspective when considering the results reported here is the representation of red tide blooms in OSMOSE-WFS. OSMOSE-WFS and WFS EwE both agree that the bulk of the natural mortality M of adult gag grouper is not due to predation by HTL groups explicitly considered in OSMOSE-WFS. The M of adult gag mainly results from 'unexplained' causes in WFS EwE (Chagaris and Mahmoudi, 2013), while it mainly comes from starvation in OSMOSE-WFS. Mortality due to unexplained causes in WFS EwE and starvation mortality in OSMOSE-WFS for 3+ yeas old gag are on the order of the red tide mortality on gag grouper over the period 2005-2009 reported in Gray et al. (2013). Given that red tide outbreaks may significantly impact a wide range of species in the West Florida Shelf (Walter et al., 2013), components of total mortality in future versions of OSMOSE-WFS may include red tide mortality in addition to natural mortality due to various causes ($M_{diverse}$), starvation mortality, predation mortalities and fishing mortality.

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Tables

Table 1. High trophic level (HTL) groups explicitly considered in the OSMOSE-WFS model. 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 scat (*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 2. Feeding size ranges of the high trophic level (HTL) groups explicitly considered in OSMOSE-WFS expressed as predator/prey size ratios. L_{thres} is the 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 predator to prey body size ratios that have been modified since Grüss et al. (2013) are highlighted in grey.

HTL group	L_{thres} (cm TL)	$(L_{pred}/L_{prey})_{min}$		$(L_{pred}/L_{prey})_{max}$	
		Juveniles	*Adults*	*Juveniles*	*Adults*
King mackerel	97.5	2.9	4.5	18	30
Amberjacks	90.3	4.5	4.5	12	12
Red grouper	34.1	3	4.5	50	30
Gag grouper	46.8	1.5	3.9	200	23
Red snapper	34.6	2.5	5	400	100
Sardine-herring-scad complex	9.3	10	100	150	10000
Anchovies and silversides	4.6	12	12	500	500
Coastal omnivores	15.3	2	2	80	80
Reef carnivores	17.4	1.5	1.5	50	50
Reef omnivores	15.5	30	30	1000	1000
Shrimps	8	3	5	10000	242
Large crabs	13.1	1.1	1.1	50	50

Table 3. Target biomass of the 12 high trophic level (HTL) groups considered in OSMOSE-WFS, associated pedigree and coefficient of variation, and larval mortality rates of the different HTL groups estimated through the calibration of OSMOSE-WFS. Biomass values come from the calibration of the WFS Ecopath model. Coefficients of variations were set from biomass pedigree categories according to the criteria specified in Okey and Mahmoudi (2002).

HTL group	Target biomass (tons)	Pedigree category of the biomass estimate	Associated coefficient of variation	Minimum possible biomass (tons)	Maximum possible biomass (tons)	Larval mortality rates (month^{-1})
King mackerel	9 703	Approximate or indirect method	0.25	4 852	14 555	15.40
Amberjacks	1 328	Approximate or indirect method	0.25	663	1 991	15.28
Red grouper	19 759	Approximate or indirect method	0.25	9 880	29 639	11.94
Gag grouper	9 189	Approximate or indirect method	0.25	4 594	13 783	12.67
Red snapper	8 786	Approximate or indirect method	0.25	4 393	13 179	11.63
Sardine-herring-scad complex	289 000	From other model	0.4	57 800	520 200	0.68
Anchovies and silversides	162 120	From other model	0.4	32 424	291 816	6.14
Coastal omnivores	303 450	From other model	0.4	60 690	446 210	2.86
Reef carnivores	276 980	From other model	0.4	55 396	498 564	9.81
Reef omnivores	78 862	From other model	0.4	15 774	141 970	3.97
Shrimps	154 710	Approximate or indirect method	0.25	77 355	232 065	9.39
Large crabs	109 640	From other model	0.4	21 928	197 352	10.75

Table 4. Prey accounting for less than 1% of the diet of 0-1 year old, 1-3 years old and 3+ years old gag grouper.

