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Improving the Spatial Allocation of Functional Group Biomasses in Spatially-Explicit Ecosystem Models: Insights from Three Gulf of Mexico Models

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Improving the spatial allocation of functional group biomasses in spatially-explicit ecosystem models: insights from three Gulf of Mexico models

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ABSTRACT.—Spatially-explicit ecosystem models, such as Ecospace, Atlantis, and OSMOSE, are key tools for achieving ecosystem-based fisheries management in the Gulf of Mexico (GOM). In spatially-explicit ecosystem models, trophic interactions strongly depend on the way functional group biomasses are allocated spatially, which conditions patterns of spatial overlap between predators, prey, and competitors. Here, we review realized and ongoing improvements in the spatial allocation of functional group biomasses in Ecospace and OSMOSE models of the West Florida Shelf (“WFS Reef fish Ecospace” and “OSMOSE-WFS”) and in the Atlantis model of the GOM (“Atlantis-GOM”). A habitat capacity model, which defines the spatial distribution of functional groups dynamically based on environmental factors, was introduced in WFS Reef fish Ecospace. Moreover, generalized additive models (GAMs) relating biomasses to environmental predictors were developed to produce distribution maps for Atlantis-GOM and OSMOSE-WFS. WFS Reef fish Ecospace’s habitat capacity model itself relies on GAMs to determine relationships between marine organisms and environmental parameters. Ongoing efforts include the development of a sophisticated GAM framework, using carefully chosen environmental predictors and a blending of available fisheries-independent and fisheries-dependent survey data. This GAM framework benefits from insights contributed by empiricists and fishers and will significantly enhance WFS Reef fish Ecospace’s habitat capacity model and the distribution maps fed into Atlantis-GOM and OSMOSE-WFS. Ongoing efforts also include the construction of accurate fields of chlorophyll-*a* and plankton biomasses for WFS Reef fish Ecospace, Atlantis-GOM, and OSMOSE-WFS, employing a blending of ocean observations (satellite and in situ data) and outputs from a biogeochemical model.

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Ecosystem-based fisheries management (EBFM) is becoming a central paradigm worldwide, including in the Gulf of Mexico (GOM) (Pitcher et al. 2009, Schirripa et al. 2012, Karnauskas et al. 2013, Keith et al. 2013). EBFM considers trophic interactions and the influence of the abiotic environment on species dynamics to define fisheries management strategies (Link 2002, 2010, Marasco et al. 2007). Ecosystem modeling approaches, including Ecopath with Ecosim (EwE) with Ecospace (Pauly et al. 2000, Christensen and Walters 2004), Atlantis (Fulton et al. 2004, 2007), and OSMOSE (Shin and Cury 2001, 2004), are key tools for achieving EBFM, due to their ability to provide an integrated, holistic understanding of marine ecosystems and of how to potentially mitigate fishing pressure on these ecosystems. They are increasingly being used in the GOM to integrate ecosystem considerations into stock assessments and to inform decisions made by the Gulf of Mexico Fishery Management Council (Schirripa et al. 2012, Samhouri et al. 2014), and to conduct damage assessment and guide restoration activities following the DEEPWATER HORIZON oil spill (Rose and Sable 2013, NOAA 2015).

The simulation of trophic interactions between functional groups (i.e., groups of species sharing similar ecological niches and life-history characteristics) is recognized to be the most important feature of ecosystem models (Plaganyi 2007, Travers et al. 2007, Christensen and Walters 2011). Trophic interactions in ecosystem models depend on parameters that describe diet preferences (e.g., diet matrix, gape size), predator and prey behavior (e.g., effective search rate and handling time), and prey vulnerability (e.g., EwE vulnerability parameters) (Plaganyi 2007, Shin et al. 2010, Christensen and Walters 2011). In spatially-explicit ecosystem models, trophic interactions are also strongly dependent on the allocation of functional group biomasses over space (i.e., in the horizontal dimension), which, along with fish movement patterns, conditions patterns of spatial overlap between predators, prey, and competitors (Fig. 1; Fulton et al. 2007, Shin et al. 2010).

The GOM is a large marine ecosystem enveloped by the exclusive economic zones of the United States (US), Cuba, and Mexico, which is challenging to model due to its high biodiversity and the considerable number of threats that the region is facing (Fautin et al. 2010, National Ocean Service 2011). Nine spatially-explicit ecosystem models have been developed for the region, including seven EwE with Ecospace models (of which one is a model for the West Florida Shelf called “WFS Reef fish Ecospace”; Chagaris 2013, Chagaris et al. 2015), one Atlantis model for the entire GOM referred to as “Atlantis-GOM” (Ainsworth et al. 2015), and one OSMOSE model of the West Florida Shelf called “OSMOSE-WFS” (Grüss et al. 2015, 2016) (Table 1). WFS Reef fish Ecospace, Atlantis-GOM, and OSMOSE-WFS are all intended to integrate ecosystem considerations into stock assessments, as well as to inform the Gulf of Mexico Fishery Management Council and restoration efforts related to EBFM (Fig. 2).

Here, we review realized and ongoing improvements in the spatial allocation of functional group biomasses in the WFS Reef fish Ecospace, Atlantis-GOM, and OSMOSE-WFS models. Reliable spatial allocation of functional group biomasses in spatially-explicit ecosystem models is important, because it allows a realistic representation of patterns of spatial overlap between predators, prey, and competitors, and consequently, lends more confidence to the predictions of spatially-explicit ecosystem models. In the following, we first briefly summarize how functional group biomasses are usually allocated over space in the Ecospace, Atlantis, and OSMOSE

Figure 1. Parameters controlling predator-prey interactions in Ecopath with Ecosim (EwE) with Ecospace, Atlantis, and OSMOSE models. In all three models, predator-prey interactions, as well as interactions between predators and their competitors, strongly depend on patterns of spatial overlap between functional groups, which are conditioned by habitat capacity (EwE with Ecospace) or distribution maps (Atlantis and OSMOSE), along with fish movement patterns.

modeling platforms. We then detail the WFS Reef fish Ecospace, Atlantis-GOM, and OSMOSE-WFS models, and the methodologies currently employed to allocate functional group biomasses in these models, which all involve generalized additive models (GAMs) and are more advanced than the methodologies employed in other spatially-explicit ecosystem models. Finally, we describe ongoing research making better use of research survey data, ocean observations, insights contributed by empiricists and fishers, and GAMs to allocate functional group biomasses spatially in WFS Reef fish Ecospace, Atlantis-GOM, and OSMOSE-WFS. Our study aims to promote the general use of better methodologies and data inputs to condition the spatial allocation of functional group biomasses in the different spatially-explicit ecosystem models employed in the GOM.

