Improving the spatial allocation of marine mammal and sea turtle biomasses in spatially explicit ecosystem models

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ABSTRACT: Ecosystem-based fisheries management (EBFM) is gaining traction worldwide, including in the Gulf of Mexico (GOM). Ecosystem models, such as applications of the Atlantis and Ecospace modeling approaches, are key tools for assisting EBFM. Patterns of spatial overlap between exploited fish species, other species of concern such as marine mammals and sea turtles, and human activities can have a large influence on the predictions made by ecosystem models, but these patterns are usually not well defined. We developed methods for producing distribution maps for the cetacean, sirenian, and sea turtle groups represented in the Atlantis model of the GOM, and employed a method, initially designed for fish and invertebrates, for generating preference functions for the dolphin species represented in the Ecospace model of the West Florida Shelf. Preference functions specify the preferences of species for certain environmental conditions and are used by Ecospace to allocate species biomasses in space. We also took advantage of our mapping outputs to estimate the percentage of spatial overlap between the hotspots of cetaceans and sea turtles in the US GOM and their areas of bycatch in the US pelagic longline fishery. The present study provides new insights into the spatial distribution patterns of marine mammals and sea turtles in the GOM large marine ecosystem, including the first quantitatively supported maps of Florida manatee (sirenian) distribution along the entire US GOM coast. Efforts such as ours should be continued for improving the reliability of ecosystem models and, thereby, advancing EBFM worldwide.

KEY WORDS: Distribution maps · Preference functions · Ecosystem models · Cetaceans · Florida manatee · Sea turtles · Gulf of Mexico · Ecosystem-based fisheries management

INTRODUCTION

Ecosystem-based fisheries management (EBFM), which considers trophic dynamics, interactions between marine species and human activities, and environmental influences on species ecology, is gaining traction worldwide, including in the Gulf of Mexico (GOM) large marine ecosystem (LME) (Fig. 1) (Patrick & Link 2015, Grüss et al. 2017, Harvey et al. 2017). In the GOM, EBFM efforts include plans to mitigate bycatch in commercial fisheries such as the shrimp trawl and pelagic longline fisheries, measures
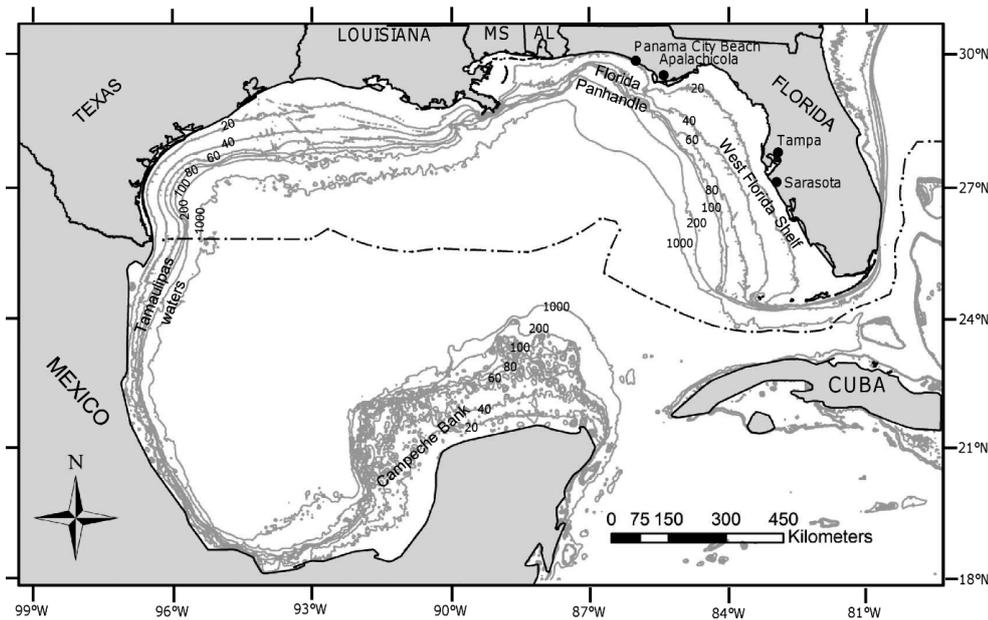
Fig. 1. Gulf of Mexico large marine ecosystem. Depth contours are labeled at 20, 40, 60, 80, 100, 200, and 1000 m. Important features are labeled and include the Campeche Bank, Tamaulipas waters, the Florida Panhandle, and the West Florida Shelf. MS: Mississippi; AL: Alabama. Black dashed-dotted line: US exclusive economic zone

to mitigate the lionfish (*Pterois* spp.) invasion, and strategies for developing marine protected areas (MPAs) (Grüss et al. 2017). Ecosystem modeling platforms are key tools for assisting EBFM, due to their ability to simulate the impacts of anthropogenic and environmental stressors and resource management for multiple ecosystem components at multiple temporal and spatial scales (Christensen & Walters 2011, Collie et al. 2016). There now exists a wide variety of ecosystem modeling frameworks, ranging from simple extended single-species models to complex trophodynamic and biogeochemical-based end-to-end modeling platforms (see Plagányi 2007 and O'Farrell et al. 2017 for a review).