Age class	High trophic level groups accounting for less than 1% of the diet of this age class	Low trophic level groups accounting for less than 1% of the diet of this age class
0-1 year old gag grouper	Red grouper, gag grouper, red snapper	Phytoplankton, meiofauna, small infauna, bivalves
1-3 years old gag grouper	Red grouper, gag grouper, red snapper	Phytoplankton, meiofauna, small infauna, bivalves, ichthyoplankton
3+ years old gag grouper	Red grouper, gag grouper, red snapper	Small infauna, bivalves

Figures

Fig. 1. Biomasses predicted by WFS Ecopath (gray boxplots) and OSMOSE-WFS (black boxplots) for the 12 high trophic level (HTL) groups that are explicitly considered in OSMOSE-WFS. Biomasses predicted by WFS Ecopath correspond to mean biomasses +/- standard deviations in this model, where standard deviations were estimated from biomass pedigree categories according to the criteria specified in Okey and Mahmoudi (2002). Biomasses simulated with OSMOSE-WFS correspond to mean biomasses +/- standard deviations for 10 replicates after 30 to 50 years of simulation in the reference situation. (a) km: king mackerel – am: amberjacks – rg: red grouper – gg: gag grouper – rs: red snapper; (b) shsc: sardine-herring-scad complex – as: anchovies and silversides – co: coastal omnivores – rc: reef carnivores – ro: reef omnivores – shr: shrimps – lc: large crabs.

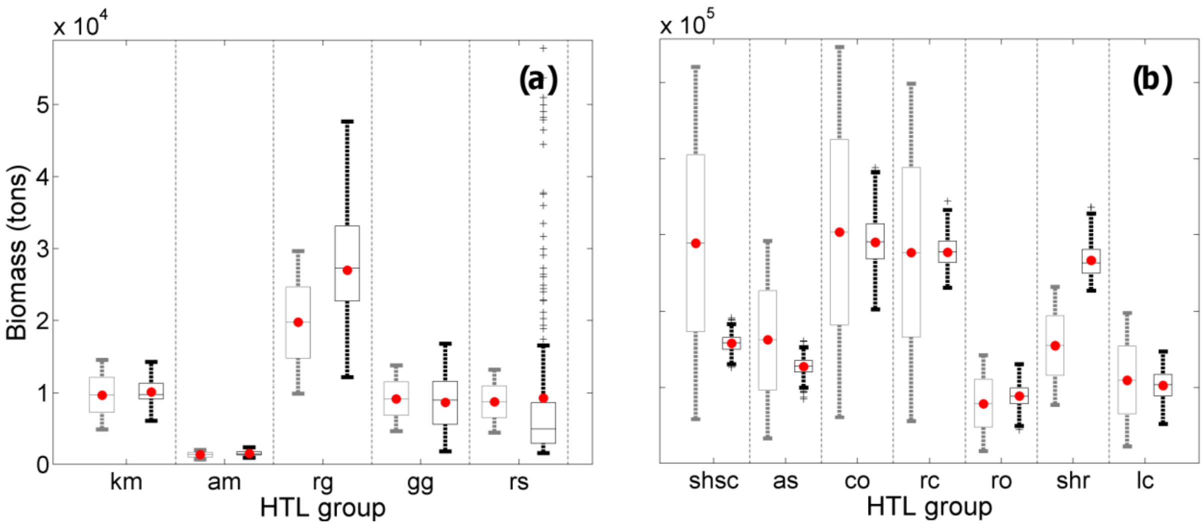


Fig. 2. Biomass trajectories predicted by OSMOSE-WFS.

