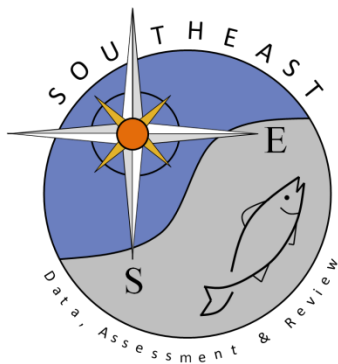


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Estimating natural mortality rates and simulating fishing scenarios for Gulf of Mexico red grouper (*Epinephelus morio*) using the ecosystem model OSMOSE-WFS[☆]



Arnaud Grüss^{a,b,*}, Michael J. Schirripa^b, David Chagaris^c, Laure Velez^{d,e}, Yunne-Jai Shin^{d,e,f}, Philippe Verley^d, Ricardo Oliveros-Ramos^{d,g}, Cameron H. Ainsworth^h

^a Cooperative Institute for Marine and Atmospheric Studies, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

^b Southeast Fisheries Science Center, Sustainable Fisheries Division, 75 Virginia Beach Drive, Miami, FL 33149-1099, USA

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

^d Institut de Recherche pour le Développement, UMR MARBEC 248 and EME 212, Centre de Recherche Halieutique Méditerranéenne et Tropicale, Avenue Jean Monnet, CS 30171, 34203 Sète cedex, France

^e Université de Montpellier, Place Eugène Bataillon, Bâtiment 24, CC 093, 34095 Montpellier cedex 05, France

^f University of Cape Town, Marine Research Institute Ma-Re, Department of Biological Sciences, Private Bag X3, Rondebosch, Cape Town 7701, South Africa

^g Instituto del Mar del Perú (IMARPE), Gamarra y General Valle s/n Chucuito, Callao, Peru

^h University of South Florida, College of Marine Science, 140 7th Avenue South, St. Petersburg, FL 33701, USA

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ABSTRACT

The ecosystem model OSMOSE-WFS was employed to evaluate natural mortality rates and fishing scenarios for Gulf of Mexico (GOM) red grouper (*Epinephelus morio*). OSMOSE-WFS represents major high trophic level (HTL) groups of species of the West Florida Shelf, is forced by the biomass of plankton and benthos groups, and has a monthly time step. The present application of the model uses a recently developed 'stochastic mortality algorithm' to resolve the mortality processes of HTL groups. OSMOSE-WFS predictions suggest that the natural mortality rate of juveniles of GOM red grouper is high and essentially due to predation, while the bulk of the natural mortality of adult red grouper results from causes not represented in OSMOSE-WFS such as, presumably, red tides. These results were communicated to GOM red grouper stock assessments. Moreover, OSMOSE-WFS indicate that altering the fishing mortality of GOM red grouper may have no global impact on the biomass of the major prey of red grouper, due to the high complexity and high redundancy of the modeled system. By contrast, altering the fishing mortality of GOM red grouper may have a large impact on the biomass of its major competitors. Increasing the fishing mortality of red grouper would increase the biomass of major competitors, due to reduced competition for food. Conversely, decreasing the fishing mortality of red grouper would diminish the biomass of major competitors, due to increased predation pressure on the juveniles of the major competitors by red grouper. The fishing scenarios that we evaluated may have slightly different impacts in the real world, due to some discrepancies between the diets of red grouper and its major competitors predicted by OSMOSE-WFS and the observed ones. Modifications in OSMOSE-WFS are suggested to reduce these discrepancies.

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1. Introduction

Ecosystem-based fisheries management (EBFM) is becoming a central paradigm in the Gulf of Mexico (GOM) (Karnauskas et al.,

2013; Schirripa et al., 2013). EBFM considers trophic interactions and the influence of the abiotic environment on fish dynamics to define fisheries management strategies (Link, 2002, 2010; Marasco et al., 2007). Ecosystem simulation models are key tools for achieving EBFM, for

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* Corresponding author at: Cooperative Institute for Marine and Atmospheric Studies, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA. Tel.: +1 305 421 4262.

E-mail addresses: agruss@rsmas.miami.edu (A. Grüss), michael.schirripa@noaa.gov (M.J. Schirripa), Dave.Chagaris@MyFWC.com (D. Chagaris), laure.velez@ird.fr (L. Velez), yunne-jai.shin@ird.fr (Y.-J. Shin), philippe.verley@ird.fr (P. Verley), ricardo.oliveros@gmail.com (R. Oliveros-Ramos), ainsworth@usf.edu (C.H. Ainsworth).

their ability to provide an integrated, holistic understanding of marine ecosystems and of how to potentially mitigate pressures on these ecosystems (Cury et al., 2008; Link, 2010; Plagányi, 2007). They are increasingly being used in the GOM to integrate environmental and ecosystem considerations into fisheries stock assessments and to influence fisheries management decisions (Samhuri et al., 2014; Schirripa et al., 2013). Currently, the ecosystem model OSMOSE-WFS (Grüss et al., 2015a) is being employed to assist the stock assessment of GOM red grouper (*Epinephelus morio*) conducted under the auspices of Southeast Data Assessment and Review (SEDAR) (SEDAR 42; <http://www.sefsc.noaa.gov/sedar/>), as well as the GOM Fishery Management Council.

OSMOSE (Object-oriented Simulator of Marine ecOSystem Exploitation) is a spatially-structured, individual-based and multispecies modeling approach, which is increasingly being used by marine ecosystem modelers (Shin and Cury, 2001, 2004; Travers-Trolet et al., 2014; <http://www.osmose-model.org>). The key features of OSMOSE are the consideration of size-based predator–prey interactions, and the explicit representation of the whole life cycle of the major high trophic level (HTL) groups of fish and invertebrate species of a given ecosystem (Shin and Cury, 2001, 2004). OSMOSE-WFS is a steady-state application of the OSMOSE modeling approach with a monthly time step, which describes the trophic structure of the West Florida Shelf ecosystem over the period 2005–2009 (Fig. 1; Grüss et al., 2015a).

In June 2014, a new version of the OSMOSE modeling approach ('OSMOSE version 3 update 1' or 'OSMOSE v3u1') was released (<http://www.osmose-model.org>). One of the differences between OSMOSE v3u1 and earlier versions of OSMOSE is the use of a recently developed mortality algorithm, called the 'stochastic mortality algorithm', which assumes that all types of mortalities are processes that are simultaneous, and that there is competition and stochasticity in the predation process (<http://www.osmose-model.org>). The OSMOSE-WFS model was updated to meet the specifics of OSMOSE and, therefore, had to be recalibrated so that biomasses of the HTL groups represented in the model keep matching observed biomasses over the period 2005–2009 (Grüss et al., 2015a).

In the present study, we describe the updated steady-state version of the OSMOSE-WFS model, and we use this model to estimate natural mortality rates and simulate fishing scenarios for GOM red grouper, with the intent to inform SEDAR 42 and the GOM Fishery Management Council. In the U.S. waters of the GOM, almost all red groupers are found on the West Florida Shelf (Coleman et al., 1996, 2011; Lombardi-Carlson et al., 2008; Sagarese et al., 2014); therefore, the use of the OSMOSE-WFS model is appropriate to evaluate natural mortality rates and fishing scenarios for GOM red grouper. In the following, we: (1) briefly describe the structure, assumptions and parameterization of the new steady-state version of the OSMOSE-WFS model, with a focus on the stochastic mortality algorithm; (2) fit the model to the biomasses observed in the West Florida Shelf in 2005–2009; (3) evaluate the calibrated OSMOSE-WFS model by comparing the predicted diets to observed diets, and the predicted trophic levels (TLs) to TLs from an Ecopath model of the West Florida Shelf ('WFS Reef fish Ecopath'; Chagaris, 2013; Chagaris et al., 2015); (4) generate estimates of annual natural mortality for different life stages of red grouper with OSMOSE-WFS, and compare these estimates with those produced for SEDAR 42 using Lorenzen (2005)'s approach and to those predicted by WFS Reef fish Ecopath; (5) construct an equilibrium catch curve for GOM red grouper, which we employ to estimate the annual fishing mortality rate of the fish population resulting in maximum sustainable yield (MSY), i.e., its F_{msy} ; and (6) investigate the long-term, equilibrium consequences of changing the annual fishing mortality of red grouper on the biomass and fishery catches of the HTL groups represented in OSMOSE-WFS.

2. Material and methods

2.1. Structure, assumptions and parameterization of OSMOSE-WFS

In order to use the latest release of the OSMOSE modeling approach (OSMOSE v3u1), we updated the steady-state version of the OSMOSE-WFS model which was described in detail by Grüss et al. (2015a). Therefore, we provide here only a brief presentation of the structure, assumptions and parameterization of the new steady-state version of

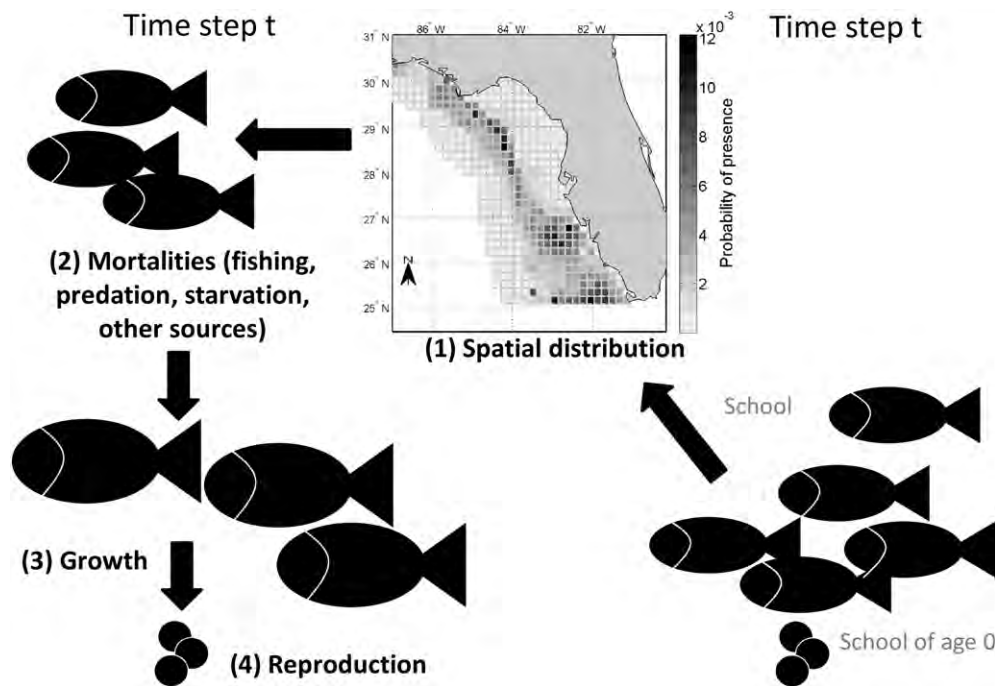


Fig. 1. Succession of events within each time step (month) in the OSMOSE-WFS model. The distribution map used to symbolize the first event (spatial distribution) shows the spatial domain of OSMOSE-WFS, which is also the spatial domain considered implicitly in the non-spatial WFS Reef fish Ecopath model (Chagaris, 2013); this spatial domain 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.

Table 1

Parameters of the low trophic level (LTL) groups of species considered in OSMOSE-WFS, their mean biomass in the West Florida Shelf region in 2005–2009 taken from WFS Reef fish Ecopath (Chagaris, 2013), and their availability coefficients to all high trophic level (HTL) groups (α) estimated via 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	0.2237
Diatoms	0.02–0.2	1*	2,309,400	1.10^{-4}
Small copepods	0.2–1.3 ^{a,b,c}	2.09*	1,550,700	0.0263
Large mesozooplankton	1–3 ^d	2.28*	1,148,400	0.4082
Meiofauna	0.065–0.5 ^e	2.13*	2,315,800	0.0188
Small infauna	0.5–20 ^e	2.25*	3,283,800	4.10^{-5}
Small mobile epifauna	0.5–20 ^f	2.25*	1,979,600	4.10^{-5}
Bivalves	0.2–95 ^{f,g}	2*	8,508,800	3.10^{-5}
Echinoderms and large gastropods	20–95 ^{f,h}	2.5*	3,085,908	3.10^{-4}

^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.

OSMOSE-WFS. Details can be found in the Appendices (Appendices A and B and Tables C, D and E).

OSMOSE-WFS is a two-dimensional individual-based and multispecies model with a monthly time step providing a representation of trophic interactions in the West Florida Shelf ecosystem over the period 2005–2009. OSMOSE-WFS explicitly represents the whole life cycle of the major pelagic–demersal and benthic HTL groups of fish and invertebrate species of the West Florida Shelf (Fig. 1). The model is forced by the biomasses of low trophic level (LTL) groups of species (plankton and benthos), which were estimated from SeaWiFS (Sea-viewing Wide Field-of-view Sensor) data and the WFS Reef fish Ecopath model

Table 2

High trophic level (HTL) groups explicitly considered in OSMOSE-WFS. Species of a given HTL group exhibit similar life history traits, body size ranges, diet and exploitation patterns. Some individual species constitute their own group, as they are emblematic to the West Florida Shelf and of high economic importance. A reference species was identified for each of the HTL groups (indicated in bold). Growth, reproduction, mortality and diet parameters of each group are those of the reference species of the group (given in Appendix B).