The trophodynamic Ecopath with Ecosim (EwE) with Ecospace approach (Walters et al. 1999, Coll et al. 2015, Colléter et al. 2015) and the biogeochemical-based end-to-end Atlantis approach (Fulton et al. 2011, Weijerman et al. 2016) are among the most frequently used ecosystem modeling platforms. Both EwE with Ecospace and Atlantis represent all marine organisms, from bacteria and primary producers to apex predators. The Ecopath component of EwE is a static mass-balance description of a food web that provides initial conditions for dynamic modeling, including steady-state biomasses per km^2 (Christensen & Pauly 1992, Christensen & Walters 2004). The Ecosim component simulates the dynamics of the marine ecosystem of interest at monthly time steps by altering fishing effort, fishing mortality, and environmental forcing functions (Walters et al. 1997, 2000). Finally, Ecospace replicates Ecosim dynamics over a 2-dimensional domain and simulates dispersal,

migration, ontogenetic habitat shift, and advection patterns, while also representing trophic interactions and spatio-temporal changes in fishing effort (Walters et al. 1999, 2010). By contrast, Atlantis takes a biogeochemical approach, and employs irregular 3-dimensional polygons to characterize biogeography and a detailed biological sub-model to simulate the spatio-temporal dynamics of animal abundances and biomasses as well as nutrient, detritus, and bacteria cycles (Fulton et al. 2004, 2007, 2011). The sophistication of EwE with Ecospace and Atlantis allows these modeling approaches to tackle a wide number of EBFM issues, including MPA effectiveness (e.g. Salomon et al. 2002, Martell et al. 2005, Savina et al. 2013, Olsen et al. 2018), the consequences of bycatch reduction measures (e.g. Fulton et al. 2007, Walters et al. 2010, Morzaria-Luna et al. 2012, 2013), and management strategy evaluations integrating ecosystem considerations (e.g. Fulton et al. 2014, Masi et al. 2018).

The sophistication of EwE with Ecospace and Atlantis, however, also demands a very large number of inputs, which are not necessarily readily available for all the studied marine organisms (Grüss et al. 2016). For example, to allocate species biomasses over space and simulate spatial overlap among marine organisms, their prey, their predators, and human activities, Ecospace must be given preference functions that specify the preferences of species groups for certain environmental conditions (Christensen et al. 2014). These preference functions are then combined with spatio-temporal environmental data in a calculation of species group spatial distributions by
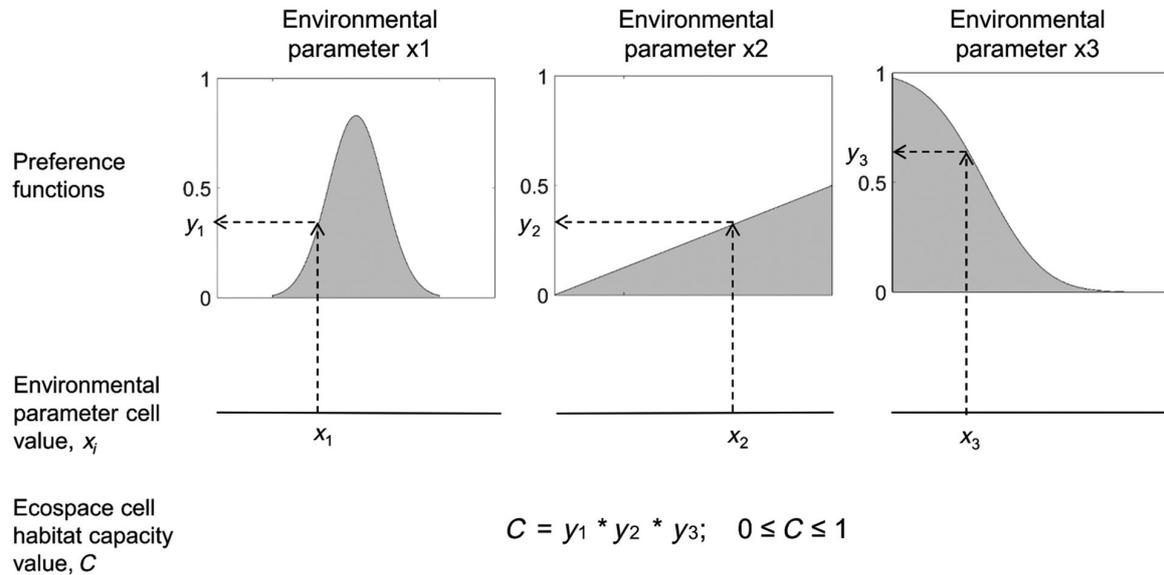
Fig. 2. Habitat capacity computations in the Ecospace modeling platform. During model run, spatial estimates of environmental parameters are read from data layers for each monthly time step, and the habitat capacity in each cell of the Ecospace model is computed as the product of preferences for the environmental parameter values. The preference functions used in Ecospace's habitat capacity model are calculated beforehand from the predictions of generalized additive models integrating environmental covariates in the original scale (i.e. not in the link scale), as described in detail in the main text. Figure inspired by Christensen et al. (2014) and Grüss et al. (2016)