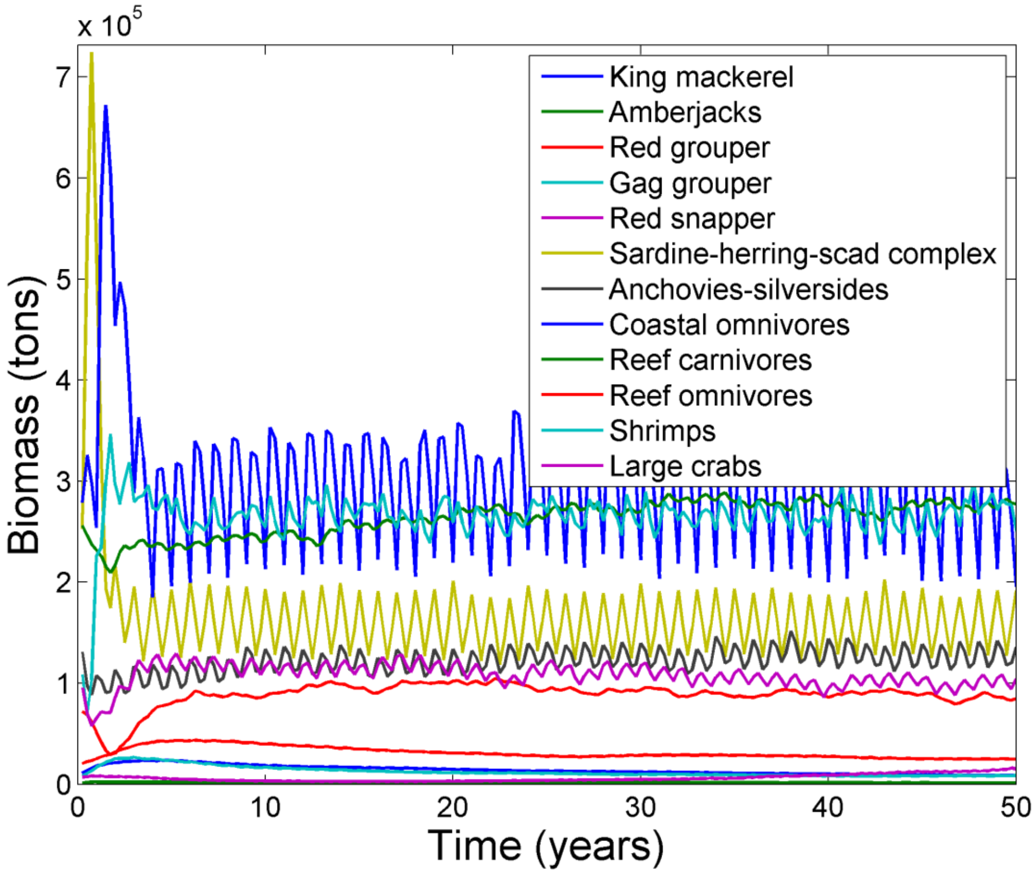


Fig. 3. Annual instantaneous mortality rates predicted by OSMOSE-WFS after 30 to 50 years of simulation for (a) 0-1 year old, (b) 1-3 years old and (c) 3+ years old gag grouper (*Mycteroperca microlepis*). *M*: total instantaneous natural mortality rate - P_{total}: total instantaneous predation mortality rate - M_{others}: instantaneous natural mortality rate due to all other causes.