SPATIAL ALLOCATION OF FUNCTIONAL GROUP BIOMASSES: REALIZED IMPROVEMENTS.

ECOSPACE

The Ecospace Modeling Approach.—EwE with Ecospace is a trophodynamic modeling package that explicitly accounts for trophic interactions, fisheries, and environmental forcing (Table 2; Pauly et al. 2000, Christensen and Walters 2004). The spatial allocation of functional group biomasses in Ecospace is based on habitat capacity (habitat suitability), as well as on movement patterns and other factors (relative vulnerabilities to predation in non-preferred habitat, and relative feeding rates in non-preferred habitat) (Walters et al. 1999, Christensen and Walters 2004).

Table 1. Characteristics of the spatially-explicit ecosystem models of the Gulf of Mexico (GOM).

Model	Area modeled	Functional groups considered	Methods used to generate habitat capacity fields (Ecospace) or distribution maps (Atlantis and OSMOSE)
Vidal and Pauly (2004)'s Ecospace model	Entire GOM large marine ecosystem	Marine mammals (2 groups), seabirds (1), sea turtles (1), fish (20, of which 3 are non-adult life stages), invertebrates (11, of which 4 are zooplankton groups and 1 is a non-adult life stage), marine plants (2), phytoplankton (1), detritus (2)	Traditional approach consisting of defining the preferences of functional groups to habitat types, from information available in the biological and ecological literature, queries in global information systems on marine organisms, and experts' opinion.
Walters et al. (2010)'s Ecospace model	Northern GOM (0–1000 m)	Fish (50, of which 21 are non-adult stanzas), invertebrates (9, of which 2 are zooplankton groups), marine plants (2), phytoplankton (1), detritus (1)	Traditional approach consisting of defining the preferences of functional groups and stanzas to habitat types, from information available in the biological and ecological literature, queries in global information systems on marine organisms, research survey records, and experts' opinion.
Suprenand et al. (2015)'s Ecospace model	Northern GOM (0–1000 m)	Fish (50, of which 21 are non-adult stanzas), invertebrates (9, of which 2 are zooplankton groups), marine plants (2), phytoplankton (1), detritus (1)	Traditional approach consisting of defining the preferences of functional groups and stanzas to habitat types, from information available in the biological and ecological literature, queries in global information systems on marine organisms, research survey records, and experts' opinion.
de Mutsert et al. (2015)'s Ecospace model	Louisiana coastal zone (0–690 m)	Marine mammals (1 group), seabirds (1), fish (34, of which 16 are non-adult stanzas), invertebrates (15, of which 1 is a zooplankton group and 6 are non-adult stanzas), marine plants (2), phytoplankton (1), detritus (1)	(1) Use of Ecospace's habitat capacity model, which defines spatial distributions dynamically based on environmental parameters, for the majority of the functional groups represented in the model. (2) Uniform spatial distribution for the remaining functional groups.
de Mutsert et al. (2016)'s Ecospace model	Louisiana coastal zone (0–1829 m)	Marine mammals (1 group), sea turtles (1), fish (43, of which 15 are non-adult stanzas), invertebrates (12, of which 1 is a zooplankton group and 3 are non-adult stanzas), marine plants (1), phytoplankton (1), detritus (1)	(1) Use of Ecospace's habitat capacity model, which defines spatial distributions dynamically based on environmental parameters, for the majority of the functional groups represented in the model. (2) Uniform spatial distribution for the remaining functional groups.
Barataria Bay Ecospace model (Lewis et al. 2016)	Barataria Bay, Louisiana	Fish (20, of which 3 are non-adult life stages), invertebrates (4, of which 1 is a zooplankton group and 1 is a non-adult life stage), marine plants (2), phytoplankton (1), detritus (1)	(1) Use of Ecospace's habitat capacity model, which defines spatial distributions dynamically based on environmental parameters, for the majority of the functional groups represented in the model. (2) Uniform spatial distribution for the remaining functional groups.

Table 1. Continued.

Model	Area modeled	Functional groups considered	Methods used to generate habitat capacity fields (Ecospace) or distribution maps (Atlantis and OSMOSE)
WFS Reef fish Ecospace (Chagaris 2013)	West Florida Shelf, defined here as the area extending from the Florida Panhandle south to a boundary that excludes the Florida Keys, and out to the 250-m isobath	Marine mammals (1 group), seabirds (1), fish (43, of which 11 are non-adult stanzas), invertebrates (18, of which 3 are zooplankton groups), marine plants (3), phytoplankton (1), detritus (3)	(1) Use of Ecospace's habitat capacity model, which defines spatial distributions dynamically based on environmental parameters, for 49 of the 70 functional groups and stanzas represented in the model (listed in Online Table 1). (2) Uniform spatial distribution for 22 functional groups (listed in Online Table 1).
Atlantis-GOM (Ainsworth et al. 2015)	Entire GOM large marine ecosystem	Marine mammals (4 groups), seabirds (2), sea turtles (3), fish (48), invertebrates (17, of which 3 are zooplankton groups and 3 are filter feeders), structural species (3), marine plants (4), phytoplankton (4), nutrient cyclers (4)	(1) Negative binomial generalized additive models fitted to fisheries-independent survey data for 40 of the 91 functional groups represented in the model (listed in Online Table 3). (2) Published spatial distribution for 11 functional groups (listed in Online Table 3). (3) Use of a simple allocation algorithm (uniform spatial distribution in coastal polygons, proportional to other functional groups, or manually set) for 30 functional groups (listed in Online Table 3). (4) Use of remote-sensing derived time series of chlorophyll-a (MODIS data) for small phytoplankton, large phytoplankton, toxic dinoflagellates, protists, and 6 other functional groups (listed in Online Table 3).
OSMOSE-WFS (Grüss et al. 2015a)	West Florida Shelf, defined here as the area extending from the Florida Panhandle south to a boundary that excludes the Florida Keys, and out to the 250-m isobath	Fish (10 groups), invertebrates (2), phytoplankton (2; implicitly considered); zooplankton (2; implicitly considered); low-trophic level benthos (5; implicitly considered)	(1) Delta generalized additive models fitted to fisheries-independent survey data for the majority of the functional groups, life stages and seasons considered in the model (listed in Online Appendix 1). (2) Use of information from the literature and experts' opinion for younger juvenile red grouper and younger juvenile gag grouper. (3) Use of remote-sensing derived time series of chlorophyll-a (SeaWiFS data) for small phytoplankton and large phytoplankton. (4) Uniform spatial distribution for small copepods, large mesozooplankton, meiofauna, small infauna, small mobile epifauna, bivalves, and echinoderms and large gastropods.