HTL group	Species
King mackerel	King mackerel (<i>Scomberomorus cavalla</i>)
Amberjacks	Greater amberjack (<i>Seriola dumerili</i>) , banded rudderfish (<i>Seriola zonata</i>), and lesser amberjack (<i>Seriola fasciata</i>)
Red grouper	Red grouper (<i>Epinephelus morio</i>)
Gag grouper	Gag grouper (<i>Mycteroperca microlepis</i>)
Red snapper	Red snapper (<i>Lutjanus campechanus</i>)
Sardine–herring–scad complex	Scaled sardine (<i>Haemulga jaguana</i>) , Spanish sardine (<i>Sardinella aurita</i>), Atlantic thread herring (<i>Opisthonema oglinum</i>), and round scad (<i>Decapterus punctatus</i>)
Anchovies and silversides	Bay anchovy (<i>Anchoa mitchilli</i>) , striped anchovy (<i>Anchoa hepsetus</i>), silversides (<i>Atherinidae</i> spp.), and alewife (<i>Alosa</i> sp.)
Coastal omnivores	Pinfish (<i>Lagodon rhomboides</i>) , spottail pinfish (<i>Diplodus holbrooki</i>), orange filefish (<i>Aluterus schoepfii</i>), fringed filefish (<i>Monacanthus ciliatus</i>), planehead filefish (<i>Monacanthus hispidus</i>), orangespotted filefish (<i>Cantherhines pullus</i>), honeycomb filefish (<i>Acanthostracion polygonius</i>), Atlantic spadefish (<i>Chaetodipterus faber</i>), scrawled cowfish (<i>Lactophrys quadricornis</i>), and pufferfish (<i>Tetraodontidae</i> spp.)
Reef carnivores	White grunt (<i>Haemulon plumieri</i>) , black sea bass (<i>Centropristis striata</i>), rock sea bass (<i>Centropristis philadelphica</i>), belted sandfish (<i>Serranus subligarius</i>), longtail bass (<i>Hemanthias leptus</i>), butter hamlet (<i>Hypoplectrus unicolor</i>), creole fish (<i>Paranthias furcifer</i>), slippery dick (<i>Halichoeres bivittatus</i>), painted wrasse (<i>Halichoeres caudalis</i>), yellowhead wrasse (<i>Halichoeres garnoti</i>), bluehead (<i>Thalassoma bifasciatum</i>), reef croaker (<i>Odontoscion dentex</i>), jackknife-fish (<i>Equetus lanceatus</i>), leopard toadfish (<i>Opsanus pardus</i>), scopian fish (<i>Scorpaenidae</i> spp.), bigeyes (<i>Priacanthidae</i> spp.), littlehead porgy (<i>Calamus proridens</i>), jolthead porgy (<i>Calamus bajonado</i>), saucereye progy (<i>Calamus calamus</i>), whitebone progy (<i>Calamus leucosteus</i>), knobbed progy (<i>Calamus nodosus</i>), French grunt (<i>Haemulon flavolineatum</i>), Spanish grunt (<i>Haemulon macrostomum</i>), margate (<i>Haemulon album</i>), bluestriped grunt (<i>Haemulon sciurus</i>), striped grunt (<i>Haemulon striatum</i>), sailor's grunt (<i>Haemulon parra</i>), porkfish (<i>Anisotremus virginicus</i>), and neon goby (<i>Gobiosoma oceanops</i>)
Reef omnivores	Doctorfish (<i>Acanthurus chirurgus</i>) , other surgeons (<i>Acanthuridae</i> spp.), blue angelfish (<i>Holocanthus bermudensis</i>), gray angelfish (<i>Pomacanthus arcuatus</i>), cherubfish (<i>Cantopryge argi</i>), rock beauty (<i>Holocanthus tricolor</i>), cocoa damselfish (<i>Pomacentrus variabilis</i>), bicolor damselfish (<i>Pomacentrus partitus</i>), beau gregory (<i>Pomacentrus leucostictus</i>), yellowtail damselfish (<i>Microspathodon chrysurus</i>), seaweed blenny (<i>Parablennius marmoratus</i>), striped parrotfish (<i>Scarus croicensis</i>), bible goby (<i>Coryphopterus glaucofraenum</i>), and Bermuda chub (<i>Kyphosus sectatrix</i>)
Shrimps	Pink shrimp (<i>Farfantepenaeus duorarum</i>) , brown shrimp (<i>Farfantepenaeus aztecus</i>), white shrimp (<i>Litopenaeus setiferus</i>), and other shrimp species
Large crabs	Blue crab (<i>Callinectes sapidus</i>) , stone crabs (<i>Menippe mercenaria</i> and <i>Menippe adina</i>), horseshoe crab (<i>Limulus polyphemus</i>), hermits crab (e.g., <i>Pylopagurus operculatus</i> and <i>Clibanaris vittatus</i>), spider crabs (e.g., <i>Stenocionops furcatus</i>), and arrow crabs (e.g., <i>Stenorynchus seticornis</i>)

(Table 1 and Appendix A). In OSMOSE-WFS, basic units are schools, which are composed of animals belonging to the same HTL group, that have the same age, body size, food requirements and, at a given month, the same spatial coordinates. The central assumption in OSMOSE-WFS is that predation is an opportunistic process, which depends on: (1) the overlap between predators (HTL groups only) and potential prey items (HTL and/or LTL groups) in the horizontal dimension; (2) size adequacy between the predators and the potential prey (determined by 'predator/prey size ratios'); and (3) the accessibility of prey items to predators, which depends on their vertical distribution and morphology (this being determined by means of 'accessibility coefficients'). Thus, in OSMOSE-WFS, the food web structure of the West Florida Shelf ecosystem emerges from local predation and competition interactions.

Ten fish and two crustacean HTL groups are explicitly represented in OSMOSE-WFS as either single species or groups of species: (1) king mackerel (*Scomberomorus cavalla*); (2) amberjacks; (3) red grouper; (4) gag grouper (*Mycteroperca microlepis*); (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 (Table 2). Within each time step (month), four successive events occur in OSMOSE-WFS, as depicted in Fig. 1: (1) distribution of the schools over space using specific distribution maps; (2) mortalities (predation mortality, starvation mortality, diverse natural mortality, and fishing mortality); (3) somatic growth of fish that is estimated based on their predation success; and (4) reproduction. The assumptions, details and parameterization of OSMOSE-WFS are described in Appendix B. Below, we detail only the computation of mortalities in OSMOSE-WFS, since this is a new and central element of the present study.

2.2. Computation of mortalities in OSMOSE-WFS

In the early releases of OSMOSE (OSMOSE version 1), the different sources of mortality were applied sequentially within a time step. One major consequence is that the effective fishing mortality rates exerted on HTL groups differed from fishing mortality rates specified as inputs

and needed to be calculated a posteriori (Y.-J. Shin and P. Verley, pers. obs.). To avoid this, an ‘iterative mortality algorithm’ was employed in OSMOSE version 2, which is the OSMOSE version used in Grüss et al. (2015a), so as to apply all types of mortalities simultaneously on HTL schools (<http://www.osmose-model.org>). Though the algorithm was able to resolve mortalities for the calibration of OSMOSE, it tended to underestimate fishery catches when simulating very high levels of fishing mortality rates. 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 the output of OSMOSE-WFS, the mortality process (second event in Fig. 1) is iterated over 10 sub-time steps ($subdt$).

2.2.1. 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): $M_{diverse0}$, 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 the WFS Reef fish Ecopath model but not in OSMOSE-WFS (Chagaris, 2013; Appendix B). $M_{diverse0}$ 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 Subsection 2.3).

2.2.2. 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 (Appendix B). Schools whose body size is larger than the size of recruitment into the fisheries are fully selected by fisheries. Monthly fishing mortality rates for each HTL group are determined from a group-specific annual fishing mortality rate $F_{current}$ (Appendix B) and its seasonality. Discards were taken into account in the calculation of $F_{current}$ 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 $F_{current}$ 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 $F_{current}$ for the sardine–herring–scad complex, anchovies/silversides and reef carnivores. The seasonality of $F_{current}$ 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. C).

2.2.3. 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 it 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, 2001, 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 3); 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 $subdt$ ($B_{j,i,subdt}^{Preyed}$) is equal to:

$$B_{j,i,subdt}^{Preyed} = \frac{B_{j,i,subdt}^{Access}}{\sum_j B_{j,i,subdt}^{Access}} Y_{i,subdt}^* \quad (1)$$

where $B_{j,i,subdt}^{Access}$ is the biomass of j accessible to school i at sub-time step $subdt$. Otherwise, $B_{j,i,subdt}^{Preyed}$ is equal to $B_{j,i,subdt}^{Access}$, which is given by:

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

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. (2015a) (Table D), while the accessibility of a given LTL group j to school i (in %) is evaluated as:

$$\delta_{j,i} = \rho_{j,i} \alpha_j \quad (3)$$

where $\rho_{j,i}$ is the theoretical accessibility coefficient of LTL group j to the life-stage group to which school i belongs, which was taken from Grüss et al. (2015a) (Table E); 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 Subsection 2.3).

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

$$Y_{i,subdt} = \sum_j B_{j,i,subdt}^{Preyed} \quad (4)$$

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:

$$M_{predation\ j,i,t} = Z_{j,t} \frac{\sum_{subdt} B_{j,i,subdt}^{Preyed} / W_j}{N_{j,t}^{Dead}} \quad (5)$$

where $N_{j,t}^{Dead}$ 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:

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

Table 3
Feeding size ranges of the high trophic level (HTL) groups explicitly considered in OSMOSE-WFS expressed as predator/prey size ratios; adapted from Grüss et al. (2015a). L_{thres} is 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 (initial values used in Grüss et al. (2015a) are indicated in parentheses).

	L_{thres} (cm TL)	$(L_{pred}/L_{prey})_{min}$		$(L_{pred}/L_{prey})_{max}$	
		Juveniles	Adults	Juveniles	Adults
King mackerel	73.4	5 (2.9)	5 (4.5)	8 (18)	9 (30)
Amberjacks	90.3	4.5	4.5	8 (12)	8 (12)
Red grouper	34.1	6.5 (4.5)	6.5 (4.5)	40	30
Gag grouper	46.8	4 (1.8)	4 (3.9)	18 (100)	16
Red snapper	34.6	3.5	6.5 (9)	28 (100)	21 (30)
Sardine–herring–scad complex	9.3	20 (10)	100	200 (150)	10,000
Anchovies and silversides	4.6	20	20	300 (500)	300 (500)
Coastal omnivores	15.3	20 (50)	20 (50)	50 (80)	50 (80)
Reef carnivores	17.4	5.5 (4.5)	5.5 (4.5)	30 (50)	30 (50)
Reef omnivores	15.5	100	100	300 (1000)	300 (1000)
Shrimps	8	4.5	4.5 (7.5)	10,000	100 (242)
Large crabs	13.1	9 (1.1)	9 (1.1)	60 (50)	60 (50)

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

2.2.4. 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):

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

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:

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

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).

Table 4
Reference biomass of the 12 high trophic level (HTL) groups considered in OSMOSE-WFS, associated valid intervals (defined by minimum and maximum biomasses), and larval mortality rates of the different HTL groups estimated by the calibration of OSMOSE-WFS. Minimum and maximum biomasses account for variability and uncertainty of reference biomass estimates over the period 2005–2009.

HTL group	Reference biomass (tons)	Minimum biomass (tons)	Maximum biomass (tons)	Source of biomass estimates	Larval mortality rates (month ⁻¹)
King mackerel	9703	4852	14,555	SEDAR 16 (2009)	17.02
Amberjacks	1328	663	1991	SEDAR (2011)	17.83
Red grouper	19,759	9880	29,639	SEDAR (2009a)	16.09
Gag grouper	9189	4594	13,783	SEDAR (2009c)	17.54
Red snapper	8786	4393	13,179	SEDAR (2009b)	12.63
Sardine–herring–scad complex	289,000	57,800	520,200	WFS Reef fish Ecopath	8.96
Anchovies and silversides	162,120	32,424	291,816	WFS Reef fish Ecopath	7.73
Coastal omnivores	303,450	60,690	446,210	WFS Reef fish Ecopath	7.57
Reef carnivores	276,980	55,396	498,564	WFS Reef fish Ecopath	7.37
Reef omnivores	78,862	15,774	141,970	WFS Reef fish Ecopath	14.08
Shrimps	154,710	77,355	232,065	Nance (2009)	15.53
Large crabs	109,640	21,928	197,352	WFS Reef fish Ecopath	14.79

2.3. Calibration of OSMOSE-WFS

As in Grüss et al. (2015a), we used a recently developed evolutionary algorithm (EA; Oliveros-Ramos and Shin, submitted for publication) to calibrate OSMOSE-WFS to a reference state corresponding to the mean observed conditions in the West Florida Shelf region over the period 2005–2009. In brief, the calibration process: (1) ensures that the biomasses of the HTL groups predicted by OSMOSE-WFS are on average within valid intervals (see Table 4 for the minimum and maximum biomass values in 2005–2009); and (2) allows the estimation of 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'; $M_{diverse0}$ parameters) and the availability coefficients of LTL groups to all HTL groups (α parameters) (see Grüss et al., 2015a for further details).

As OSMOSE is very sensitive to the minimum and maximum predator/prey size ratios (L_{pred}/L_{prey} 's) of HTL groups, the value of these parameters in OSMOSE-WFS, which were initially taken from Grüss et al. (2015a) (Table 3), were refined during the calibration process to help the EA ensure that the biomasses simulated by OSMOSE-WFS are on average within valid intervals.