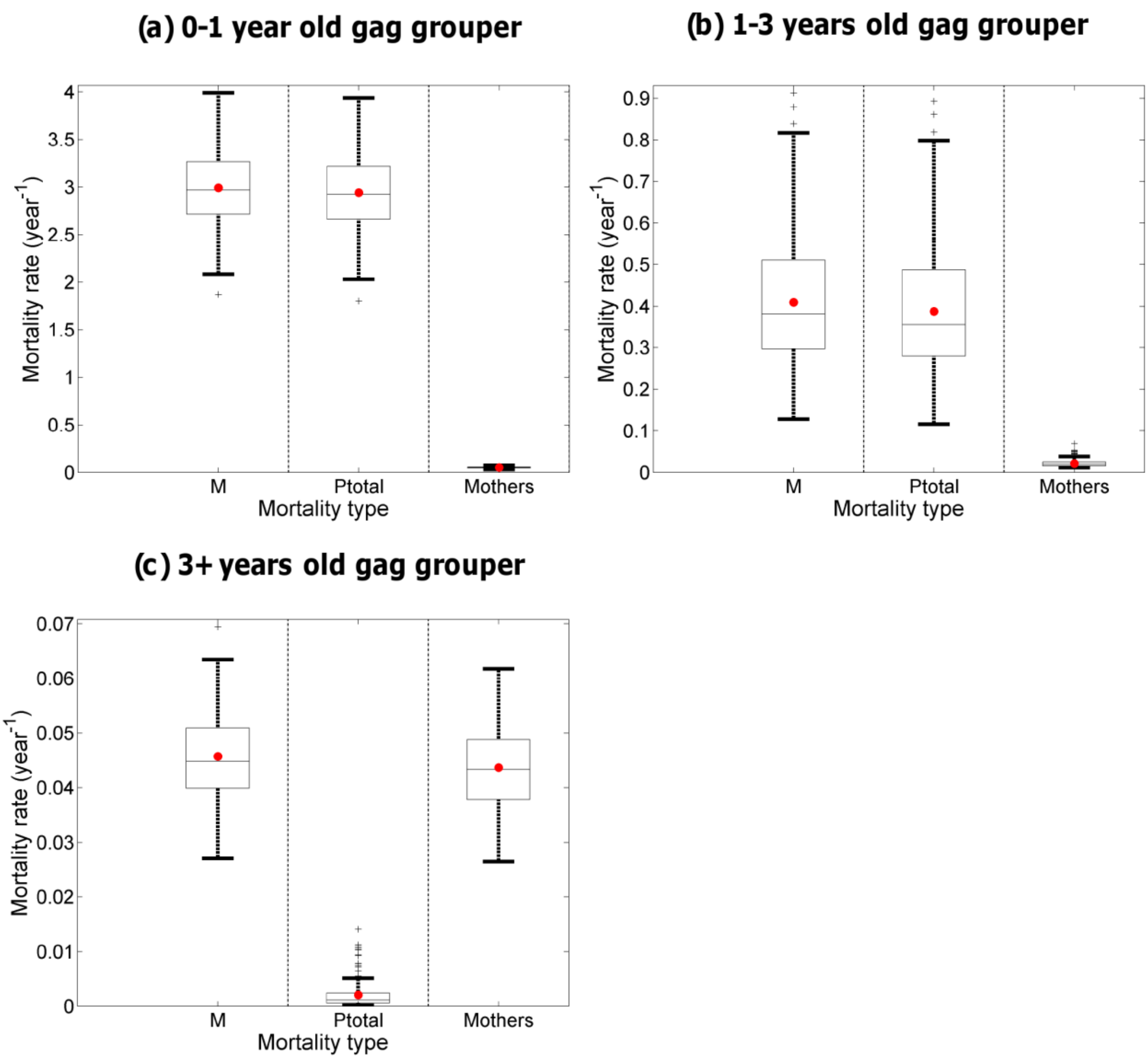


Fig. 4. Main contributors to the predation mortalities of (a) 0-1 year old, (b) 1-3 years old and (c) 3+ years old gag grouper.