Figure 2. Spatial domains of the spatially-explicit models intended to inform stock assessments and ecosystem-based fisheries management and restoration efforts in the Gulf of Mexico. (A) Spatial polygons of the Atlantis model of the Gulf of Mexico referred to as “Atlantis-GOM” (filled in dark gray). (B) Spatial cells of the Ecospace and OSMOSE models of the West Florida Shelf, respectively referred to as “WFS Reef fish Ecospace” and “OSMOSE-WFS” (filled in dark gray).

Until recently, the only way to define habitat capacity in Ecospace was to designate each spatial cell as a discrete habitat type and then specify the preference of each functional group for habitat types (Christensen and Walters 2004, Christensen et al. 2008). In reality, multiple habitats types can be present in each spatial cell of Ecospace, especially when spatial cells are large, and the abovementioned approach is not capable of capturing habitat gradients and the preferences by functional groups across those gradients (Christensen et al. 2014). Thus, a “habitat capacity model” was introduced in Ecospace, which allows for a flexible and realistic representation of habitat capacity for each functional group as it relates to environmental characteristics (Christensen et al. 2014).

A spatial-temporal data framework was also recently introduced in Ecospace (Steenbeek et al. 2013). Through this feature, spatio-temporal data sets can be loaded into Ecospace and used to drive the environmental layers for which functional groups have response functions. Thus, the combination of the habitat capacity model and the spatial-temporal data framework allows environmental layers in Ecospace to be dynamic and to affect the movement of functional groups according to defined response shapes (Steenbeek et al. 2013). In the habitat capacity model, each functional group may be assigned one function for each environmental map layer, and these functions are combined across all layers to produce a single habitat capacity map (Fig. 3). The values of the computed habitat capacity map are then used to determine the relative foraging arena size of each spatial cell of Ecospace for each functional group, and movement toward areas with more foraging habitat is favored (Christensen et al. 2014).

The spatial allocation of the biomasses of primary producers in Ecospace also depends on the spatial allocation of their productivity (i.e., production/biomass or P/B). The development of the spatial-temporal data framework enables Ecospace to read remote-sensing derived spatio-temporal time series of chlorophyll-*a* to drive primary producers’ P/B (Steenbeek et al. 2013).

WFS Reef Fish Ecospace.—WFS Reef fish Ecospace is an Ecospace model focused on regulated species of the West Florida Shelf, including gag grouper [*Mycteroperca*

Figure 3. Example of habitat capacity model calculations in Ecospace. Schematic diagram of habitat capacity calculations for adult red snapper (*Lutjanus campechanus*) in the WFS Reef fish Ecospace model. During model run, cell-specific environmental parameter values (here: bathymetry, rugosity and bottom temperature) can be read from data layers for each time step, and cell-specific habitat capacity is computed as the product of the environmental parameter values. Figure inspired by Christensen et al. (2014).

microlepis (Goode and Bean, 1879)], red grouper [*Epinephelus morio* (Valenciennes, 1828)], red snapper [*Lutjanus campechanus* (Poey, 1860)], and other reef fishes, coastal migratory pelagics, and highly migratory pelagics (Fig. 2; Chagaris 2013, Chagaris et al. 2015). The model consists of 70 biomass pools (Table 1, Online Table 1).

WFS Reef fish Ecospace belongs to the first Ecospace models that have tested and then integrated the habitat capacity model and the spatial-temporal data framework. WFS Reef fish Ecospace employs the habitat capacity model for 49 of the functional groups that it considers (Online Table 1, Chagaris 2013). Maps for readily available variables constitute the environmental layers of WFS Reef fish Ecospace's habitat capacity model. Functional group distribution patterns in WFS Reef fish Ecospace are thus determined by the relationship with those environmental variables, the abundance of prey and predators, and the proximity to younger stanzas (Christensen et al. 2014). For example, with respect to adult red snapper, a dome-shaped function is used to relate habitat capacity to bathymetry, and habitat capacity also increases linearly with rugosity and decreases with bottom temperature in a non-linear manner (Fig. 3, Chagaris 2013).

To define relationships between habitat capacity for a given functional group and environmental variables, Chagaris (2013) either used the fits of a binomial GAM (Wood 2006) fitted to presence/absence survey data, or relied on the ecological literature, FishBase/SeaLifeBase (Froese and Pauly 2016, Palomares and Pauly 2016), and experts' opinion, when no survey data were available. When the former option was selected, Chagaris (2013) utilized a single appropriate research survey data set to fit a GAM for each functional group (Online Tables 1, 2). However, in some cases, very few presence/absence data were available to fit relationships between the probability of presence of a functional group and environmental factors, such that these relationships are uncertain.

Ecospace's spatial-temporal data framework enables WFS Reef fish Ecospace to read remote-sensing derived spatio-temporal time series of chlorophyll-*a* to drive phytoplankton P/B [Moderate Resolution Imaging Spectroradiometer (MODIS) data] (Chagaris 2013).

Table 2. Overview of the Ecopath with Ecosim (EwE) with Ecospace, Atlantis, and OSMOSE modeling approaches.