2.4. Evaluation of OSMOSE-WFS

To evaluate the OSMOSE-WFS model, we compared the diets predicted by the calibrated model to observed diets, and the predicted trophic levels (TLs) to TLs from the WFS Reef fish Ecopath model, as in Grüss et al. (2015a). Observed diets were reconstructed from stomach

contents data collected by the Florida Fish and Wildlife Research Institute (FWRI) and information available in published studies. Observed diets were directly entered in the WFS Reef fish Ecopath model to obtain TLs to be compared with the TLs predicted by OSMOSE-WFS. Details of the evaluation of OSMOSE-WFS are given in Appendix F.

As OSMOSE is a stochastic modeling approach, 10 simulation replicates were considered to estimate diet compositions and TLs. Moreover, the systems that are modeled in OSMOSE generally stabilize after a period equal to around twice the maximum age of the longest-lived HTL group being explicitly considered (Y.-J. Shin and P. Verley, pers. obs.). The longest-lived HTL group currently represented in OSMOSE-WFS is red snapper, which lives up to 57 years (SEDAR 7, 2005). Therefore, OSMOSE-WFS was run for 134 years to ensure that the model reaches a steady state and only the outcomes of the last 20 years of simulation were analyzed. The maximum number of schools per annual cohort was set to 240. The same set-up applied for the simulations presented in Subsections 2.5, 2.6 and 2.7.

2.5. Estimation of natural mortality rates for GOM red grouper

We estimated the following annual natural mortality rates for GOM red grouper with OSMOSE-WFS: (1) its total annual predation mortality rate ($M_{predation}$); (2) its annual rate of natural mortality unexplained by predation (M_{others}); and (3) its total annual natural mortality rate (M). M_{others} was evaluated for the purpose of comparison with WFS Reef fish Ecopath, and is given by:

$$M_{others} = M_{diverse} + M_{starvation} \quad (9)$$

where $M_{diverse}$ is mortality due to marine organisms and events (e.g., red tide events, diseases) that are not explicitly considered in OSMOSE-WFS; and $M_{starvation}$ is the annual starvation mortality rate. The total annual natural mortality rate M is given by:

$$M = M_{predation} + M_{others}. \quad (10)$$

An age-specific vector of M for GOM red grouper was estimated with OSMOSE-WFS and compared with the age-specific vector of M produced for SEDAR 42 using Lorenzen (2005)'s approach (SEDAR 42, in prep.). Age 0 in OSMOSE-WFS includes all red grouper individuals that are older than 1 month and younger than 1 year; 0–1 month old red groupers belong to the 'ichthyoplankton' (Appendix F). The Lorenzen (2005)'s approach employed for SEDAR 42 relates M -at-age to the mean length-at-age by an exponential decay, and takes into consideration: (i) von Bertalanffy growth parameters (the maximum length, instantaneous growth rate at small size and theoretical age of zero length estimated for SEDAR 42); (ii) first age of vulnerability into the fishery (assumed to be age 5 in SEDAR 42); (iii) maximum age (29 years; SEDAR, 2009a); and (iv) target M at maximum age (0.14 year^{-1} ; calculated for SEDAR 42 from Hoenig, 1983).

Moreover, M , $M_{predation}$ and M_{others} were estimated for younger juveniles (individuals older than 1 month and smaller than 14.8 cm), older juveniles (individuals larger than 14.8 cm and smaller than 34.1 cm) and adults (individuals larger than 34.1 cm) of red grouper, and compared with natural mortality rates estimated for these red grouper stanzas in the WFS Reef fish Ecopath model (Chagaris, 2013). In WFS Reef fish Ecopath, M is the sum of $M_{predation}$ and unexplained mortality (i.e., mortality unexplained by fishing and predation, and due to starvation, diseases, etc.), which is comparable to M_{others} evaluated with OSMOSE-WFS.

2.6. Estimation of an equilibrium catch curve and reference points for GOM red grouper

To estimate an equilibrium catch curve (i.e., fishery catches at equilibrium as a function of annual fishing mortality rate F) and reference

points for GOM red grouper, we made the F of red grouper vary from 0 to 2 year^{-1} in increments of 0.01 while holding the F of all the other HTL groups represented in OSMOSE-WFS at their $F_{current}$ values, and estimated the resulting biomass and fishery catches of red grouper at equilibrium. Generalized additive models using penalized cubic regression splines (Wood, 2006) were then fitted to simulated biomass and fishery catch data points, from which maximum sustainable yield (MSY), the annual fishing mortality rate resulting in MSY (F_{msy}), the virgin biomass (i.e., biomass at zero fishing mortality; B_0), the biomass at which collapse occurs ($B_{collapse}$) and the corresponding value of annual fishing mortality ($F_{collapse}$) were estimated. Collapse is defined here as biomass of less than 10% of unfished levels (i.e., $B_{collapse}/B_0 = 0.1$).

2.7. Evaluation of fishing scenarios for GOM red grouper

We used OSMOSE-WFS to investigate the long-term, equilibrium consequences of applying an annual fishing mortality to GOM red grouper equal to half its F_{msy} , its F_{msy} or twice its F_{msy} . We evaluated the impacts of these three fishing scenarios on the biomass and fishery catches of red grouper, but also on the biomass of the other HTL groups represented in OSMOSE-WFS and the total fishery catches predicted by OSMOSE-WFS.

3. Results

3.1. Calibration of OSMOSE-WFS

The calibration of OSMOSE-WFS model resulted in the biomasses of all HTL groups falling on average within valid intervals after 115 to 134 years of simulation (Fig. 2). Among the different simulation replicates, the biomasses of all HTL groups were always on average within valid intervals, except in a few replicates for king mackerel, amberjacks and gag grouper. OSMOSE-WFS reached a steady state after around 60 years of simulation (Fig. 3).

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

We can distinguish between two categories of monthly larval mortality rates (i.e., $M_{diverse0}$ parameters for the first eggs–larvae stage; Table 4). The first category includes king mackerel, amberjacks, red grouper, gag grouper, red snapper, reef omnivores, shrimps and large crabs, which have a very high $M_{diverse0}$ ($>12 \text{ month}^{-1}$). The sardine–herring–scad complex, anchovies/silversides, coastal omnivores and reef carnivores make up the second category and are characterized by a relatively low $M_{diverse0}$ ($<9 \text{ month}^{-1}$).

3.2. Evaluation of OSMOSE-WFS

The new calibrated OSMOSE-WFS model provided in output the diet composition of 18 HTL groups and stanzas for the period 2005–2009. Given that the analysis of the diets is similar to that performed with the previous version of OSMOSE-WFS in Grüss et al. (2015a), all predicted diet compositions are detailed in the Appendices, along with the diets reconstructed from empirical data (Appendix G). As was the case in Grüss et al. (2015a), OSMOSE-WFS and observations more or less agree as to the species composition of the diet of HTL groups and stanzas, and fully as to the body size and ecological niche of prey of the different HTL groups (Appendix G).

The values of the mean TLs of HTL groups predicted by the new version of OSMOSE-WFS are similar to, though usually slightly higher than those predicted by WFS Reef fish Ecopath (Fig. 4). This is especially the case for those species groups that belong to the base of the food web,

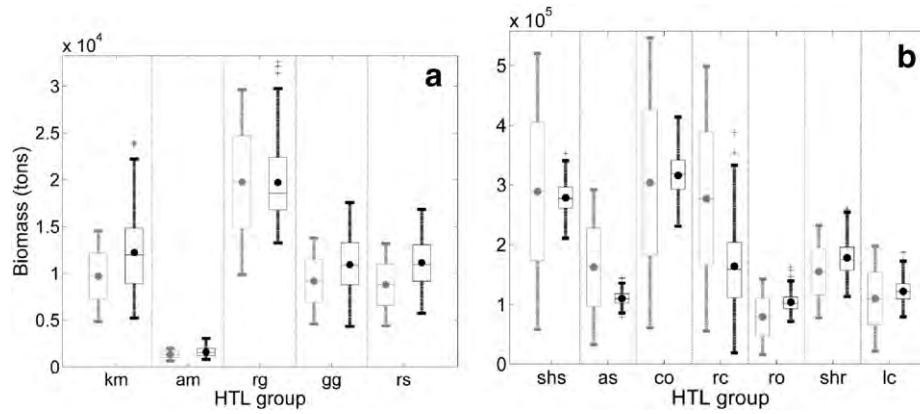


Fig. 2. Biomasses observed over the period 2005–2009 (gray boxplots) and predicted by OSMOSE-WFS (black boxplots) for the 12 high trophic level (HTL) groups explicitly considered in OSMOSE-WFS. Mean observed biomasses (gray dots) are associated with valid intervals, i.e., minimum and maximum possible 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) \pm standard deviations for 10 replicates after 115 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.

i.e., the sardine–herring–scad complex, anchovies/silversides, coastal omnivores, reef omnivores and shrimps. On the other hand, the ranks of the TL values in OSMOSE-WFS are akin to those in WFS Reef fish Ecopath: king mackerel, amberjacks, red grouper, gag grouper and red snapper have the highest TLs, followed by reef carnivores and large crabs, and then by the sardine–herring–scad complex, anchovies/silversides, coastal omnivores, reef omnivores and shrimps (Fig. 4). In OSMOSE-WFS, the biomass of all HTL groups but shrimps distributes across a large range of TLs (Fig. 4).

The evaluation of the OSMOSE-WFS model confirms three categories of HTL groups in the West Florida Shelf ecosystem: (1) ‘large predators’, including king mackerel, amberjacks, red grouper, gag grouper and red snapper; (2) ‘small predators’, comprised of reef carnivores and large crabs; and (3) ‘forage fish and invertebrates’, consisting of the sardine–herring–scad complex, anchovies/silversides, coastal omnivores, reef omnivores and shrimps (Appendix G and Fig. 4).

In OSMOSE-WFS, red grouper, gag grouper and red snapper (i.e., the species of the ‘snapper–grouper complex’ explicitly considered in the model; Farmer et al., submitted for publication, in review) belong to ‘large predators’. These three species are predicted to have similar diets and predators and, therefore, to compete strongly with one another (Appendix G and Fig. H). In OSMOSE-WFS, LTL prey items dominate the

diet of younger juveniles of red grouper and gag grouper, and anchovies/silversides are the main HTL prey of these two stanzas (Appendix G). The model predicts that the older juveniles of red grouper and gag grouper and the adults of red grouper, gag grouper and red snapper all feed essentially upon HTL prey, including mainly the sardine–herring–scad complex, anchovies/silversides and coastal omnivores (Appendix G). Competition between red grouper, gag grouper and red snapper is less strong in the real world, according to observed diets (Appendix G). In particular, observations indicate that the proportion of HTL prey in the diet of juvenile red grouper is significantly lower than that in the diets of juvenile gag grouper and juvenile red snapper. Furthermore, according to observed diets, juvenile gag grouper consumes more HTL fish than HTL invertebrates, while the proportions of HTL fish and HTL invertebrates in the diet of juvenile red snapper are similar. Finally, observations indicate that adults of red grouper and gag grouper are mostly piscivorous (as is the case in OSMOSE-WFS), whereas adult red snapper feeds mainly on HTL invertebrates (as is not the case in OSMOSE-WFS; Appendix G).

Adult gag grouper is a major predator of all life stages of red grouper, gag grouper and red snapper in OSMOSE-WFS (see Fig. H and next subsection). Moreover, OSMOSE-WFS predicts that adult red grouper has the potential to exert a significant predation pressure on younger

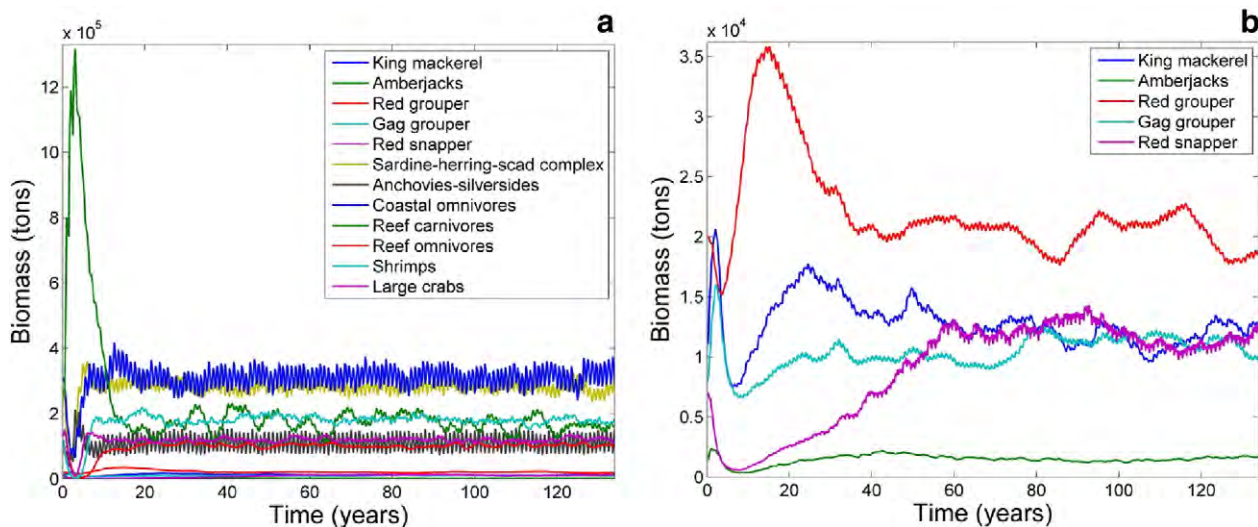


Fig. 3. Mean trajectories of biomasses in OSMOSE-WFS after 0 to 134 years of simulation (a) for all HTL groups; and (b) for king mackerel, amberjacks, red grouper, gag grouper and red snapper. 10 simulation replicates were run to produce these plots.