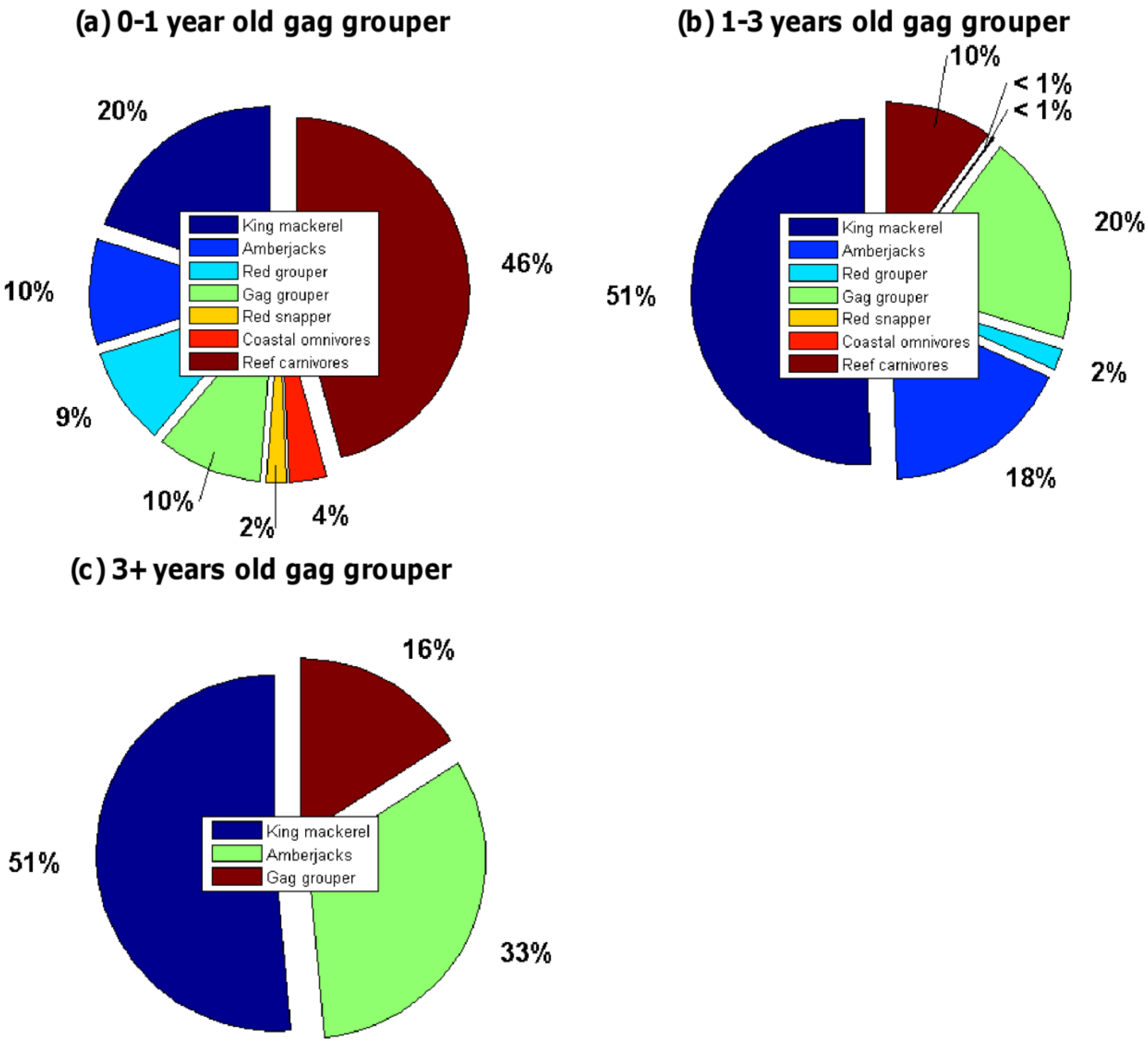
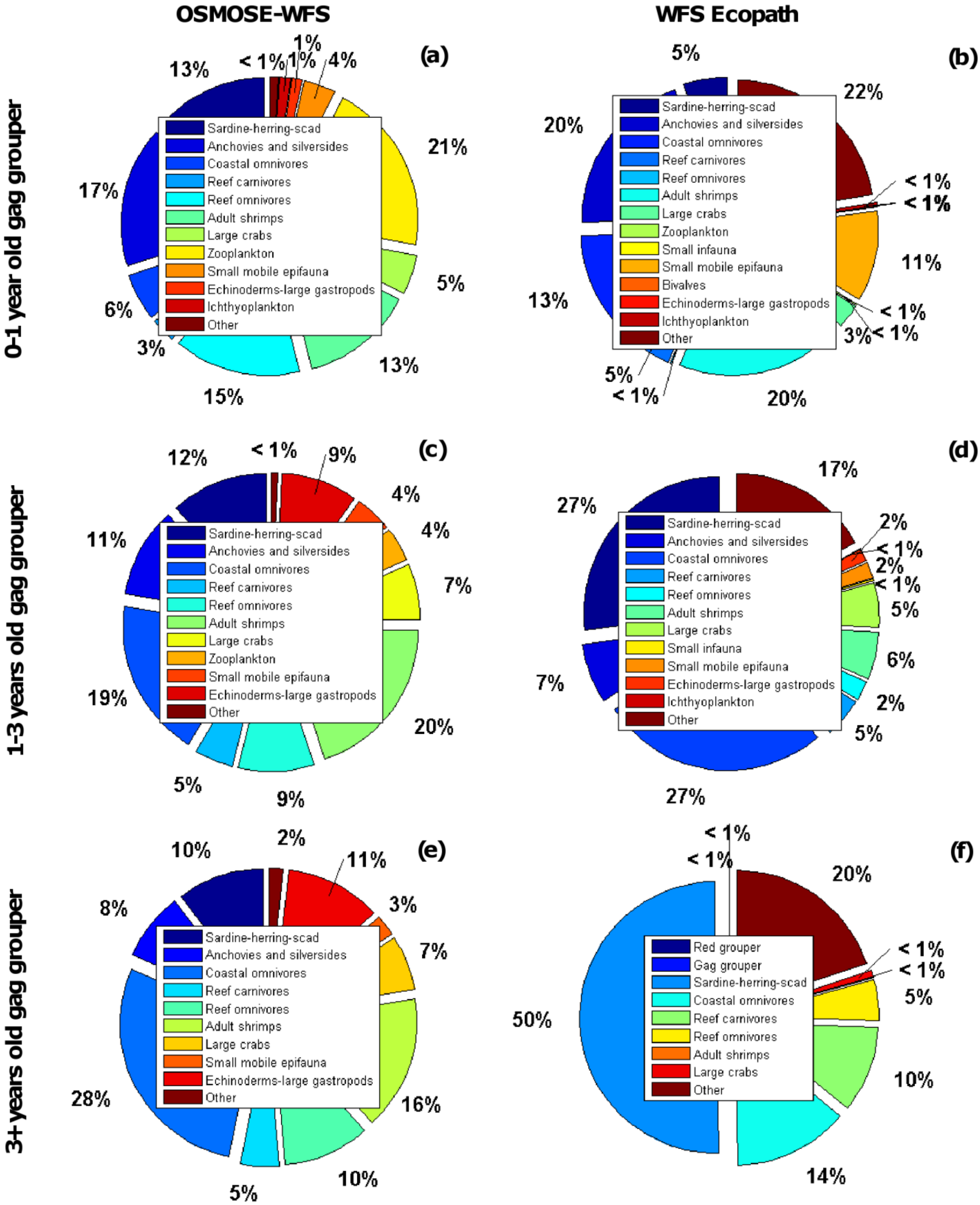


Fig. 5. Diet composition of (a,b) 0-1 year old, (c,d) 1-3 years old and (e,f) 3+ years old gag grouper (*Mycteroperca microlepis*), predicted by (a,c,e) OSMOSE-WFS and (b,d,f) WFS Ecopath, expressed as percentage of prey in mass. In the case of OSMOSE-WFS 'Other' refers to model groups accounting for less than 1% of the diet of a given age class of gag grouper (listed in Table 4), while in the case of WFS Ecopath 'Other' refers to model groups (HTL or LTL groups) not represented in OSMOSE-WFS.