Ecosystem modeling approach	Overview
EwE with Ecospace	<ul style="list-style-type: none">• EwE is a modeling tool that considers a comprehensive palette of the functional groups of a given marine ecosystem: primary producers (phytoplankton groups, marine plants), invertebrates, fishes, marine mammals, seabirds, detritus groups and, often, microbial groups. Functional groups are described as either single biomass pools or multi-stanza groups to account for ontogenetic differences in habitat and/or diet. The Ecopath component of the EwE modeling package is a static mass-balance representation of a marine food web that provides an initial state for dynamic modeling (Christensen and Pauly 1992). Trophic interactions in Ecopath are determined through a fixed diet matrix (Fig. 1).• The Ecosim component of EwE simulates ecosystem dynamics over monthly time steps by changing fishing mortality, fishing effort, and environmental forcing functions (Walters et al. 1997, 2000). Trophic interactions in Ecosim are modeled based on the “foraging arena theory”, which asserts that spatio-temporal restrictions in prey and predator activity result in the partitioning of each prey population into vulnerable and invulnerable components, such that predation mortality rates are dependent on (and limited by) rates of exchange between these prey components (Walters et al. 1997, Ahrens et al. 2012). Thus, trophic interactions in Ecosim depend not only on the Ecopath diet matrix, but also on prey vulnerabilities (which express the maximum increase in predation mortality under conditions of high predator/prey abundance), the effective search rate and handling time for the predators, and the risk-sensitive behavior of prey (Fig. 1).• Ecospace replicates biomass dynamics of Ecosim over a two-dimensional spatial grid and represents mixing (dispersal, migration, ontogenetic habitat shifts, advection) of biomasses among spatial cells, while also including trophic interactions processes and spatial fishing effort dynamics (Fig. 1; Walters et al. 1999, 2010). Ecospace applications integrating multi-stanza population-dynamics models represent spatial age structure using an individual-based modeling approach; for multistanza species, the numbers in each age class are divided into packets of individuals and the age and size dynamics of each packet are simulated in each spatial cell at the start of each month (Walters et al. 2010). The spatial allocation of functional group biomasses at the beginning of each month in Ecospace is a complex process, which is based on habitat capacity, as well as on movement patterns (base annual dispersal rates, relative dispersal rates in “non-preferred” and “preferred” habitats, and migration and advection patterns such as the north-south and east-west components of migrations) and other factors (relative vulnerabilities to predation in non-preferred habitat, and relative feeding rates in non-preferred habitat) (Walters et al. 1999, Christensen and Walters 2004).

Table 2. Continued.

Ecosystem modeling approach	Overview
Atlantis	<ul style="list-style-type: none"> Atlantis is a sophisticated biogeochemical-based marine ecosystem modeling approach (Fulton et al. 2004, 2007). Within the Atlantis modeling platform, numerous sub-models simulate features and processes crucial to a functioning marine ecosystem, including biochemical processes (e.g., nutrient cycling, oxygen availability), food-web interactions, fisheries, dependence of functional groups on biogenic and physical habitat, and physical and biophysical features (e.g., light penetration, stratification). Atlantis therefore bridges low and high trophic level drivers and processes. This versatility allows simulating important physical processes and their impacts on fishes and fisheries in a way inaccessible to simpler ecosystem modeling frameworks (Fulton et al. 2011). Like EwE with Ecospace models, Atlantis models explicitly consider a comprehensive suite of the functional groups of a given marine ecosystem (i.e., primary producers, invertebrates, fishes, marine mammals, etc.), which are aggregated by trophic, life history, or niche similarities. Atlantis uses an irregular grid structure (polygons) to represent important bioregional features while saving computation time in homogeneous space. Trophic interactions in Atlantis are conditioned by: (1) a diet matrix, which determines the availability of prey to predators; (2) gape limitation, which directs predation mortality to functional groups and age classes that fall within an accessible body size range determined as a fraction of predator body weight; (3) “clearance” parameters, which dictate predation efficiency when prey items are scarce; and (4) distribution maps, vertical distribution profiles and migration rates, which define the spatial distribution of functional group biomasses in the horizontal and vertical dimensions and, therefore, influence patterns of overlap between predators, prey and competitors in Atlantis’ three-dimensional domain (Fig. 1; Fulton et al. 2004, 2007, Ainsworth et al. 2011).
OSMOSE	<ul style="list-style-type: none"> OSMOSE (Object-oriented Simulator of Marine eCOSystem Exploitation) is a two-dimensional, individual-based, multispecies modeling approach (Shin and Cury 2001, 2004). OSMOSE models usually have a two-week or a monthly time step. The basic units of OSMOSE models are schools, which consist of marine organisms belonging to the same functional group, which have the same age, body size, food requirement and, at a given time step, the same spatial coordinates. One major difference between OSMOSE and the EwE and Atlantis modeling platforms is that OSMOSE models explicitly consider only a limited number of high trophic level (HTL) functional groups (e.g., 10–15 fish and invertebrate groups), due to the fact that each school simulated in OSMOSE is represented from the egg stage to the terminal age, which entails intensive calculation capacities and integration of extensive information on entire life cycles. However, fields of plankton and benthos biomasses are provided to OSMOSE models as prey pools on which schools can feed, in addition to, and simultaneously with, explicit prey (Brochier et al. 2013, Fu et al. 2013, Travers-Trolet et al. 2014). The OSMOSE modeling platform also differs from EwE and Atlantis in that it does not employ a diet matrix to condition trophic interactions, but rather makes the assumption that a predator school is opportunistic and can potentially feed on any prey provided that: (1) the predator and potential prey overlap in the horizontal dimension; (2) there is size adequacy between them (determined by “predator/prey size ratios,” which have the same rationale as gape limitation in Atlantis); and, (3) the vertical distribution and morphology of the potential prey makes it accessible to the predator (this being determined by means of “accessibility coefficients”). Spatial co-occurrence between predators and prey in OSMOSE is conditioned by the use of distribution maps developed for specific functional groups (HTL and plankton and benthos groups), life stages and seasons (Fig. 1; Travers-Trolet et al. 2014).