Ecospace's habitat capacity model (Fig. 2) (Christensen et al. 2014, Grüss et al. 2016). To fulfill the same capacity, Atlantis must be directly provided with distribution maps that specify the annual or seasonal distribution of species groups in the horizontal plane (Drexler & Ainsworth 2013, Grüss et al. 2014).

In the GOM, a methodology was recently proposed and applied to produce distribution maps and preference functions in bulk for the Atlantis model of the GOM, called 'Atlantis-GOM', which has a very coarse spatial resolution, and the Ecospace model of the West Florida Shelf (WFS), called 'WFS Reef fish Ecospace', which has a much finer spatial resolution (see Fig. 3) (Grüss et al. 2016). This methodology consists of (1) compiling a large monitoring database by gathering all fisheries-independent data collected using random-station designs, and fisheries-dependent data obtained by randomly sampling fisheries operations in the US GOM; (2) fitting statistical habitat models, including generalized additive models (GAMs), to this large monitoring database; and (3) employing the fitted statistical habitat models to generate distribution maps and preference functions (Grüss et al. 2018a,b,c). However, the large monitoring database compiled for the US GOM includes only limited data for marine mammals and sea turtles; thus, distribution maps and preference functions for marine mammals and sea turtles could not be produced for Atlantis and Ecospace. Nevertheless, producing reli-

able distribution maps and preference functions for marine mammals and sea turtles for Atlantis and Ecospace remains a priority, because the patterns of spatial overlap among marine mammals and sea turtles and exploited fish species and human activities (e.g. fishing) can have a large influence on the predictions made by Atlantis and Ecospace for assisting EBFM (e.g. when evaluating the performance of bycatch mitigation measures).

The Atlantis-GOM model represents 3 cetacean groups (dolphins, Odontoceti, and Mysticeti), 1 sirenian group (manatee) and 3 sea turtle groups (loggerhead, Kemp's ridley and leatherback sea turtles), while the WFS Reef fish Ecospace model represents only one cetacean species (common bottlenose dolphin *Tursiops truncatus*) (see Table 1). In the GOM, several cetacean line-transect shipboard and aerial monitoring programs have been implemented, which provide density estimates for cetaceans (reviewed in Roberts et al. 2016). A blending of these data was used in Roberts et al. (2016) and Mannocci et al. (2017) to develop Tweedie GAMs for the US GOM and the GOM LME, respectively; these Tweedie GAMs model species absolute density (individuals per unit area) as a function of environmental parameters. The predictions made by these GAMs are available to generate distribution maps for the cetacean groups represented in Atlantis-GOM and preference functions for common bottlenose dolphin

for WFS Reef fish Ecospace. Presence-only data are available for sea turtle species for the entire GOM LME from the Ocean Biogeographic Information System (OBIS) (OBIS 2017). MaxEnt is a statistical approach frequently employed for modeling species distributions from presence-only and environmental data (Phillips et al. 2006, 2017), which is appropriate to employ with the OBIS sea turtle data for the GOM LME; then, MaxEnt predictions can be used to construct distribution maps for the sea turtle groups represented in Atlantis-GOM. Finally, presence-only data are also collected for manatees, via an ensemble of aerial surveys in WFS waters in winter only (Martin et al. 2015), and via other ways (e.g. citizen scientists) in the other US GOM States all year round (Fertl et al. 2005, Carmichael et al. 2017, Hieb et al. 2017). Manatees undertake extensive migrations in spring and fall (Irvine & Campbell 1978, Laist & Reynolds 2005, Laist et al. 2013); therefore, the Atlantis-GOM ecosystem model must be provided with seasonal distribution maps for that group. Given the complex nature of the presence-only data available for the manatee (particularly the fact that data are available for the WFS only for the winter season) and the very coarse resolution of the Atlantis-GOM ecosystem model, it is reasonable to base the production of seasonal distribution maps for the manatee for Atlantis-GOM on rules of thumb rather than a statistical method.