OSMOSE-WFS
WFS Ecopath
0-1 year old gag grouper
1-3 years old gag grouper
3+ years old gag grouper
(a)
(b)
(c)
(d)
(e)
(f)
Sardine-herring-scad
Anchovies and silversides
Coastal omnivores
Reef carnivores
Reef omnivores
Adult shrimps
Large crabs
Zooplankton
Small infauna
Small mobile epifauna
Bivalves
Echinoderms-large gastropods
Ichthyoplankton
Other
Red grouper
Gag grouper

Fig. 6. Mean trophic level (TL) of the HTL groups explicitly considered in OSMOSE-WFS in the reference situation predicted by OSMOSE-WFS (black diamonds) and by WFS Ecopath (grey circles). For OSMOSE-WFS, standard deviations around mean TLs are also represented.

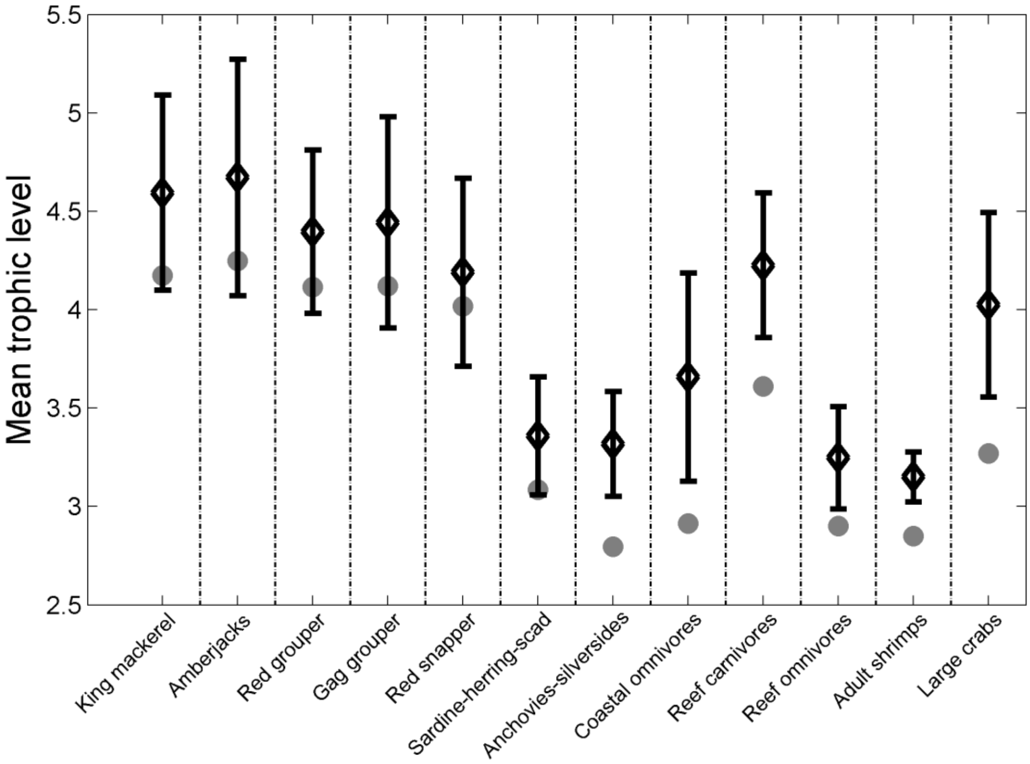


Fig. 7. Distribution of gag grouper biomass across trophic levels predicted by OSMOSE-WFS. The vertical black line represents the mean trophic level of the species.