ATLANTIS

The Atlantis Modeling Approach.—Atlantis is a sophisticated biogeochemical-based ecosystem modeling approach, which integrates physical, chemical, ecological, and fisheries dynamics in a three-dimensional, spatially-explicit domain (Table 2; Fulton et al. 2004, 2007). In Atlantis, the allocation of functional group biomasses in the horizontal dimension at each time step is based on a set of distribution maps defined for specific species groups and seasons and on migration rates (Fulton et al. 2004, 2007). The distribution maps provided to Atlantis are maps reflecting the preferences of functional groups for specific habitat types, and/or density maps. Habitat preference maps are generated based on the potential use of habitat types by each functional group and the relative area coverage for each habitat type in the different Atlantis polygons (Fulton et al. 2007, Horne et al. 2010). Density maps in Atlantis are usually produced directly from fisheries-independent survey data (e.g., Brand et al. 2007, Horne et al. 2010, Link et al. 2011) or remote-sensing derived time series of chlorophyll-*a* in the case of phytoplankton groups (e.g., Brand et al. 2007, Ainsworth et al. 2011). Smith et al. (2015) generated density maps for their Atlantis model of the Southern Benguela system from maps constructed in a previous study through an ad hoc, non-statistical method combining diverse data sources (Pecquerie et al. 2004). An original approach was adopted by Ainsworth et al. (2011) to create density maps for the Atlantis model of the northern Gulf of California, where a biomass allocation algorithm was developed to extrapolate available fisheries-independent survey data estimates to other areas. While Ainsworth et al. (2011)'s algorithm constitutes an improvement over the other methodologies for producing density maps for Atlantis, it has the disadvantage of limiting the spatial coverage of the modeled system to the vicinity of areas that are consistently sampled by fisheries-independent surveys—just as the other methodologies described above.

The Atlantis-GOM Model.—The Atlantis-GOM model is an Atlantis model with a 12-hr time step, which was primarily designed to investigate the food web impacts of the DEEPWATER HORIZON oil spill (Ainsworth et al. 2015). Atlantis-GOM polygons cover the entire GOM large marine ecosystem, namely the US, Mexican, Cuban, and international waters of the GOM (Fig. 2). Atlantis-GOM explicitly considers 91 functional groups (Table 1, Online Table 3).

Drexler and Ainsworth (2013) developed a methodology to produce seasonal density maps for a large number of the functional groups of the Atlantis-GOM model for which research survey data are available. This methodology consisted of fitting negative binomial GAMs relating the biomass of a functional group to long-term environmental data (sediment type, bottom depth, bottom temperature, bottom dissolved oxygen, and chlorophyll-*a*), using a large trawl survey data set. Negative binomial models were chosen due to the zero-inflated nature of the trawl survey data set, which is common when working with fisheries-independent survey data. Drexler and Ainsworth (2013)'s methodology allowed the prediction of the spatial distribution of the biomass of 40 of the 91 functional groups represented in Atlantis-GOM over the entire GOM shelf (0–200 m) (Fig. 4A, Online Table 3).

Drexler and Ainsworth (2013)'s methodology was also employed to generate density maps for 17 of the benthic functional groups represented in Atlantis-GOM that inhabit (partially or exclusively) waters deeper than 200 m (Fig. 4B, Online Table 3). In that case, relationships were fitted between the biomass of a benthic functional

Figure 4. Distribution maps produced for the Atlantis-GOM and OSMOSE-WFS models, using generalized additive models. (A) Density map for pink shrimp (*Penaeus duorarum* Burkenroad, 1939) in summer in Atlantis-GOM. (B) Density map for infaunal meiobenthos (all seasons) in Atlantis-GOM. (C) Density map for adult red grouper (*Epinephelus morio*) (all seasons) in OSMOSE-WFS.

group and sediment type, bottom depth, bottom temperature, and food availability, using a deep-water fisheries-independent survey data set (Ainsworth et al. 2015).

Drexler and Ainsworth (2013)'s methodology represents a significant improvement over traditional methodologies for producing density maps for Atlantis. The GAM framework designed by Drexler and Ainsworth (2013) does not restrict mapping to the vicinity of the US shelf areas or deep sea areas that are consistently sampled by fisheries-independent surveys, but instead delivers density maps for the entire US, Mexican, and Cuban shelves, and for the whole deep sea region of the GOM (though within reasonable longitude, latitude, and depth limits for each functional group based on the ecological literature, and FishBase/SeaLifeBase). While this approach offers a practical and efficient means to inferring biomass distributions across unsampled locations, it also introduces additional uncertainties in the distribution maps produced. Drexler and Ainsworth (2013) utilized only one trawl survey data set for the majority of functional groups represented in Atlantis-GOM found in inshore areas (Online Table 2), because these data can be readily extracted from a comprehensive public database. Relying on a single survey data set to generate a density map for a given functional group is not ideal; consequently, a very limited number of non-zero biomass estimates are used to fit the response of some functional groups to environmental factors. Fitting responses to environmental factors to a very limited number of non-zero data points can lead to unreliable predictions (Wood 2006). Moreover, the trawl survey considered employs a benthic trawl gear to which many

functional groups considered in Atlantis-GOM are only slightly vulnerable; fitting GAMs to benthic trawl data for those groups may provide relatively inaccurate density maps. Finally, Drexler and Ainsworth (2013) utilized the same set of environmental predictors for all of the functional groups that they considered, due to the fact that spatial estimates for these environmental factors are easily available for the entire GOM. However, based on the ecological literature, other environmental predictors may be more relevant to fit GAMs for some of the functional groups considered in Drexler and Ainsworth (2013).

When Drexler and Ainsworth (2013)'s GAM framework was not able to produce density maps, functional groups' initial spatial distributions in Atlantis-GOM were set using ad hoc methodologies (Table 1, Online Table 3).

OSMOSE

The OSMOSE Modeling Approach.—OSMOSE is a spatially-explicit, individual-based, multispecies modeling approach, with basic units that are schools, which consist of organisms belonging to the same functional group, have the same age, size, food requirement, and at a given time step, the same spatial coordinates (Table 2; Shin and Cury 2001, 2004). The distribution maps that determine the spatial allocation of schools in OSMOSE at each time step are either maps of presence/absence or density maps (Shin et al. 2004, Marzloff et al. 2009, Fu et al. 2013, Travers-Trolet et al. 2014). When schools do not need to be reallocated over space (within a season, or if their distribution is constant throughout the year), they move to immediately adjacent cells within their distribution area according to a random walk. Traditionally, the maps of presence/absence used in OSMOSE are generated from the ecological literature and experts' opinion, or directly from fisheries-independent survey and fisheries data (Shin et al. 2004, Brochier et al. 2013, Fu et al. 2013, Travers-Trolet et al. 2014). The density maps employed in Marzloff et al. (2009) were produced directly from trawl and acoustic survey data. Thus, the approaches that have been traditionally adopted to construct distribution maps for OSMOSE models are not objective and/or they limit the spatial coverage of the modeled system to the vicinity of areas that are consistently sampled by fisheries-independent surveys and/or fisheries.