In this study, we present the 3 methods we developed for constructing distribution maps for the cetacean, sirenian, and sea turtle groups represented in the Atlantis-GOM model, and we employ another method initially designed for fish and invertebrates (Grüss et al. 2018a) for generating preference functions for the common bottlenose dolphin for the WFS Reef fish Ecospace model. The first method we developed was for the 3 cetacean groups represented in Atlantis-GOM and relied on the GAMs fitted in Roberts et al. (2016) and Mannocci et al. (2017). The second method we developed was for the manatee and relied on sighting records and results from previous studies. The seasonal distribution maps generated using the second method are the first quantitatively supported maps of Florida manatee distribution along the entire US GOM. Finally, the third method we developed was for the 3 sea turtle groups represented in Atlantis-GOM and consisted of fitting MaxEnt models to presence-only data from OBIS and environmental data. As an example management application, we also used the results for some cetaceans and sea turtles to estimate the percentage of spatial overlap between the hotspots of these marine organisms in the US GOM and their areas of bycatch in the US pelagic longline fishery.

MATERIALS AND METHODS

Study ecosystem models and species

The GOM is one of the world's 64 LMEs, bordered by Mexico, Cuba, and the US (Fig. 1). The spatial domain of the Atlantis-GOM model (Ainsworth et al. 2015) covers the entire GOM LME (Fig. 3a), and is made of 63 irregular polygons and 2 'boundary poly-
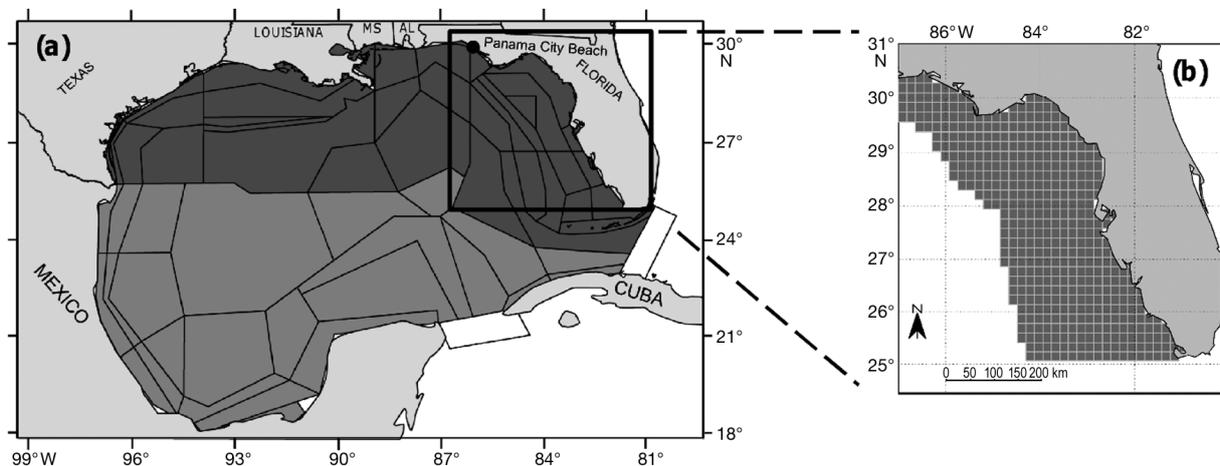

Fig. 3. Spatial domains of the ecosystem models considered in this study. (a) Spatial polygons of the Atlantis model of the Gulf of Mexico (GOM) referred to as 'Atlantis-GOM'. Dark gray shading: Atlantis-GOM polygons in the US GOM; lighter gray: polygons located outside the US GOM (i.e. in the Mexican or Cuban GOM or in international waters). The 2 'boundary polygons' of Atlantis-GOM, which do not interact with the rest of the model, are filled in white. MS: Mississippi; AL: Alabama. (b) Spatial cells of the Ecospace model of the West Florida Shelf referred to as 'WFS Reef fish Ecospace' (filled in dark grey)