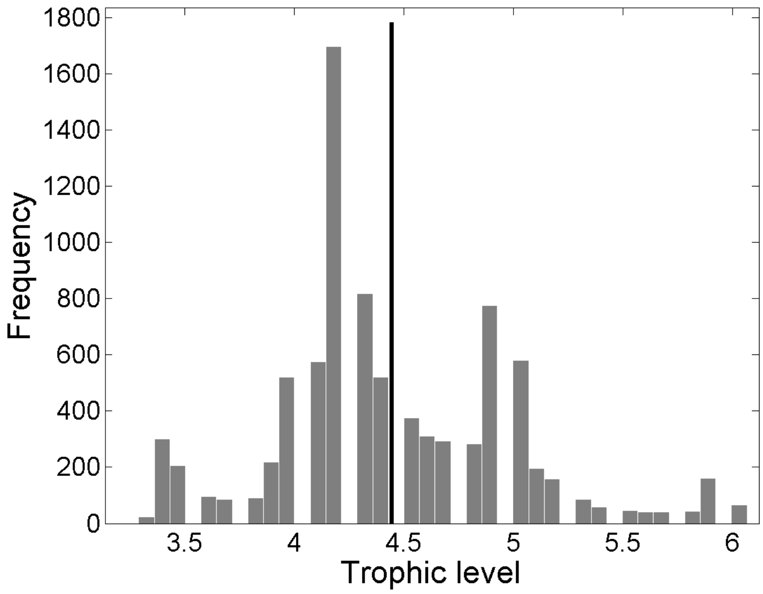
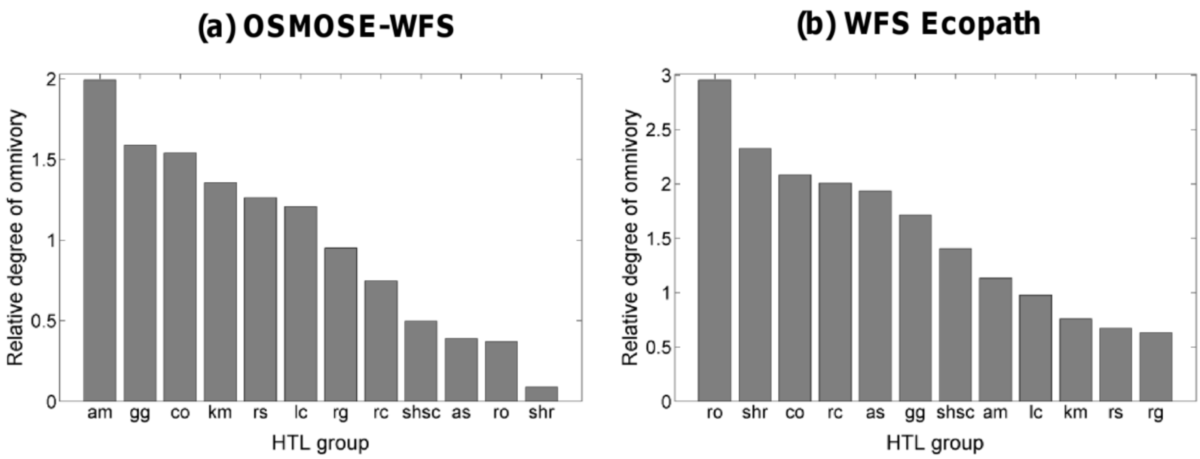


Fig. 8. Relative degree of omnivory of the HTL groups explicitly considered in OSMOSE-WFS in the reference situation predicted by (a) OSMOSE-WFS and by (b) WFS Ecopath. km: king mackerel – am: amberjacks – rg: red grouper – gg: gag grouper – rs: red snapper - shsc: sardine-herring-scad complex – as: anchovies and silversides – co: coastal omnivores – rc: reef carnivores – ro: reef omnivores – shr: shrimps – lc: large crabs.



Boxes

Box 1. Theoretical accessibility of the different age classes of the HTL groups to LTL groups (Table I), and comments on the value of some accessibility coefficients (Table II).

Table I. Theoretical accessibility of the different age classes of the HTL groups (in columns) to LTL groups (in rows), 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 I. (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%	100%	0%	0%	0%	100%	0%	100%	0%	100%	0%
Diatoms	0%	100%	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 II. Comments on the value of some accessibility coefficients.

	Comments
Juvenile king mackerel	Accessibility to the different LTL benthos groups set to 40% to account for little overlap in the vertical dimension.
Adult king mackerel	Accessibility to the different LTL benthos groups set to 10% to account for very little overlap in the vertical dimension.
Amberjacks	Accessibility to the different LTL benthos groups set to 10% to account for very little overlap in the vertical dimension.
Juvenile red grouper	Accessibility to bivalves and to echinoderms and large gastropods 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 feeding on the two mentioned LTL benthos groups.
Adult red grouper	Accessibility to bivalves and to echinoderms and large gastropods 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 feeding on the two mentioned LTL benthos groups.
Adult gag grouper	Accessibility to the different LTL benthic groups set to 40% to account for little overlap in the vertical dimension.
Juvenile red snapper	Accessibility to meiofauna, small infauna and small mobile epifauna set to 40% to account for little overlap in the vertical dimension. Accessibility to bivalves and to echinoderms and 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 feeding on the two mentioned LTL benthos groups.
Adult red snapper	Accessibility to meiofauna, small infauna and small mobile epifauna set to 40% to account for little overlap in the vertical dimension. Accessibility to bivalves and to echinoderms and 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 feeding on the two mentioned LTL benthos groups.
Sardine-herring-scad complex	Accessibility to the different LTL benthos groups set to 10% to account for very little overlap in the vertical dimension.
Anchovies and silversides	Accessibility to meiofauna, small infauna and small mobile epifauna set to 40% to account for little overlap in the vertical dimension. Accessibility to bivalves, and echinoderms and large gastropods set to 10% to account for very little overlap in the vertical dimension.