In the different OSMOSE applications, the distribution maps of plankton and benthos groups—which serve as potential additional food in OSMOSE—(1) emerge from simulations with a spatially-explicit biogeochemical model, when OSMOSE is coupled to such a model (plankton groups in Travers-Trolet et al. 2014); (2) are generated directly from maps of chlorophyll-*a* concentration obtained from remote-sensing derived time series (phytoplankton groups in Marzloff et al. 2009); (3) are produced from an extrapolation of acoustic survey data (zooplankton groups in Marzloff et al. 2009); or (4) are pseudo maps where biomass density is uniform over space, when no information is available (e.g., plankton groups in Fu et al. 2013).

The OSMOSE-WFS Model.—OSMOSE-WFS is a model with a monthly time step simulating dynamics on the West Florida Shelf in the 2000s (Fig. 2; Grüss et al. 2015, 2016). OSMOSE-WFS explicitly considers 10 fish groups and two invertebrate groups (Table 1, Online Appendix 1). OSMOSE-WFS is also forced by the biomass of two phytoplankton, two zooplankton, and five low-trophic level benthic groups.

Grüss et al. (2014) devised a methodology similar to that of Drexler and Ainsworth (2013) to generate seasonal density maps for the functional groups and life stages explicitly considered in OSMOSE-WFS. Grüss et al. (2014)'s methodology consists of

fitting delta GAMs relating the abundance of a functional group/life stage to long-term environmental data (sediment type, bottom depth, bottom temperature, bottom dissolved oxygen, and chlorophyll-*a*). Delta GAMs result from the fitting of two independent models, a binomial GAM fitted to presence/absence data and a quasi-Poisson GAM fitted to non-zero abundance data, allowing predictions to be combined using the delta method (Lo et al. 1992) to yield spatial abundance estimates. To fit GAMs, Grüss et al. (2014) utilized: (1) one longline data set for older juvenile and adult red groupers and older juvenile gag grouper; (2) one video data set for adult gag grouper; and (3) one trawl data set for all the other functional groups and life stages explicitly considered in OSMOSE-WFS, except younger juveniles of red and gag groupers (Fig. 4C, Online Table 2, Online Appendix 1). Delta models were chosen due to the zero-inflated observations in survey data sets; they were preferred to negative binomial GAMs that require a considerable computation time (Grüss et al. 2014).

The GAM framework designed in Grüss et al. (2014) represents a substantial improvement over the methodologies that have been traditionally employed to construct distribution maps for OSMOSE models. However, it suffers from the same flaws as Drexler and Ainsworth (2013)'s GAM framework; namely: (1) it uses a single fisheries-independent survey data set to generate a density map for a given functional group, such that a limited number of non-zero data points is available to fit quasi-Poisson GAMs for some functional groups and life stages; (2) it relies on longline, video, or trawl data sets, which are not ideal to map the spatial distributions of some functional groups; and (3) it takes into consideration the same set of environmental predictors for all the functional groups and life stages represented in OSMOSE-WFS.

The distribution maps of plankton and low-trophic level benthic groups provided to the OSMOSE-WFS model were constructed based on simple assumptions due to a lack of spatio-temporal empirical estimates of plankton and benthos biomass for the West Florida Shelf (Grüss et al. 2015). Distribution maps for phytoplankton groups were produced for OSMOSE-WFS from monthly maps of chlorophyll-*a* concentration constructed from SeaWiFS (Sea-viewing Wide Field-of-view Sensor) measurements. In the absence of detailed spatial information for the zooplankton and low-trophic level benthic groups, a uniform distribution over the entire West Florida Shelf was assumed for the different months of the year. The simple distribution maps generated for plankton groups by Grüss et al. (2015) allow for very limited spatio-temporal variability in plankton biomasses in OSMOSE-WFS compared to reality. This prevents OSMOSE-WFS from satisfactorily simulating patterns of spatial overlap between HTL groups and plankton groups (Grüss et al. 2015).

SPATIAL ALLOCATION OF FUNCTIONAL GROUP BIOMASSES: ONGOING IMPROVEMENTS TO THE SPATIAL ALLOCATION OF THE BIOMASSES OF NON-PLANKTONIC FUNCTIONAL GROUPS

Over recent years, there has been considerable effort to improve the spatial allocation of the biomasses of non-planktonic functional groups in the WFS Reef fish Ecospace, Atlantis-GOM, and OSMOSE-WFS models. This has largely involved GAMs, which are useful to define non-linear relationships between marine organisms and their environment, and to create objective distribution maps spanning both sampled and unsampled areas for Atlantis-GOM and OSMOSE-WFS (though

within reasonable longitude, latitude and bottom depth limits for each functional group/life stage). However, current GAM methodologies need to be enhanced to: (1) significantly increase the number of data points used to fit GAMs; (2) utilize appropriate research survey data sets for the different functional groups and life stages represented in ecosystem models; and (3) consider a set of environmental predictors known to influence the spatial distributions of the functional groups/life stages under consideration.

To tackle the three issues mentioned above, a project has been initiated in the GOM to address the following (Fig. 5):

1. Foster interactions between ecosystem modelers, empiricists, and fishers to be able to optimize the quantity and quality of data and information used to fit GAMs.
2. Blend all available fisheries-independent and fisheries-dependent survey data of the GOM to obtain a large database (referred to as the “comprehensive survey database”).
3. Use the insights contributed by empiricists and fishers, and review the literature to determine pertinent environmental predictors for the different functional groups and life stages represented in WFS Reef fish Ecospace, Atlantis-GOM, and OSMOSE-WFS.
4. Fit GAMs for the different functional groups and life stages represented in the three ecosystem models using the comprehensive survey database and pertinent environmental predictors.
5. Employ fitted binomial GAMs to parameterize WFS Reef fish Ecospace’s habitat capacity model, and to predict the spatial patterns of probability of presence of functional groups and life stages in the GOM to be able to generate distribution maps for Atlantis-GOM and OSMOSE-WFS.

The project initiated in the GOM does not currently involve any Mexican or Cuban representatives. However, in the future, the project will be expanded to include Mexico and Cuba.