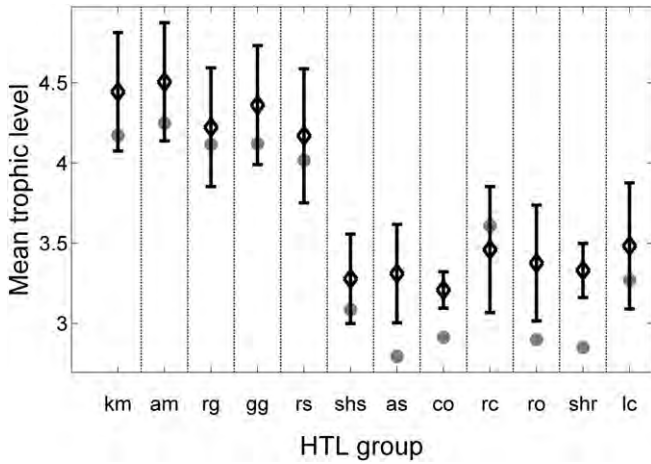


Fig. 4. Mean trophic levels (TLs) predicted by OSMOSE-WFS (black diamonds) and by WFS Reef fish Ecopath (gray circles). For OSMOSE-WFS, 10 replicates and only the last 20 years of simulations (i.e., years 114 to 134) were considered to estimate TLs. km: king mackerel – am: amberjacks – rg: red grouper – 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.

juveniles of red grouper and gag grouper and on juveniles of red snapper, and that adult red snapper can feed on younger juveniles of red and gag groupers (see next subsection and Fig. H). Observed diets indicate that red grouper preys upon itself, gag grouper, yellowedge grouper (*Epinephelus flavolimbatus*) and black grouper (*Mycteroperca bonaci*), and that gag grouper feeds on itself, red grouper and ‘other snappers’ (e.g., *Lutjanus griseus*) (Appendix G). According to observations, red snapper does not prey on juveniles of red and gag groupers (Appendix G).

3.3. Estimation of natural mortality rates for GOM red grouper

The annual natural mortality rate M of GOM red grouper provided in output of OSMOSE-WFS decreases exponentially with age, as is the case for that estimated using Lorenzen (2005)’s approach (Fig. 5a and b). However, the M -at-age curve predicted by OSMOSE-WFS differs markedly from that produced for SEDAR 42. The M ’s estimated by OSMOSE-WFS are significantly higher than those constructed for SEDAR 42 for 0 to 5 years old red grouper, especially for 0–1 year old red grouper ($1.73 \pm 0.38 \text{ year}^{-1}$ in OSMOSE-WFS vs. 0.58 year^{-1} with Lorenzen’s approach; Fig. 5a). On the other hand, the M ’s of 5+ year old red grouper are higher in Lorenzen’s model than in OSMOSE-WFS (Fig. 5b). In OSMOSE-WFS, predation mortality ($M_{predation}$) dominates other sources

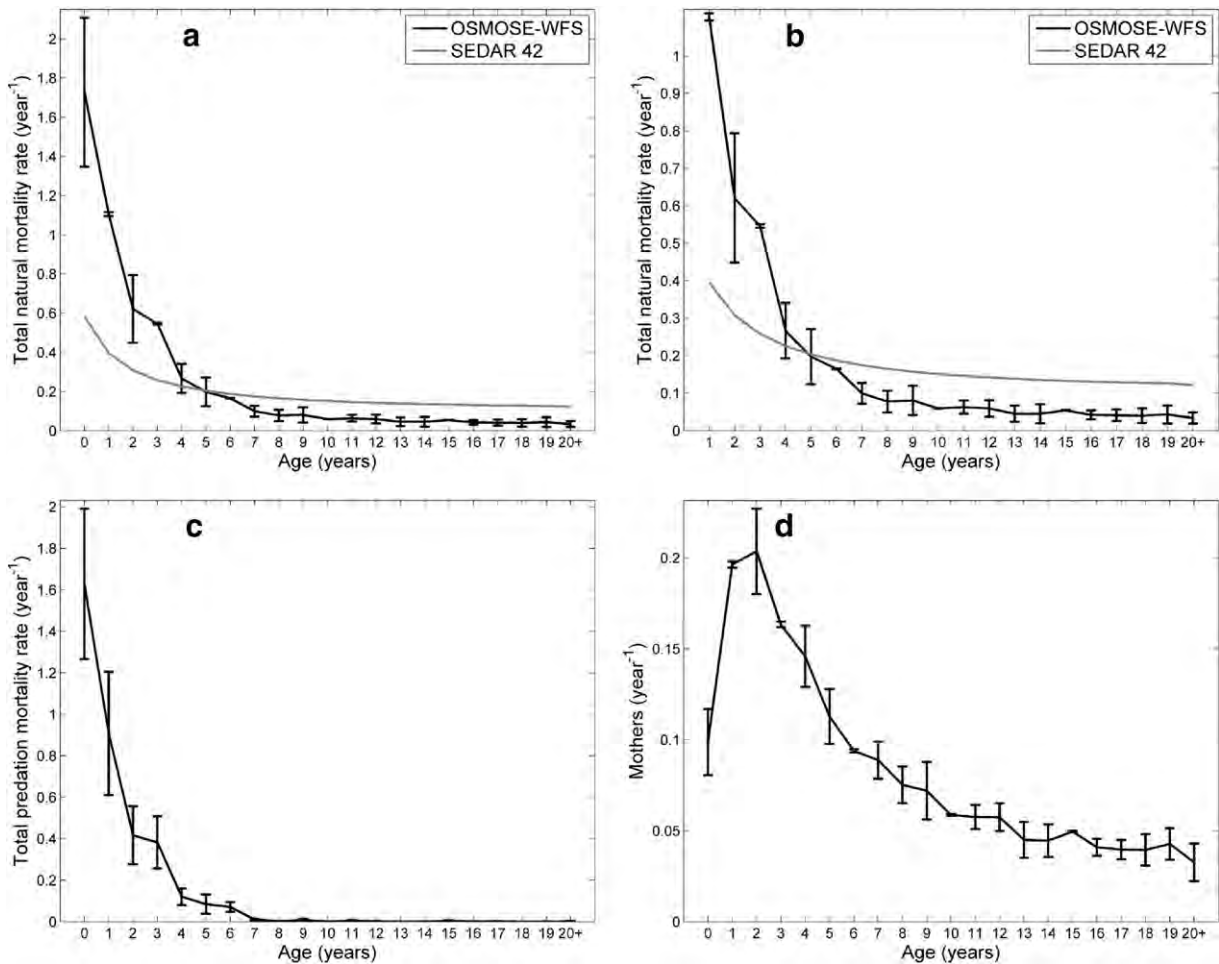


Fig. 5. Annual natural mortality rates at age of red grouper predicted by OSMOSE-WFS. (a) Total natural mortality at age of red grouper predicted by OSMOSE-WFS compared with that produced for SEDAR 42 using Lorenzen (2005)’s approach. (b) Total natural mortality at age of red grouper from age 1 predicted by OSMOSE-WFS compared with that produced for SEDAR 42. (c) Total predation mortality at age of red grouper predicted by OSMOSE-WFS. (d) Natural mortality at age of red grouper due to causes other than predation (M_{others}) predicted by OSMOSE-WFS. For OSMOSE-WFS, 10 replicates and only the last 20 years of simulations (i.e., years 114 to 134) were considered. Note that age 0 in OSMOSE-WFS includes all red grouper individuals that are older than 1 month and younger than 1 year; 0–1 month old red groupers belong to the ‘ichthyoplankton’ (Appendix F).

of natural mortality (M_{others}) for 0–4 year old red grouper, whereas the opposite occurs for 4+ years old red grouper (Fig. 5c and d). The $M_{predation}$ of red grouper decreases exponentially with age (Fig. 5c). The $M_{predation}$ of 0–1 year old red grouper (excluding individuals less than 1 month old) is extremely high ($1.63 \pm 0.36 \text{ year}^{-1}$), while the $M_{predation}$ of 7+ years old red grouper is extremely low ($\leq 0.01 \text{ year}^{-1}$ on average). The M_{others} of red grouper increases from $0.10 \pm 0.02 \text{ year}^{-1}$ to $0.20 \pm 0.03 \text{ year}^{-1}$ from age 0 to age 2, and then decreases exponentially with age (Fig. 5d).

The M of younger juvenile red grouper (i.e., 0–1 year old individuals in Fig. 5) is very high in both WFS Reef fish Ecopath and OSMOSE-WFS (2 year^{-1} and $1.73 \pm 0.38 \text{ year}^{-1}$, respectively; Fig. 6a). The total natural mortality of younger juvenile red grouper essentially results from predation in OSMOSE-WFS vs. ‘unexplained’ causes in WFS Reef fish Ecopath (Fig. 6a). The main predators of younger juvenile red grouper in OSMOSE-WFS are, in order of importance: adult king mackerel (responsible for 41% of the predation mortality of younger juvenile red grouper), adult gag grouper (24%), adult red grouper (16%), adult red snapper (7%) and amberjacks (6%) (Fig. 7a). 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 red grouper (Fig. 7b). 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.

The M of older juvenile red grouper is high in both OSMOSE-WFS and WFS Reef fish Ecopath ($0.74 \pm 0.20 \text{ year}^{-1}$ and 0.77 year^{-1} ,

respectively; Fig. 6b). This mortality rate results mainly from predation in OSMOSE-WFS vs. ‘unexplained’ causes in WFS Reef fish Ecopath (Fig. 6b). In both models, major predators of older juvenile red grouper include adult king mackerel (responsible for 50% of the total predation mortality of the stanza in OSMOSE-WFS and 44% in WFS Reef fish Ecopath) and adult gag grouper (32% in OSMOSE-WFS and 30% in WFS Reef fish Ecopath) (Fig. 7c and d). Another major predator of older juvenile red grouper in OSMOSE-WFS is the amberjacks’ group (responsible for 17% of the total predation mortality of the stanza; Fig. 7c). 22% of the total predation mortality of older 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 (Fig. 7d).

The 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 ($0.10 \pm 0.02 \text{ year}^{-1}$ and 0.14 year^{-1} , respectively; Fig. 6c). In OSMOSE-WFS, the M of adult red grouper is mainly due to starvation plus M_{others} due to organisms and events (e.g., red tide events) not represented in OSMOSE-WFS. 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 with its mortality rate due to ‘unexplained’ causes (Figs. 6c and 7f). The M_{others} of adult red grouper in OSMOSE-WFS was estimated from the predation mortality rate due to those animals which are modeled 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

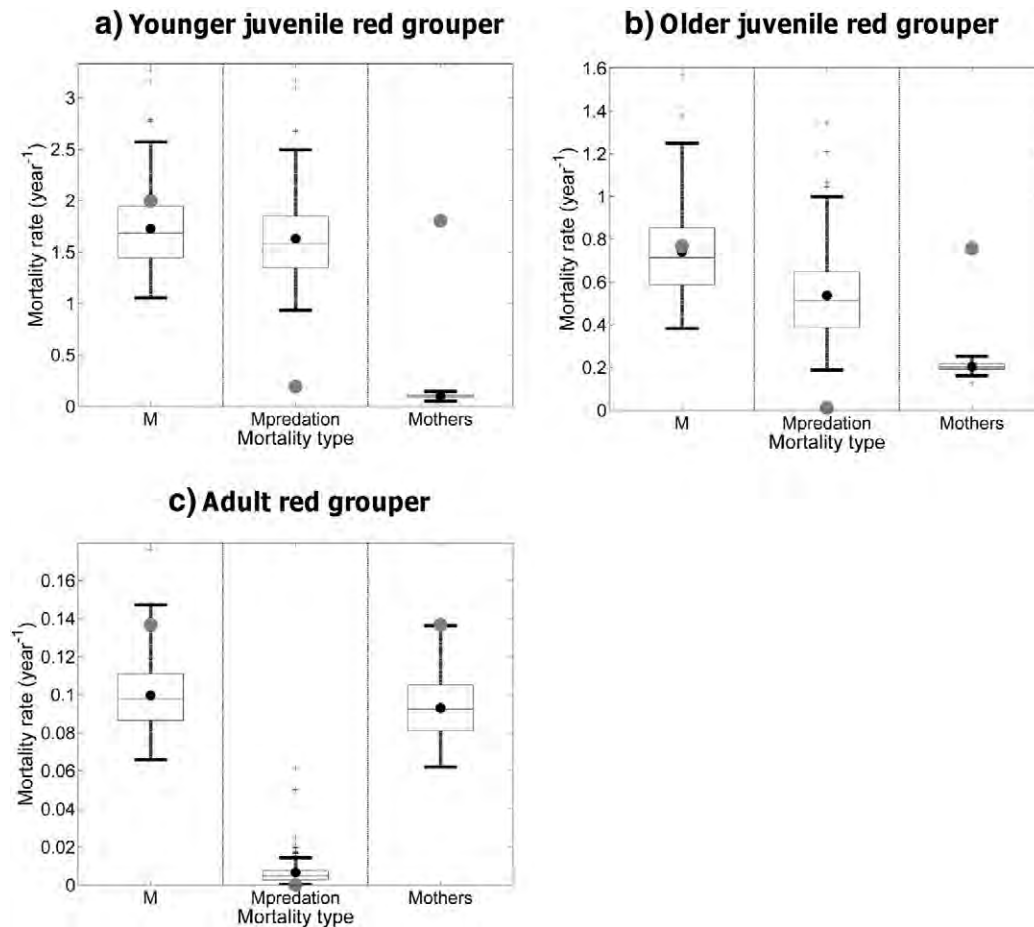


Fig. 6. Annual natural mortality rates of (a) younger juvenile, (b) older juvenile and (c) adult red grouper predicted by OSMOSE-WFS (black boxplots) and WFS Reef fish Ecopath (large gray dots). Mean natural mortality rates predicted by OSMOSE-WFS are indicated by small black dots. For OSMOSE-WFS, 10 replicates and only the last 20 years of simulations (i.e., years 114 to 134) were considered. M : total natural mortality rate – $M_{predation}$: total predation mortality rate – M_{others} : natural mortality rate due to all other causes.