Box 2. Accessibility of the different age classes of the HTL groups to each other (Table I), and comments on the value of some accessibility coefficients (Table II).

Table I. Accessibility of the different age classes of the HTL groups (in columns) to each other (in rows), determined from the literature and expert opinion (J. Simons, Center for Coastal Studies, Texas A&M University-Corpus Christi). The accessibility coefficients that have been modified since Grüss et al. (2013) are highlighted in grey.

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

Table II. (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%
Juvenile red grouper	40%	80%	80%	80%	0%	0%
Adult 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%	10%	10%	10%	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 II. Comments on the value of some accessibility coefficients.

	Comments
Juvenile king mackerel	Accessibility to shrimps set to 40% to account for little overlap in the vertical dimension. Accessibility to anchovies and silversides set to 10% to account for very little overlap in the horizontal dimension; anchovies and silversides are found primarily in very coastal areas (estuaries and bays), whereas king mackerel occurs in more offshore waters. Accessibility to large crabs set to 0% to account for very little overlap in the vertical dimension, and the 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 to shrimps set to 40% to account for little overlap in the vertical dimension. Accessibility to anchovies and silversides set to 10% to account for very little overlap in the horizontal dimension; anchovies and silversides are found primarily in very coastal areas (estuaries and bays), whereas king mackerel occurs in more offshore waters. Accessibility to large crabs set to 0% to account for very little overlap in the vertical dimension, and the 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 to shrimps set to 40% to account for little overlap in the vertical dimension. Accessibility to anchovies and silversides set to 10% to account for very little overlap in the horizontal dimension; anchovies and silversides are found primarily in very coastal areas (estuaries and bays), whereas amberjacks occur in more offshore waters. Accessibility to large crabs set to 10% to account for very little overlap in the vertical dimension. Accessibility to 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 to 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.
Juvenile red grouper	Accessibility to juvenile and adult king mackerels and to amberjacks 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.
Adult red grouper	Accessibility to juvenile and adult king mackerels and to amberjacks 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 to juvenile and adult king mackerels and to amberjacks set to 0%, to account for the fact that gag 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 to shrimps and large crabs set to 40% to account for little overlap in the vertical dimension. Accessibility to juvenile and adult king mackerels and to amberjacks set to 0%, to account for the fact that gag 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 to large crabs set to 40% to account for little overlap in the vertical dimension.
Sardine-herring-scad complex	Accessibility to red grouper, gag grouper, red snapper, coastal omnivores, reef carnivores and reef omnivores set to 40% to account for little overlap in the vertical dimension. Accessibility to anchovies and silversides set to 10% to account for very little overlap in the horizontal dimension; anchovies and silversides are found primarily in very coastal areas (estuaries and bays), whereas species of the sardine-herring-scad complex generally occur in more offshore waters. Accessibility to shrimps and large crabs set to 10% to account for very little overlap in the vertical dimension.
Anchovies and silversides	Accessibility to red grouper, gag grouper, red snapper, coastal omnivores, reef carnivores and reef omnivores set to 40% to account for little overlap in the vertical dimension. Accessibility to anchovies and silversides set to 10%, because predation on post-larval stages of anchovies

	and silversides (i.e., individuals older than 1 month) is unlikely; anchovies and silversides only feed on very small prey items belonging to low trophic levels (Froese and Pauly, 2010). Accessibility to shrimps and large crabs set to 10% to account for very little overlap in the vertical dimension.
Coastal omnivores	Accessibility to king mackerel, amberjacks, the sardine-herring-scad complex and shrimps set to 40% to account for little overlap in the vertical dimension. Accessibility to anchovies and silversides set to 10% to account for little overlap in the vertical and horizontal dimension. Accessibility to 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 feeding on large crabs.
Reef carnivores	Accessibility to anchovies and silversides set to 10% to account for little overlap in the vertical and horizontal dimension.
Reef omnivores	Accessibility to anchovies and silversides set to 10% to account for little overlap in the vertical and horizontal dimension.
Shrimps	Accessibility to all HTL groups 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 to the sardine-herring-scad complex, anchovies and silversides and coastal omnivores set to 10% to account for very little overlap in the vertical dimension. Accessibility to all other HTL 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).