FOSTERING COMMUNICATION BETWEEN ECOSYSTEM MODELERS, EMPIRICISTS, AND FISHERS

A strong collaboration between ecosystem modelers and fishers greatly contributes to the success of the ecosystem modeling efforts, as demonstrated, for example, by the Atlantis experience in Southeast Australia (Fulton et al. 2007, 2014). The “Gulf of Mexico Ecosystem Modeling workshop” or “GOMEMOw” took place on January 15, 2016, at the Rosenstiel School of Marine & Atmospheric Science in Miami, Florida. This event gathered ecosystem modelers, empiricists, non-governmental employees, and fishers of the GOM. GOMEMOw provided ecosystem modelers a comprehensive idea of the diversity of fisheries-independent and fisheries-dependent survey data available in the GOM (Online Table 2), and how these data are collected and analyzed. The workshop also helped empiricists and fishing industry representatives understand how Ecospace, Atlantis and OSMOSE models operate, and how these models use survey data and products derived from them. Finally, the structure and assumptions of GAMs to be fitted to survey data to parameterize WFS Reef fish

Figure 5. Schematic diagram of ongoing efforts to improve the spatial allocation of the biomasses of non-planktonic functional groups in spatially-explicit models of the Gulf of Mexico (GOM).

Ecospace's habitat capacity model and produce distribution maps for Atlantis-GOM and OSMOSE-WFS were scrutinized and discussed.

After GOMEMOW, the vested community that attended the workshop has been in continued communication. This communication is particularly useful to ensure that the critical influence of some environmental factors on the probability of presence of functional groups is not overlooked in the GAMs to be fitted to survey data. This communication is also facilitating the compilation of the "comprehensive survey database" for the GOM (see next subsection).

COMPILING A COMPREHENSIVE SURVEY DATABASE FOR THE GOM AND A LARGE DATABASE OF ENVIRONMENTAL PARAMETERS

The rationale behind the construction of the comprehensive survey database is to be able to utilize a maximum number of data points to fit the response of functional groups to environmental factors (Farmer and Karnauskas 2013, Sagarese et al. 2014). Fitting responses to environmental factors to a maximum amount of data will optimize the predictive power of GAMs (Wood 2006). Also, blending all available fisheries-independent and fisheries-dependent survey data of the GOM into a single database will allow the parameterization of WFS Reef fish Ecospace's habitat capacity model and the production of distribution maps for Atlantis-GOM and OSMOSE-WFS for functional groups and life stages for which this was not possible before (e.g., younger juvenile gag grouper).

The insights contributed by empiricists and fishers regarding environmental influences on the spatial distributions of marine organisms and a thorough review of the literature are allowing the development of a large database of environmental

parameters to be considered when fitting GAMs. Using a specific set of environmental predictors for each of the different functional groups and life stages considered in WFS Reef fish Ecospace, Atlantis-GOM, and OSMOSE-WFS provide greater realism in the distribution maps and habitat capacity models constructed for these ecosystem models.

FITTING GAMs USING THE COMPREHENSIVE SURVEY DATABASE AND PERTINENT ENVIRONMENTAL PREDICTORS

Relying on the comprehensive survey database imposes constraints on the type of GAMs to be used to relate abundances to environmental factors. Negative binomial or delta GAMs are not applicable in this context, because the different fisheries-dependent and fisheries-independent surveys that are conducted in the GOM use disparate sampling procedures and gears (Online Table 2). Binomial GAMs relying on presence/absence data were found to be more appropriate through discussions at GOMEMOW, as long as they integrate the confounding factors of “gear” and year (Online Appendix 2; Farmer and Karnauskas 2013, Sagarese et al. 2014). The use of binomial GAMs entails that the distribution maps for Atlantis-GOM and OSMOSE-WFS will be constructed from predictions of probability of presence rather than from biomass or abundance predictions, as is often done in other mapping literature (Maxwell et al. 2009, Hattab et al. 2013, Cormon et al. 2014, Sagarese et al. 2014).

PARAMETERIZING WFS REEF FISH ECOSPACE’S HABITAT CAPACITY MODEL AND PRODUCING DISTRIBUTION MAPS FOR ATLANTIS-GOM AND OSMOSE-WFS

With respect to WFS Reef fish Ecospace, for each of the functional groups and stanzas represented in the model, the fits of binomial GAMs will define an individual function for each environmental map layer in Ecospace’s habitat capacity model.

With respect to Atlantis-GOM and OSMOSE-WFS, fitted binomial GAMs will be used to predict probabilities of presence over the entire West Florida Shelf (OSMOSE-WFS) and the entire GOM (Atlantis-GOM) including areas where biomass survey estimates do not exist, though within reasonable longitude, latitude, and bottom depth limits for each functional group and life stage [based on the ecological literature, FishBase/SeaLifeBase, and the BioGoMx information system (Moretzsohn et al. 2016)]. The probability of presence predicted by binomial GAMs will be averaged over the extent of each Atlantis-GOM spatial polygon and according to the OSMOSE-WFS grid cells (Fig. 2) to obtain distribution maps for input into Atlantis and OSMOSE-WFS.

IMPROVING THE SPATIAL ALLOCATION OF PLANKTONIC GROUP BIOMASSES

The current distribution maps of plankton groups that are provided to OSMOSE-WFS only allow for very limited spatio-temporal variability in plankton biomasses and thus need to be improved. High spatio-temporal variability in plankton biomasses is less of a concern in WFS Reef fish Ecospace, because the model is provided with MODIS chlorophyll-*a* time series maps through Ecospace’s spatial-temporal data framework, which drive the spatial allocation of phytoplankton P/B. MODIS chlorophyll-*a* time series are also used to generate distribution maps for the phytoplankton

Figure 6. Diagrammatic representation of the Adaptive Ecosystem Climatology (AEC) developed for the Gulf of Mexico.

groups represented in Atlantis-GOM. However, remote-sensing derived data usually do not offer a satisfactory spatial coverage of some areas of the GOM, due to clouds, near-coast land/bottom contamination, and sensor failures (Cannizzaro et al. 2013).

To address the abovementioned issues, ecosystem models of the GOM are benefiting from the development of a comprehensive “Adaptive Ecosystem Climatology” (AEC) for the GOM (Adaptive Ecosystem Climatology 2016). AEC was initiated because climatologies, remote-sensing observations, and biogeochemical models all have inherent limitations and errors (Kantha and Clayson 2000, Cannizzaro et al. 2013). AEC melds satellite data, in situ data, and output from a data assimilative, coupled physical-biogeochemical model (NCOM-CoSiNE; de Rada et al. 2009) for the period 1980–2012. AEC mitigates the shortcomings of these individual components and combines their strengths to enhance ecosystem models and other tools of the GOM (Fig. 6). Ocean properties available from the coupled model and satellite imagery include physical oceanographic and primary ecosystem components. AEC starts with a three-dimensional, dynamically balanced, gridded, static climatology for each calendar day. Using this static climatology as a background “first guess,” recent ocean observations (satellite or in situ) are assimilated to adjust the climatology toward conditions at the time of interest, to provide updated, representative fields (adaptive climatology).