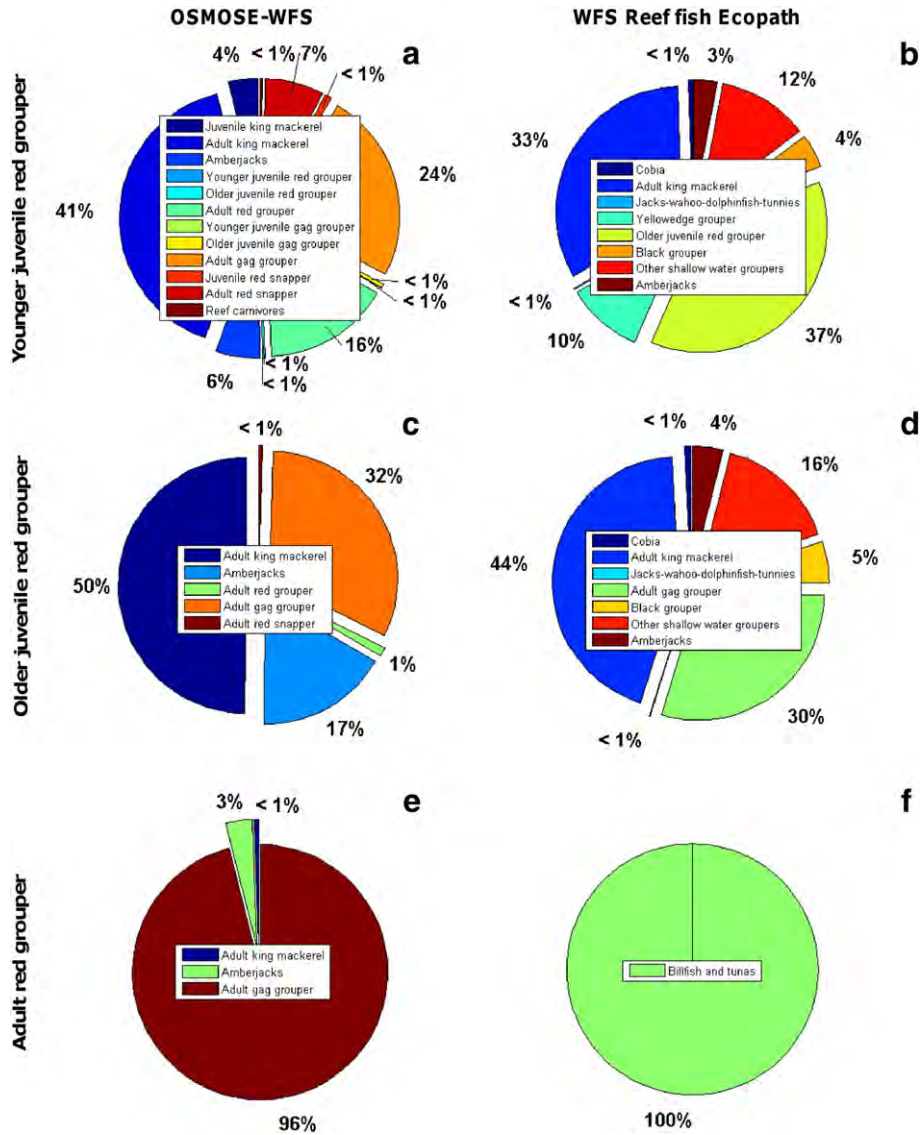


Fig. 7. Contributors to the predation mortality of (a, b) younger juvenile, (c, d) older juvenile and (e, f) adult red grouper predicted by (a, c, e) OSMOSE-WFS and (b, d, f) WFS Reef fish Ecopath. For OSMOSE-WFS, 10 replicates and only the last 20 years of simulations (i.e., years 114 to 134) were considered.

96%, 3% and less than 1% of the total predation mortality of the stanza (Fig. 7e).

3.4. Estimation of an equilibrium catch curve and reference points for GOM red grouper

An equilibrium catch curve was constructed for GOM red grouper with OSMOSE-WFS (Fig. 8a), from which the F_{msy} of the fish population was estimated to be 0.13 year^{-1} . Given that the current annual fishing mortality of red grouper ($F_{current}$) is equal to 0.22 year^{-1} in OSMOSE-WFS, then the model predicts that $F_{current} / F_{msy} = 1.69$ for red grouper, i.e., that GOM red grouper was overexploited over the period 2005–2009 from an ecosystem perspective. The F_{msy} of GOM red grouper estimated with OSMOSE-WFS is smaller than that proxy of F_{msy} estimated in previous stock assessments of the fish population (0.19 year^{-1} ; SEDAR, 2009a). Moreover, previous stock assessments of GOM red grouper suggest that the fish population was overexploited in the early 2000s, but fully exploited or underexploited starting from 2005 (SEDAR, 2009a). The fishing mortality at which GOM red grouper biomass collapses (i.e., at which GOM red grouper biomass is less than 10% of unfished levels) was estimated to be 0.25 year^{-1} (Fig. 8b).

3.5. Evaluation of fishing scenarios for GOM red grouper

Fishing red grouper at half its F_{msy} or at its F_{msy} in OSMOSE-WFS considerably increases the biomass of the species (Fig. 9a and b) and also slightly improves red grouper fishery catches (Fig. 10a). In agreement with what would be predicted by a single-species model, increases in red grouper biomass are more pronounced and improvement in red grouper catches are smaller when $F = 0.5 \cdot F_{msy}$ than when $F = F_{msy}$. Conversely, imposing an F to red grouper equal to twice its F_{msy} in OSMOSE-WFS dramatically reduces the biomass and catches of red grouper (Figs. 9c and 10a).

Fishing red grouper at half its F_{msy} in OSMOSE-WFS has different consequences for large predators, small predators, and forage fish and invertebrates (Figs. 9a and 10b). With regard to large predators, this fishing scenario has a negligible impact on the biomass of king mackerel and results in a small increase of the biomass of amberjacks (Fig. 9a). By contrast, imposing an F to red grouper equal to half its F_{msy} leads to dramatic reductions in the biomasses of gag grouper and red snapper (Fig. 9a). Under this fishing mortality scenario, the predation mortality rates of younger juvenile gag grouper and juvenile red snapper due to red grouper significantly increase (Fig. 11a and b), while the starvation

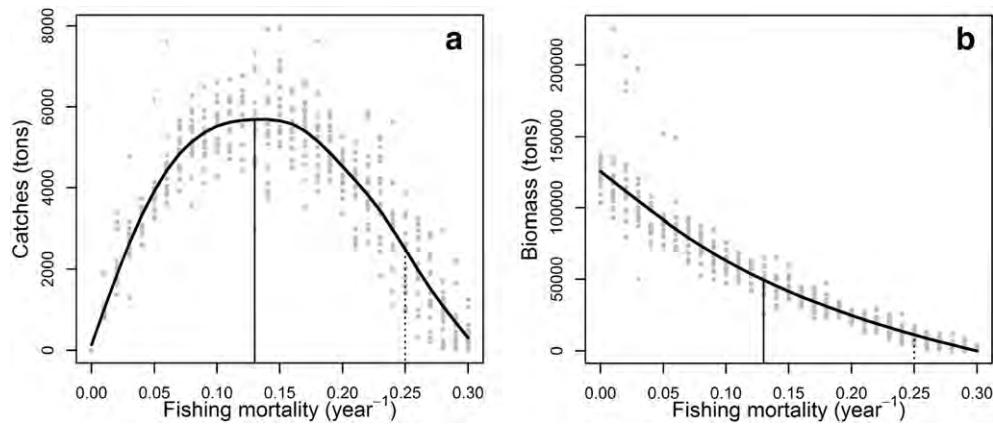


Fig. 8. (a) Catch and (b) biomass at equilibrium as a function of annual fishing mortality for Gulf of Mexico red grouper, estimated with OSMOSE-WFS. For all panels, the vertical full line indicates the annual fishing mortality rate resulting in the maximum sustainable yield of red grouper (F_{msy}), while the vertical dotted line indicates the annual fishing mortality rate at which the red grouper population collapses ($F_{collapse}$).

mortality rates of gag grouper and red snapper decrease and the mean body size of both species slightly increases (Table 5). With regard to small predators, fishing red grouper at half its F_{msy} results in a small decrease of the biomass of reef carnivores and does not affect the biomass of large crabs (Fig. 9a). The biomasses of forage fish and invertebrates do not differ when red grouper is fished at its $F_{current}$ or at half its F_{msy} . Finally, total fishery catches in OSMOSE-WFS are unaffected by decreasing the F of red grouper to half of its F_{msy} (Fig. 10b).

In general, fishing red grouper at its F_{msy} has qualitatively the same effects as fishing the species at half its F_{msy} (Figs. 9b, 10b and 11 and Table 5). An exception to this general pattern occurs for reef carnivores, whose biomass is not impacted by reducing the F of red grouper to its F_{msy} (Fig. 9b). Decreases in the biomass of gag grouper and red snapper are smaller when red grouper is fished at its F_{msy} than when it is fished at half its F_{msy} (Fig. 9b).

Fishing red grouper at twice its F_{msy} affects large predators, but not small predators and forage fish and invertebrates (Figs. 9c and 10b). This fishing scenario leads to a slight decrease in the biomasses of king mackerel and amberjacks (Fig. 9c). By contrast, this scenario results in a moderate increase in the biomass of gag grouper and in a considerable enhancement of the biomass of red snapper (Fig. 9c). Enhancements in gag grouper and red snapper biomasses are accompanied by a slight increase in the predation mortality rates of younger juvenile red grouper due to gag grouper and red snapper, a dramatic increase in the predation mortality rates of older juvenile red grouper due to gag grouper and red snapper, and a significant increase in the predation mortality rate of adult red grouper due to gag grouper (Fig. 11c and d). In contrast, increasing the F of red grouper to twice of its F_{msy} leads to a decrease in the starvation mortality rate of all red grouper stanzas, and to virtually no change in the mean body size of the red grouper population (Table 5). Under this fishing scenario, total fishery catches in OSMOSE-WFS are not impacted (Fig. 10b).

4. Discussion

4.1. Calibration and evaluation of OSMOSE-WFS

While making sure that the mean biomasses predicted by OSMOSE-WFS at steady-state are on average within valid intervals, the recalibration of OSMOSE-WFS allowed a re-estimation of unknown parameters, i.e., the availability coefficients of LTL groups to all HTL groups and the mortality rates of eggs and larvae of HTL groups ('larval mortality rates'). The availability coefficients of LTL groups are all estimated to be low except for small phytoplankton and large mesozooplankton. These parameters account for a lot of processes not explicitly represented in

OSMOSE-WFS, including, inter alia, micro- and meso-scale turbulences, diel migration and avoidance of predators, which are all highly difficult to quantify (Travers-Trolet et al., 2014). However, the low value estimated for most of these parameters may also reflect an overestimation of the LTL biomass input in OSMOSE-WFS (Marzloff et al., 2009). The larval mortality rates estimated during calibration are generally very high, except those of the sardine–herring–scad complex, anchovies/silversides, coastal omnivores and reef carnivores. Larval mortality rates also depend on numerous processes not considered in OSMOSE-WFS (e.g., non-fertilization of eggs, sinking, advection away from suitable habitat), which are all hard to quantify. The lowest larval mortality rates estimated during calibration may merely reflect the fact that most of the mortality of the sardine–herring–scad complex, anchovies/silversides, coastal omnivores and reef carnivores is accounted for explicitly in OSMOSE-WFS (Travers-Trolet et al., 2014).

Updating an OSMOSE model entails its recalibration, but also its evaluation in its new configuration. As in Grüss et al. (2015a), OSMOSE-WFS's output were compared with observed diet data, and to TLs from the WFS Reef fish Ecopath model. With regard to diet compositions, OSMOSE-WFS is in full agreement with observations as to the body size and ecological niche of prey of the different HTL groups represented in the model. On the other hand, OSMOSE-WFS and observations are more or less in agreement with regard to the species composition of the diet of HTL groups and stanzas, as was the case in Grüss et al. (2015a). This should not necessarily be viewed as a flaw of OSMOSE-WFS since empirical diet studies have many sources of uncertainty, including the small number of stomach contents sampled, with generally very limited spatio-temporal coverage, and the frequent presence of unidentifiable and inseparable partially digested material in the stomachs analyzed (Scharf et al., 1997; McQueen and Griffiths, 2004; Baker et al., 2014; J. Simons, Center for Coastal Studies, Texas A&M University-Corpus Christi, pers. comm.).