Monthly distribution maps are currently being produced for the plankton groups considered in OSMOSE-WFS through the use of AEC. This endeavor involves: (1) constructing monthly maps of plankton concentration from estimates of the NCOC-CoSiNE model; (2) correcting for biases in the absolute values of plankton concentration predicted by NCOC-CoSiNE from the estimates of primary production and grazing loss (in mass units) provided in the output of CoSiNE; (3) blending the resulting spatial estimates of plankton concentration with ocean observations (satellite and in situ data) available through AEC, using objective analysis and optimum interpolation (Gandin 1963, Bretherton et al. 1976); and (4) vertically integrating the resulting spatial estimates of plankton concentration and transforming them into spatial estimates of plankton biomass to be used in OSMOSE-WFS (Online Appendix 3).

The in situ measurements, satellite chlorophyll-*a*, and temperature fields available through AEC are also being melded to produce vertically integrated fields of chlorophyll-*a* for both the inshore and offshore regions of the GOM. Enhanced maps of chlorophyll-*a* will be provided to WFS Reef fish Ecospace's spatial-temporal data framework to drive phytoplankton P/B, and will be employed to construct distribution maps for the Atlantis-GOM's phytoplankton groups. These efforts will improve the spatio-temporal dynamics of phytoplankton simulated in WFS Reef fish Ecospace and Atlantis-GOM and, therefore, the patterns of spatial overlap between phytoplankton groups and their predators simulated in each model.

DISCUSSION

Patterns of spatial overlap between predators, prey, and competitors have a critical influence on the trophic interactions simulated by spatially-explicit ecosystem models (Plaganyi 2007, Shin et al. 2010). Therefore, significant attention must be paid to the spatial allocation of functional group biomasses in spatially-explicit models. In recent years, substantial progress has been made in the GOM on this topic; a habitat capacity model and a spatial-temporal data framework have been introduced in the WFS Reef fish Ecospace model, while GAM methodologies have been designed to produce reliable distribution maps for the Atlantis-GOM and OSMOSE-WFS models. WFS Reef fish Ecospace's habitat capacity model relies on functional relationships between marine organisms and their abiotic environment, which can be defined using GAMs. Nevertheless, further progress is underway. Ongoing efforts include the development of a sophisticated GAM framework integrating all available fisheries-independent and fisheries-dependent survey data of the GOM and carefully chosen environmental predictors. Ongoing efforts also include the construction of accurate fields of chlorophyll-*a* and plankton biomasses for WFS Reef fish Ecospace, Atlantis-GOM, and OSMOSE-WFS, employing a recently developed AEC of the GOM.

All the improvements underway in the GOM rely on the blending of data from very different sources. Numerous fisheries surveys and ocean observations take place in the GOM and are useful to get insights into specific issues. For example, benthic trawl surveys provide a clear picture of the spatial distributions of shrimp species and of other species that are susceptible to bottom trawl gears, unlike most pelagic species (GSFMC 2011, SEDAR 2011). MODIS and SeaWiFS satellite data offer a highly satisfactory coverage of the offshore waters of the GOM, but not of some coastal areas of the region due to clouds, near-coast land/bottom contamination, and sensor failures (Cannizzaro et al. 2013). Thus, each of the fisheries surveys and ocean observations conducted in the GOM taken individually has limitations and flaws and, therefore, limited value to inform EBFM, which needs a comprehensive understanding of the ecology of the different functional groups of the GOM and of the abiotic environment (Bjorndal et al. 2011, Karnauskas et al. 2013, NOAA 2015). It is critical that fisheries scientists and oceanographers of the GOM work more closely together to integrate their knowledge and data (Schirripa et al. 2012, Yáñez-Arancibia et al. 2013, NOAA 2015). Blending all available fisheries-independent and fisheries-dependent survey data sets into one comprehensive database, and melding all available ocean observations and outputs from a biogeochemical model to produce fields of chlorophyll-*a* and plankton biomasses, represent concrete and valuable examples of integrated ecosystem research.

Beyond the technical aspects of enhanced collaboration between ecosystem modelers, empiricists, and oceanographers of the GOM, improved communication among scientists and fishers is essential. Exchanges between ecosystem modelers, empiricists, and fishers are facilitating the compilation of the comprehensive survey database and of a large database of environmental variables for the GOM. They are also ensuring that the critical influence of some environmental factors on the probability of presence of functional groups will not be overlooked in GAMs.

In the present study, we focused on the WFS Reef fish Ecospace, Atlantis-GOM, and OSMOSE-WFS models, which are the spatially-explicit ecosystem models that are intended to inform stock assessments, EBFM, and restoration decisions related to EBFM in the GOM. However, the issues that were reviewed here are relevant to any spatially-explicit ecosystem model. The GAM framework using the comprehensive survey database and the AEC framework described here, which were designed to serve the WFS Reef fish Ecospace, Atlantis-GOM, and OSMOSE-WFS models, could also benefit other spatially-explicit models of the GOM.

In the present study, we focused on the parameterization of habitat capacity maps in Ecospace and the construction of distribution maps for Atlantis and OSMOSE, while trophic interactions in spatially-explicit ecosystem models also strongly depend on parameters conditioning diet preferences, predator, and prey behavior and prey vulnerability, and on movement parameters (Fig. 1; Plaganyi 2007, Shin et al. 2010). Furthermore, spatially-explicit ecosystem models, especially highly-sophisticated models such as Atlantis models, rely on hundreds of parameters and data inputs, of which many have a large impact on model predictions (Fulton et al. 2007, Shin et al. 2010, Walters et al. 2010, Steele et al. 2013). A substantial number of spatially-explicit ecosystem models have already been developed in the GOM, and considerable effort has been expended to improve the structure and assumptions of these models. Therefore, it may now be time to focus resources on enhancing the different types of inputs provided to spatially-explicit ecosystem models of the GOM, in the spirit of the present study.

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