OSMOSE-WFS and WFS Reef fish Ecopath are in good agreement with regard to the value of TLs. However, mean TLs are usually slightly higher in the former model than in the latter. This is probably due to the representation of a smaller number of functional (HTL and LTL) groups in OSMOSE-WFS (21 vs. 70 in WFS Reef fish Ecopath), and, especially, of a smaller number of functional groups belonging to the base of the West Florida Shelf food web (i.e., species groups with a small TL, and LTL groups). In OSMOSE-WFS, the broad distribution of the TLs of all HTL groups but shrimps reflects their opportunism and a high level of omnivory. The high level of omnivory of red grouper, gag grouper and red snapper (i.e., of the species of the snapper–grouper complex) is mainly due to ontogenetic changes in their feeding behavior (Appendix G).

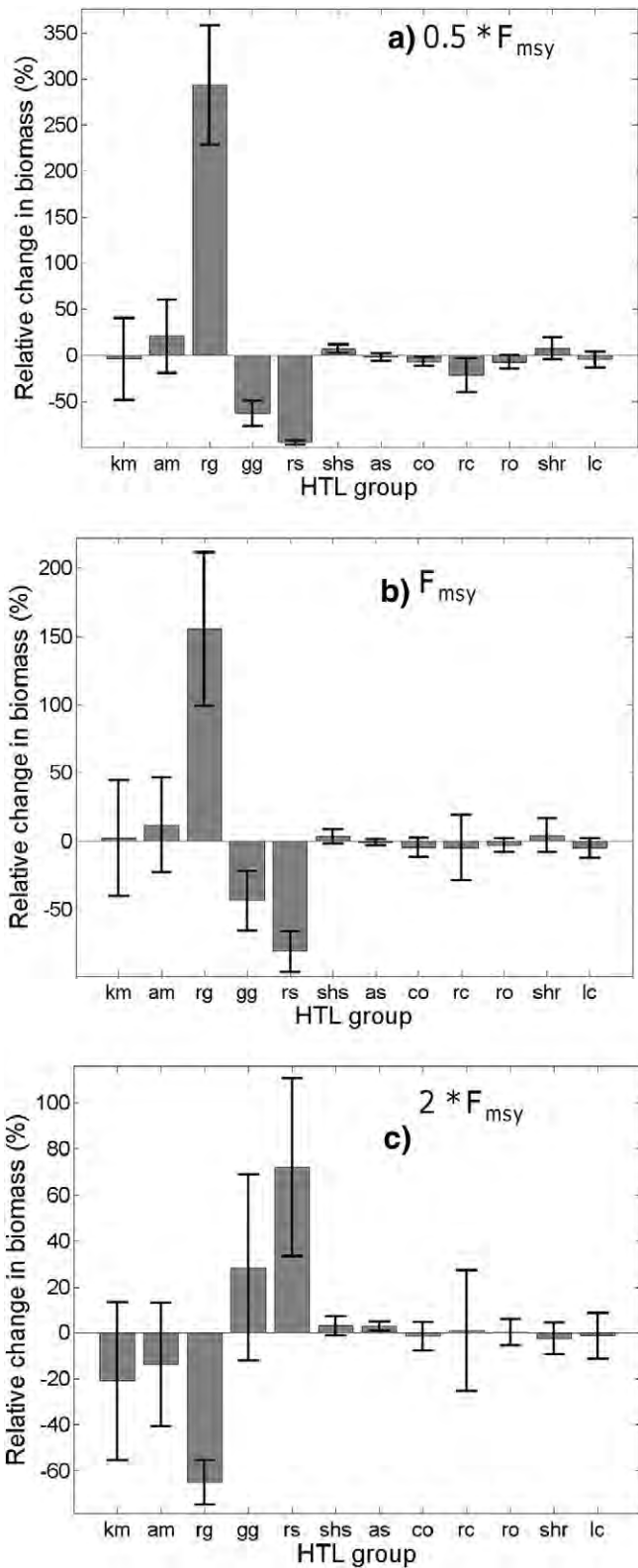


Fig. 9. Long-term changes in the biomass of the high trophic level groups represented in OSMOSE-WFS under different fishing scenarios relative to the status quo (in %). For (a), the annual fishing mortality rate F of red grouper is set to half its F_{msy} (i.e., the annual fishing mortality rate resulting in maximum sustainable yield) estimated with OSMOSE-WFS. For (b), the F of red grouper is set to its F_{msy} . For (c), the F of red grouper is set to twice its F_{msy} . 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.

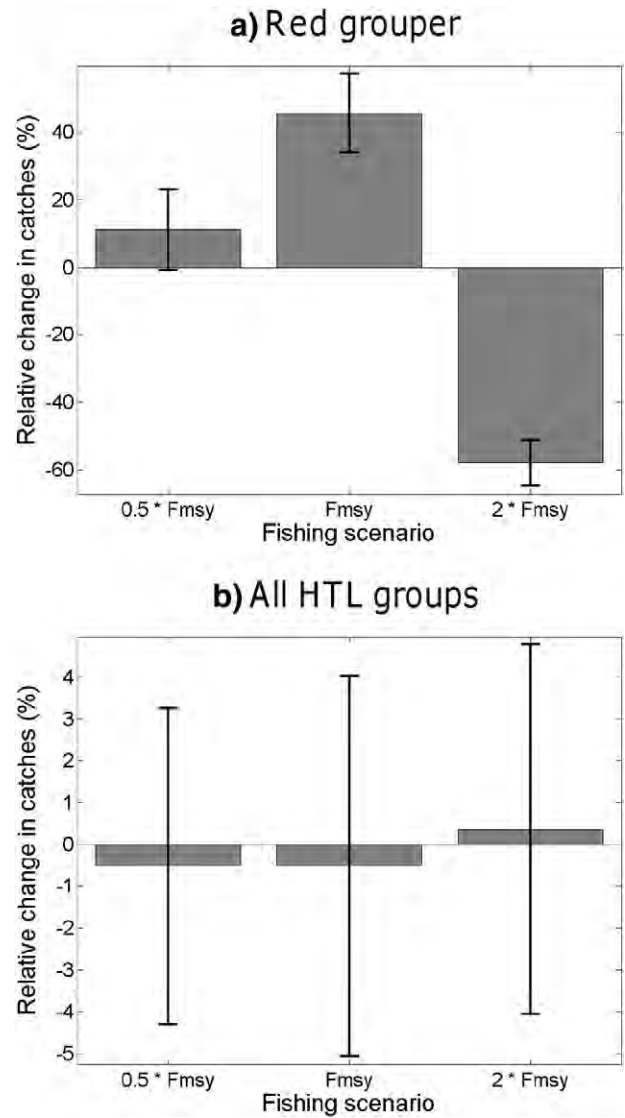


Fig. 10. Long-term changes in fishery catches in OSMOSE-WFS under different fishing scenarios relative to the status quo (in %). (a) Long-term relative changes in catches for red grouper; (b) long-term relative changes in the total fishery catches predicted by OSMOSE-WFS. $0.5 * F_{msy}$: scenario where the annual fishing mortality rate F of red grouper is set to half its F_{msy} (i.e., the annual fishing mortality rate resulting in maximum sustainable yield) estimated with OSMOSE-WFS – F_{msy} : scenario where the F of red grouper is set to its F_{msy} – $2 * F_{msy}$: scenario where the F of red grouper is set to twice its F_{msy} .

4.2. Natural mortality rates of GOM red grouper

The total annual natural mortality rate M of GOM red grouper decreases exponentially with age both in OSMOSE-WFS and in the empirical model based on Lorenzen (2005)'s approach that is used in SEDAR 42. However, juveniles of red grouper are subject to a considerably higher total natural mortality in OSMOSE-WFS, due to (1) the simulation of predation events in OSMOSE-WFS; and (2) the use of a target M at maximum age equal to 0.14 year^{-1} in the empirical model. Differences in total natural mortality between OSMOSE-WFS and the empirical model are striking for 0–1 year old individuals, whose mean M is equal to 1.73 year^{-1} in OSMOSE-WFS due to predation by a diversity of large and small predators (Fig. 7a). Adults of red grouper older than 5 years undergo higher total natural mortality in the empirical model than in OSMOSE-WFS, essentially because of the use of a target M at maximum age in the Lorenzen (2005)'s approach. Red grouper which are 5 years old or older are subject to extremely

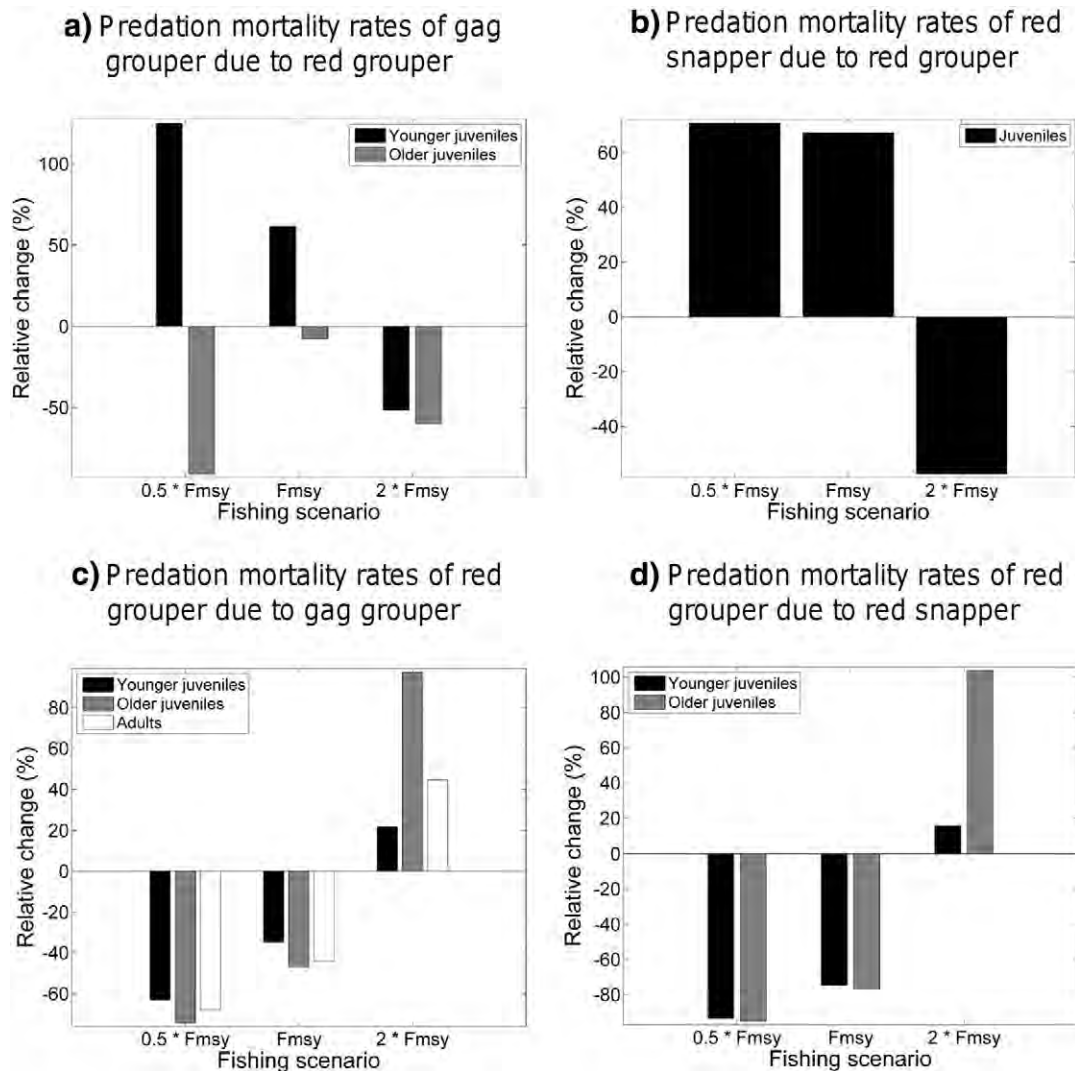


Fig. 11. Long-term changes in some predation mortality rates in OSMOSE-WFS under different fishing scenarios relative to the status quo (in %). (a) Long-term relative changes in the predation mortality rates of gag grouper due to red grouper; (b) long-term relative changes in the predation mortality rates of red snapper due to red grouper; (c) long-term relative changes in the predation mortality rates of red grouper due to gag grouper; (d) long-term relative changes in the predation mortality rates of red grouper due to red snapper. $0.5 * F_{msy}$: scenario where the annual fishing mortality rate F of red grouper is set to half its F_{msy} (i.e., the annual fishing mortality rate resulting in maximum sustainable yield) estimated with OSMOSE-WFS – F_{msy} : scenario where the F of red grouper is set to its F_{msy} – $2 * F_{msy}$: scenario where the F of red grouper is set to twice its F_{msy} .

low predation pressure in OSMOSE-WFS, and their low M is mostly due to starvation events.

OSMOSE-WFS and WFS Reef fish Ecopath agree on the magnitude of the total annual natural mortality rate M of the younger juveniles and older juveniles of red grouper, but not on the main causes of this mortality. In both models, the annual natural mortality M is very high for younger juvenile red grouper, and high for older juvenile red grouper. However, the bulk of the M of red grouper juveniles is due to explicit predation in OSMOSE-WFS, while it is due to ‘unexplained causes’ in WFS Reef fish Ecopath. Differences between the two models are due to the fact that predation mortality is conditioned by a diet matrix in Ecopath, whereas food web structure emerges from local predation and competition interactions in OSMOSE (Grüss et al., 2015a; Shin et al., 2004; Travers et al., 2010; Travers-Trolet et al., 2014). Due to their relatively small body size, juvenile life stages of red grouper are potential prey of different stanzas of a diversity of small and large predators in OSMOSE-WFS (Fig. 7a and c).

By contrast, both OSMOSE-WFS and WFS Reef fish Ecopath indicate that the M of adult red grouper is relatively low and that the bulk of this M is due to causes other than explicit predation: (1) starvation in the former model; and (2) ‘unexplained’ causes in the latter, which could

include predator–prey interactions not considered in WFS Reef fish Ecopath. In OSMOSE-WFS, the predation mortality of adult red grouper is due to adult gag grouper and, to a much lesser extent, to amberjacks and adult king mackerel. In WFS Reef fish Ecopath, only the billfish and tunas’ group feeds upon adult red grouper; this relates to the fact that it is possible to collect only a limited number of stomachs of large offshore predators on the West Florida Shelf (Chagaris, 2013; Chagaris and Mahmoudi, 2013). Results concerning the predation mortality of adult red grouper are similar to those obtained for adult gag grouper in Grüss et al. (2015a). These, and other similarities between red grouper and gag grouper noted above, support the groupings of the two species into common ‘shallow-water grouper’ and ‘snapper–grouper’ complexes (Farmer et al., submitted for publication, in review).

In July 2014, the West Florida Shelf experienced severe red tides, which resulted in the death of a large and uncertain number of numerous fish species, including red grouper and gag grouper (<http://myfwc.com/research/redtide>). The ‘unexplained causes’ of natural mortality for adult gag grouper and adult red grouper in WFS Reef fish Ecopath are likely to be red tide events mainly (Gray, 2014; Sagarese et al., 2015). The majority of the natural mortality of adult red grouper due to causes other than predation in OSMOSE-WFS is currently due

to starvation events. The explicit representation of the impacts of red tide events on the natural mortality of red grouper, gag grouper and other pertinent HTL groups in OSMOSE-WFS may provide a more accurate description of natural mortalities in the model. However, an explicit representation of red tide impacts in OSMOSE-WFS will necessitate more insights into the spatio-temporal patterns of red tides and into how these events affect the physiology of marine organisms, which calls for additional field, physiological and statistical research (Sagarese et al., 2015; Walter et al., 2015). Moreover, anecdotal reports from fishers suggest that red grouper often relocates in order to avoid red tide events (S. Sagarese, NOAA Fisheries, Miami Lab, pers. comm.). Therefore, it could be important for future OSMOSE-WFS modeling efforts to integrate red tide impacts on both emigration and natural mortality.

4.3. Consequences of changes in the fishing mortality of GOM red grouper

We constructed an equilibrium catch curve for GOM red grouper with OSMOSE-WFS, from which we determined that the fish population was overexploited over the period 2005–2009 from an ecosystem perspective. Conversely, previous stock assessments of GOM red grouper suggested that the fish population was fully exploited or underexploited between 2005 and 2009. Discrepancies between reference points estimated from an ecosystem perspective and those estimated from a single-species perspective are frequently noted in the ecosystem modeling literature (e.g., Gaichas et al., 2012; Walters et al., 2005).

Evaluations of fishing scenarios with OSMOSE-WFS indicated that altering the annual fishing mortality of GOM red grouper has a large impact on the other species of the snapper–grouper complex, i.e., gag grouper and red snapper, which OSMOSE-WFS predicts to be major competitors of red grouper. Fishing red grouper at half of its F_{msy} or at its F_{msy} increases the biomass and fishery catches of the species, but decreases the biomass of gag grouper and red snapper. Conversely, increasing the annual fishing mortality of red grouper to twice its F_{msy} reduces the biomass and catches of the species, while increasing the biomass of gag grouper and red snapper. All the fishing scenarios we evaluated had small or no impact on minor competitors (king mackerel and amberjacks) and small predators, and they did not affect forage fish and invertebrates, i.e., the major prey of red grouper. Moreover, total fishery catches in OSMOSE-WFS were unaffected under all fishing scenarios.

The results of the fishing scenarios that we obtained can be explained by: (1) the very similar diet patterns of red grouper, gag grouper and red snapper in OSMOSE-WFS; and (2) the fact that species of the snapper–grouper complex are simultaneously predators and prey of one another in the model. Firstly, the diet compositions of juveniles of red grouper, gag grouper and red snapper and of adults of the three species are similar to one another in OSMOSE-WFS (Appendix G). In particular, the sardine–herring–scad complex, anchovies/silversides and coastal omnivores are the dominant HTL groups in the diet of the three species. Thus, when the biomass of red grouper is reduced in response to increased fishing mortality, gag grouper and red snapper have the opportunity to consume a large amount of prey that are normally consumed by red grouper under baseline conditions, which leads to no change globally in the biomass of prey groups of the snapper–grouper complex (forage fish and invertebrates and, to a lesser extent, small predators).

Conversely, when the fishing mortality of red grouper is reduced and its biomass therefore dramatically increases, the species has the potential to consume a large amount of preys that are normally consumed by gag grouper and red snapper under baseline conditions. Then, one might expect that the decrease in the biomasses of gag grouper and red snapper accompanying the increase in red grouper biomass is due to enhanced competition for food. Enhanced competition for food would reduce the predation efficiency of gag grouper and red snapper, which would negatively affect the body growth of the two species and

increase their starvation mortality. An examination of the mean body sizes and starvation mortality rates of gag grouper and red snapper does not validate this hypothesis (Table 5).

The decrease in the biomasses of gag grouper and red snapper resulting from an increase in red grouper biomass can be explained by the fact that species of the snapper–grouper complex are simultaneously predators and prey of one another in OSMOSE-WFS (Fig. 11 and Table 5). In OSMOSE-WFS, adult red grouper is responsible for a non-negligible proportion of the natural mortality of younger juveniles of red grouper and gag grouper and of the natural mortality of juvenile red snapper (Appendix H). Therefore, a reduction of the fishing mortality of red grouper enhances the predation mortality rates of younger juvenile gag grouper and juvenile red snapper (Fig. 11a and b). Moreover, OSMOSE-WFS predicts that adult gag grouper exerts a significant predation pressure on all life stages of red grouper, gag grouper and red snapper, and that red snapper consumes a very small fraction of juvenile red groupers (Appendix H). Thus, the biomass of gag grouper is less impacted by a decrease in the fishing mortality (an increase in the biomass) of red grouper than the biomass of red snapper (Fig. 9).

It is reasonable to think that trophic cascades may not occur in response to changes in red grouper fishing mortality in the real world. Indeed, highly complex and redundant tropical/subtropical marine systems, such as the West Florida Shelf (Chagaris, 2013; Moretzsohn et al., 2012), are less likely to exhibit trophic cascades than other ecosystems (Kitchell et al., 2002; Sala and Sugihara, 2005). In contrast, based on the observed diets (Appendix G), we suspect that the fishing scenarios that we simulated may have slightly different impacts for red grouper, gag grouper and red snapper in the real world. Firstly, observed diets suggest that competition between species of the snapper–grouper complex is less strong in the real world than in OSMOSE-WFS. This stems from the fact that the different life stages of red grouper, gag grouper and red snapper (except adult gag grouper) feed significantly less on HTL invertebrates in OSMOSE-WFS than in reality, because (1) only two HTL invertebrates (shrimps and large crabs) are explicitly considered in OSMOSE-WFS; and (2) current predator/prey size ratios and accessibility coefficients in OSMOSE-WFS limit too much the consumption of HTL invertebrates by species of the snapper–grouper complex. Secondly, according to observed diets, red and gag groupers prey upon juveniles of species of the snapper–grouper complex, but not red snapper. It is often difficult to define the specific fish prey of red snapper, due to stomach eversion when fish ascend from the depths, and to the frequent presence of unidentifiable partially digested fish

Table 5

Long-term changes in the starvation mortality rates and mean body size of red grouper, gag grouper and red snapper in OSMOSE-WFS under different fishing scenarios relative to the status quo (in %). $0.5 * F_{msy}$: scenario where the annual fishing mortality rate F of red grouper is set to half its F_{msy} (i.e., the annual fishing mortality rate resulting in maximum sustainable yield) estimated with OSMOSE-WFS — F_{msy} : scenario where the F of red grouper is set to its F_{msy} — $2 * F_{msy}$: scenario where the F of red grouper is set to twice its F_{msy} .

	$0.5 * F_{msy}$	F_{msy}	$2 * F_{msy}$
Starvation mortality rate of younger juvenile red grouper	21.1%	11.1%	−14.0%
Starvation mortality rate of older juvenile red grouper	11.6%	6.7%	−4.0%
Starvation mortality rate of adult red grouper	28.1%	17.1%	−20.3%
Starvation mortality rate of younger juvenile gag grouper	−38.5%	−20.9%	28.1%
Starvation mortality rate of older juvenile gag grouper	−20.3%	−9.9%	2.2%
Starvation mortality rate of adult gag grouper	−10.4%	−8.3%	10.6%
Starvation mortality rate of juvenile red snapper	−70.7%	−41.7%	4.5%
Starvation mortality rate of adult red snapper	−42.1%	−25.8%	4.0%
Mean body size of red grouper	4.7%	2.2%	−0.9%
Mean body size of gag grouper	10.5%	5.0%	5.0%
Mean body size of red snapper	12.4%	3.2%	−0.7%

material in the stomachs analyzed (e.g., Bradley and Bryan, 1975; Futch and Bruger, 1976; McCawley et al., 2006). However, observed diets indicate that red snapper feeds on carnivores whose body size range is similar to that of juveniles of red and gag groupers (reef carnivores and small coastal carnivores; Appendix G), while some diet studies found species of the Serranidae family in red snapper stomachs (Futch and Bruger, 1976; Sheridan, 2008; Szedlmayer and Lee, 2004). Moreover, the populations of red grouper, gag grouper and red snapper partially overlap on the West Florida Shelf (Chagaris, 2013; Grüss et al., 2014a). Therefore, the possibility that red snapper preys upon juveniles of red and gag groupers cannot be excluded and requires further investigation.

4.4. Concluding remarks

Here, we set up an updated version of the ecosystem model OSMOSE-WFS to estimate natural mortality rates and fishing scenarios for GOM red grouper, with the intent to provide inputs to the SEDAR process (SEDAR 42) and the GOM Fishery Management Council. OSMOSE-WFS predictions suggest that the natural mortality rate of juveniles of GOM red grouper is high and essentially due to predation, while the bulk of the natural mortality of adult red grouper results from causes not represented in OSMOSE-WFS such as, presumably, red tides. These results were communicated to SEDAR 42 (Grüss et al., 2014b, 2015b).

Moreover, OSMOSE-WFS indicate that altering the fishing mortality of GOM red grouper may have no global impact on the biomass of the major prey of red grouper, due to the high complexity and high redundancy of the modeled system. By contrast, altering the fishing mortality of GOM red grouper may have a large impact on the biomass of its major competitors. Increasing the fishing mortality of red grouper would increase the biomass of its major competitors, due to reduced competition for food. Conversely, decreasing the fishing mortality of red grouper would diminish the biomass of its major competitors, due to increased predation pressure on the juveniles of the major competitors by red grouper. The results of fishing scenarios should be considered preliminary and will not be communicated to the GOM Fishery Management Council at this time, because of some discrepancies between the diets of groupers and snappers predicted by OSMOSE-WFS and the observed ones. These discrepancies may be reduced through (1) the introduction of new HTL invertebrate groups in OSMOSE-WFS, such as stomatopods (*Squilla* sp. and *Neogonodactyla* sp.) and squids (*Loligo* sp. and *Illex* sp.); and (2) the recalibration of OSMOSE-WFS focusing primarily on the adjustment of the predator/prey size ratios of species of the snapper-grouper complex and of some accessibility coefficients.

Author contributions

Designed and analyzed the models: AG, MJS, DC, LV, YJS, PV. Conceived the models: AG, MJS, DC, LV, YJS, PV, ROR. Provided inputs for the models: DC. Wrote the paper: AG, MJS, DC, LV, YJS, PV, CHA. All authors have approved the final article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jmarsys.2015.10.014>.

References

- Baker, R., Buckland, A., Sheaves, M., 2014. Fish gut content analysis: robust measures of diet composition. *Fish. Fish.* 15, 170–177.
- Bradley, E., Bryan, C.E., 1975. Life history and fishery of the red snapper (*Lutjanus campechanus*) in the northwestern Gulf of Mexico: 1970–1974. *Proceedings of the Gulf and Caribbean Fisheries Institute*, pp. 77–106.
- Chagaris, D.D., 2013. Ecosystem-based Evaluation of Fishery Policies and Tradeoffs on the West Florida Shelf (PhD Thesis) University of Florida, Gainesville, Florida.
- Chagaris, D., Mahmoudi, B., 2013. Natural Mortality of Gag Grouper from 1950 to 2009 Generated by an Ecosim Model. SEDAR 33-DW07. SEDAR, North Charleston, SC (23 pp.).
- Chagaris, D.D., Mahmoudi, B., Walters, C.J., Allen, M.S., 2015. Simulating the trophic impacts of fishery policy options on the West Florida Shelf using ecopath with Ecosim. *Mar. Coast. Fish.* 7, 44–58.
- Coleman, F.C., Koenig, C.C., Collins, L.A., 1996. Reproductive styles of shallow water groupers of the northeastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environ. Biol. Fish.* 47, 129–141.
- Coleman, F.C., Scanlon, K.M., Koenig, C.C., 2011. Groupers on the edge: shelf edge spawning habitat in and around marine reserves of the northeastern Gulf of Mexico. *Prof. Geogr.* 63, 456–474.
- Curry, P.M., Shin, Y.J., Planque, B., Durant, J.M., Fromentin, J.M., Kramer-Schadt, S., Stenseth, N.C., Travers, M., Grimm, V., 2008. Ecosystem oceanography for global change in fisheries. *Trends Ecol. Evol.* 23, 338–346.
- Farmer, N.A., Malinowski, R.P., McGovern, M.F., Rubec, P.J., 2015. Fisheries stock complexes in the Gulf of Mexico. *Mar. Coast. Fish.* (submitted for publication, in review).
- Ferrari, F.D., 1975. Taxonomic notes of the genus *Oncaea* (Copepoda: Cyclopoida) from the Gulf of Mexico and northern Caribbean Sea. *Proc. Biol. Soc. Wash.* 88, 217–232.
- Futch, R.B., Bruger, G.E., 1976. Age, growth and reproduction of red snapper in Florida waters. In: Bullis, A.H.R., Jones, A.C. (Eds.), *Proceedings on the Colloquium on Snapper–Grouper Fishery Resources of the Western Central Atlantic Ocean*, Florida Sea Grant Program Report 17, pp. 165–184.
- Gaichas, S., Gamble, R., Fogarty, M., Benoit, H., Essington, T., Fu, C., Koen-Alonso, M., Link, J., 2012. Assembly rules for aggregate-species production models: simulations in support of management strategy evaluation. *Mar. Ecol. Prog. Ser.* 459, 275–292.
- Gray, A., 2014. *Karenia brevis* harmful algal blooms: Their role in structuring the organismal community on the West Florida Shelf (MSc Thesis) University of South Florida, Saint Petersburg, Florida.
- Grice, G.D., 1960. Copepods of the genus *Oithona* from the Gulf of Mexico. *Bull. Mar. Sci.* 10, 485–490.
- Grüss, A., Drexler, M., Ainsworth, C.H., 2014a. Using delta generalized additive models to produce distribution maps for spatially-explicit ecosystem models. *Fish. Res.* 159, 11–24.
- Grüss, A., Schirripa, M.J., Chagaris, D.D., Verley, P., Shin, Y.-J., Velez, L., Ainsworth, C., Sagarese, S.R., Karnauskas, M., 2014b. Evaluation of the natural mortality rates of red grouper (*Epinephelus morio*) in the West Florida Shelf ecosystem using the individual-based, multispecies model OSMOSE-WFS. SEDAR42-DW-02. SEDAR, North Charleston, SC (70 pp.).
- Grüss, A., Schirripa, M.J., Chagaris, D., Drexler, M., Simons, J., Verley, P., Shin, Y.-J., Karnauskas, M., Oliveros-Ramos, R., Ainsworth, C.H., 2015a. Evaluation of the trophic structure of the West Florida Shelf in the 2000s using the ecosystem model OSMOSE. *J. Mar. Syst.* 144, 30–47.
- Grüss, A., Schirripa, M.J., Chagaris, D.D., Verley, P., Shin, Y.-J., Velez, L., Ainsworth, C., Sagarese, S.R., Lombardi-Carlson, L., 2015b. Estimating age- and size-specific natural mortality rates for Gulf of Mexico red grouper (*Epinephelus morio*) using the ecosystem model OSMOSE-WFS. SEDAR42-AW-05. SEDAR, North Charleston, SC (33 pp.).
- Hoening, J.M., 1983. Empirical use of longevity data to estimate mortality rates. *Fish. Bull.* 82, 898–902. <http://myfwc.com/research/redtide>. <http://www.osmose-model.org>. <http://www.sefsc.noaa.gov/sedar/>. <http://www.st.nmfs.noaa.gov/index>. <http://www.st.nmfs.noaa.gov/recreational-fisheries/index>.
- Karnauskas, M., Schirripa, M.J., Kelble, C.R., Cook, G.S., Craig, J.K., 2013. Ecosystem status report for the Gulf of Mexico. NOAA Technical Memorandum NMFS-SEFSC-653 (52 pp.).
- Kimmel, D.G., Boicourt, W.C., Pierson, J.J., Roman, M.R., Zhang, X., 2010. The vertical distribution and diel variability of mesozooplankton biomass, abundance and size in response to hypoxia in the northern Gulf of Mexico, USA. *J. Plankton Res.* 32, 1185–1202.
- Kitchell, J.F., Essington, T.E., Boggs, C.H., Schindler, D.E., Walters, C.J., 2002. The role of sharks and longline fisheries in a pelagic ecosystem of the central Pacific. *Ecosystems* 5, 202–216.
- Link, J.S., 2002. What does ecosystem-based fisheries management mean. *Fisheries* 27, 18–21.
- Link, J., 2010. *Ecosystem-based Fisheries Management: Confronting Tradeoffs*. Cambridge University Press, Cambridge, UK.
- Lombardi-Carlson, L., Fitzhugh, G., Palmer, C., Gardner, C., Farsky, R., Ortiz, M., 2008. Regional size, age and growth differences of red grouper (*Epinephelus morio*) along the west coast of Florida. *Fish. Res.* 91, 239–251.

- Lorenzen, K., 2005. Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. *Philos. Trans. R. Soc. B Biol. Sci.* 360, 171–189.
- Marasco, R.J., Goodman, D., Grimes, C.B., Lawson, P.W., Punt, A.E., Quinn II, T.J., 2007. Ecosystem-based fisheries management: some practical suggestions. *Can. J. Fish. Aquat. Sci.* 64, 928–939.
- Marzloff, M., Shin, Y.J., Tam, J., Travers, M., Bertrand, A., 2009. Trophic structure of the Peruvian marine ecosystem in 2000–2006: insights on the effects of management scenarios for the hake fishery using the IBM trophic model Osmose. *J. Mar. Syst.* 75, 290–304.
- McCawley, J.R., Cowan, J.H., Shipp, R.L., 2006. Feeding periodicity and prey habitat preference of red snapper, *Lutjanus campechanus* (Poey, 1860), on Alabama artificial reefs. *Gulf Mex. Sci.* 24, 14–27.
- McQueen, N., Griffiths, M.H., 2004. Influence of sample size and sampling frequency on the quantitative dietary descriptions of a predatory fish in the Benguela ecosystem. *Afr. J. Mar. Sci.* 26, 205–217.
- Miller, J.E., Pawson, D.L., 1984. Holothurians (Echinodermata: Holothuroidea) Memoirs of the Hourglass Cruises 5(3). Florida Department of Natural Resources, Marine Research Laboratory, St. Petersburg, Florida (119 pp.).
- Moretzsohn, F., Chavez, J.S., Tunnell Jr., J.W., 2012. GulfBase: Resource Database for Gulf of Mexico Research. World Wide Web Electronic Publication (Available from: <http://www.gulfbase.org>).
- Nance, J.M., 2009. Stock assessment report 2008. Gulf of Mexico Shrimp Fishery. Report for the Gulf of Mexico Fishery Management Council.
- Okey, T.A., Mahmoudi, B., 2002. An ecosystem model of the West Florida Shelf for use in Fisheries Management and Ecological Research: Volume II. Model Construction. Report of the Florida Marine Research Institute, St Petersburg, Florida.
- Oliveros-Ramos, R., Shin, Y.J., 2015. calibrar: an R package for the calibration of ecological models. *Methods Ecol. Evol.* (submitted for publication).
- Plagányi, É.E., 2007. Models for an ecosystem approach to fisheries. *FAO Fisheries Technical Paper No. 477*.
- Rosenberg, G., 2009. Malacolog 4.1. 1: a database of Western Atlantic marine Mollusca. WWW Database Version 4.1. 1 Available from: <http://www.malacol.com>.
- Sagarese, S.R., Grüss, A., Karauskas, M., Walter, J.F., 2014. Ontogenetic spatial distributions of red grouper (*Epinephelus morio*) within the eastern Gulf of Mexico with comments on spatio-temporal overlap with red tide events. *SEDAR 42-DW04*. SEDAR, North Charleston, SC (32 pp.).
- Sagarese, S.R., Gray, A.M., Ainsworth, C.H., Chagaris, D., Mahmoudi, B., 2015. Red tide mortality on red grouper (*Epinephelus morio*) between 1980 and 2009 on the West Florida Shelf. *SEDAR42-AW-01*. SEDAR, North Charleston, SC (12 pp.).
- Sala, E., Sugihara, G., 2005. Food web theory provides guidelines for marine conservation. In: Belgrano, A., Scharler, U., Dunne, J., Ulanowicz, B. (Eds.), *Aquatic Food Webs: An Ecosystem Approach*. Oxford University Press, Oxford, UK, pp. 170–183.
- Samhuri, J.F., Haupt, A.J., Levin, P.S., Link, J.S., Shuford, R., 2014. Lessons learned from developing integrated ecosystem assessments to inform marine ecosystem-based management in the USA. *ICES J. Mar. Sci.* 71, 1205–1215.
- Scharf, F.S., Buckel, J.A., Juanes, F., Conover, D.O., 1997. Estimating piscine prey size from partial remains: testing for shifts in foraging mode by juvenile bluefish. *Environ. Biol. Fish* 49, 377–388.
- Schirripa, M.J., Allee, B., Cross, S., Kelble, C., Parsons, A.R., 2013. Progress towards an integrated ecosystem assessment for the Gulf of Mexico. *Collect. Vol. Sci. Pap. ICCAT* 69, pp. 1867–1875.
- SEDAR, 2009a. Stock assessment of red grouper in the Gulf of Mexico. SEDAR update assessment Available from: <http://www.sefsc.noaa.gov/sedar/>.
- SEDAR, 2009b. Stock assessment of red snapper in the Gulf of Mexico. SEDAR update assessment Available from: <http://www.sefsc.noaa.gov/sedar/>.
- SEDAR, 2011. Stock assessment of greater amberjack in the Gulf of Mexico. SEDAR update assessment Available from: <http://www.sefsc.noaa.gov/sedar/>.
- SEDAR, 2014. Gulf of Mexico Gag Section III: Assessment Workshop Report. SEDAR, North Charleston, SC.
- SEDAR 16, 2009. Atlantic and Gulf of Mexico king mackerel, complete stock assessment report Available from: <http://www.sefsc.noaa.gov/sedar/>.
- SEDAR 7, 2005. Gulf of Mexico red snapper, complete stock assessment report Available from: <http://www.sefsc.noaa.gov/sedar/>.
- Sheridan, P., 2008. Seasonal foods, gonadal maturation, and length–weight relationships for nine fishes commonly captured by shrimp trawl on the Northwest Gulf of Mexico Continental Shelf. NOAA Technical Memorandum NMFS-SEFSC-566 (37 pp.).
- Shin, Y.J., Cury, P., 2001. Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. *Aquat. Living Resour.* 14, 65–80.
- Shin, Y.J., Cury, P., 2004. Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. *Can. J. Fish. Aquat. Sci.* 61, 414–431.
- Shin, Y.J., Shannon, L.J., Cury, P.M., 2004. Simulations of fishing effects on the southern Benguela fish community using an individual-based model: learning from a comparison with Ecosim. *Afr. J. Mar. Sci.* 26, 95–114.
- SUSFIO, 1977. Baseline monitoring studies, Mississippi, Alabama, Florida, outer continental shelf, 1975–1976. Volume III. Results. Prepared for the Bureau of Land Management, Washington, DC, 28 June 1977. State University System of Florida Institution of Oceanography, St. Petersburg.
- Szedlmayer, S.T., Lee, J.D., 2004. Diet shifts of juvenile red snapper (*Lutjanus campechanus*) with changes in habitat and fish size. *Fish. Bull. U. S.* 102, 366–375.
- Travers, M., Watermeyer, K., Shannon, L.J., Shin, Y.J., 2010. Changes in food web structure under scenarios of overfishing in the southern Benguela: comparison of the Ecosim and OSMOSE modelling approaches. *J. Mar. Syst.* 79, 101–111.
- Travers-Trolet, M., Shin, Y.J., Field, J.G., 2014. An end-to-end coupled model ROMS-N2P2Z2D2-OSMOSE of the southern Benguela foodweb: parameterisation, calibration and pattern-oriented validation. *Afr. J. Mar. Sci.* 36, 11–29.
- Turner, I.T., 2004. The importance of small planktonic copepods and their roles in pelagic marine food webs. *Zool. Stud.* 43, 255–266.
- Walter III, J.F., Sagarese, S.R., Harford, W.J., Grüss, A., Stumpf, R.P., Christman, M.C., 2015. Assessing the impact of the 2014 red tide event on red grouper (*Epinephelus morio*) in the northeastern Gulf of Mexico. *SEDAR42-RW-02*. SEDAR, North Charleston, SC (13 pp.).
- Walters, C.J., Christensen, V., Martell, S.J., Kitchell, J.F., 2005. Possible ecosystem impacts of applying MSY policies from single-species assessment. *ICES J. Mar. Sci.* 62, 558–568.
- Wood, S.N., 2006. *Generalized Additive Models: An Introduction with R*. Chapman & Hall, London, UK.