Table 1. Marine mammal and sea turtle groups and species explicitly considered in the Atlantis-Gulf of Mexico (GOM) ecosystem model

Species group	Species making up the group
Dolphins	Common bottlenose dolphin *Tursiops truncatus*, Atlantic spotted dolphin *Stenella frontalis*, Clymene dolphin *Stenella clymene*, Fraser's dolphin *Lagenodelphis hosei*, pantropical spotted dolphin *Stenella attenuata*, rough-toothed dolphin *Steno bredanensis*, spinner dolphin *Stenella longirostris*, striped dolphin *Stenella coeruleoalba,* false killer whale *Pseudorca crassidens*, killer whale *Orcinus orca*, melon-headed whale *Peponocephala electra*, pygmy killer whale *Feresa attenuata*, Risso's dolphin *Grampus griseus*, short-finned pilot whale *Globicephala macrorhynchus*
Odontoceti	Blainville's beaked whale *Mesoplodon densirostris*, Cuvier's beaked whale *Ziphius cavirostris*, Garvais' beaked whale *Mesoplodon europaeus*, dwarf sperm whale *Kogia sima*, pygmy sperm whale *Kogia breviceps*, sperm whale *Physeter macrocephalus*
Mysticeti	Bryde's whale *Balaenoptera edeni*, fin whale *Balaenoptera physalus*
Manatee	West Indian manatee, Florida subspecies *Trichechus manatus latirostris*
Loggerhead sea turtle	Loggerhead sea turtle *Caretta caretta*
Kemp's ridley sea turtle	Kemp's ridley sea turtle *Lepidochelys kempii*
Leatherback sea turtle	Leatherback sea turtle *Dermochelys coriacea*

gons' that do not interact with the rest of the Atlantis-GOM model (Fig. 3a). In total, 91 species groups are explicitly considered in Atlantis-GOM, including the 3 cetacean groups (dolphins, Odontoceti and Mysticeti), the sirenian group (manatee) and the 3 sea turtle groups (loggerhead, Kemp's ridley and leatherback sea turtles) considered in this study (Table 1). The dolphin group comprises 14 species, the Odontoceti group 6 species, and the Mysticeti group 2 species (Table 1).

The spatial domain of the WFS Reef fish Ecospace model covers the entire WFS region excluding the Florida Keys, has a spatial resolution of 20 km (Fig. 3b; Chagaris 2013), and is made of 465 regular cells (Fig. 3b). A total of 71 species groups are explicitly considered in WFS Reef fish Ecospace, including the dolphin species considered in this study (common bottlenose dolphin). Henceforth, we refer to the common bottlenose dolphin as 'dolphin'.

Distribution maps for Atlantis-GOM

Cetaceans

The habitat-based density models developed and validated in Roberts et al. (2016) and Mannocci et al. (2017) that we employed in this study actually combine a detection function, which models the probability of detecting a species from an observation platform given that it is present, with a Tweedie GAM, which models species absolute density as a function of environmental parameters. For each of the 22 species making up the cetacean groups represented in Atlantis-GOM (as well as for other cetacean species), Roberts et al. (2016) and Mannocci et al. (2017) fitted habitat-based density models to the aggregation of 6 systematic line-transect shipboard and aerial monitoring data sets and a set of pertinent environmental data. Through the use of detection functions, where possible, the models of Roberts et al. (2016) and Mannocci et al. (2017) corrected for availability bias (the chance that animals would be missed because they were submerged) and perception bias (the chance that animals at the surface would be missed despite being present directly along the survey trackline, e.g. because of small size or cryptic behaviors). Roberts et al. (2016) developed models for the US Atlantic and GOM regions, which were both entirely covered by shipboard and aerial monitoring data. Mannocci et al. (2017) needed to map the spatial distributions of cetacean species in a large region of the western North Atlantic (including the GOM LME) that was not entirely covered by cetacean monitoring programs. Faced with this extrapolation problem, Mannocci et al. (2017) developed models that were more general than those of Roberts et al. (2016); Mannocci et al. (2017)'s models integrated only a few environmental parameters and smooth relationships between environmental parameters and cetacean density.

To generate distribution maps usable in Atlantis-GOM for dolphins, Odontoceti, and Mysticeti, we proceeded in 3 steps. First, for each of the species belonging to the 3 cetacean groups, we constructed annual density maps with a 20 km resolution for the GOM LME (Fig. 4a), using the annual density surfaces predicted from Roberts et al. (2016)'s models within the extent of the area where cetacean moni-
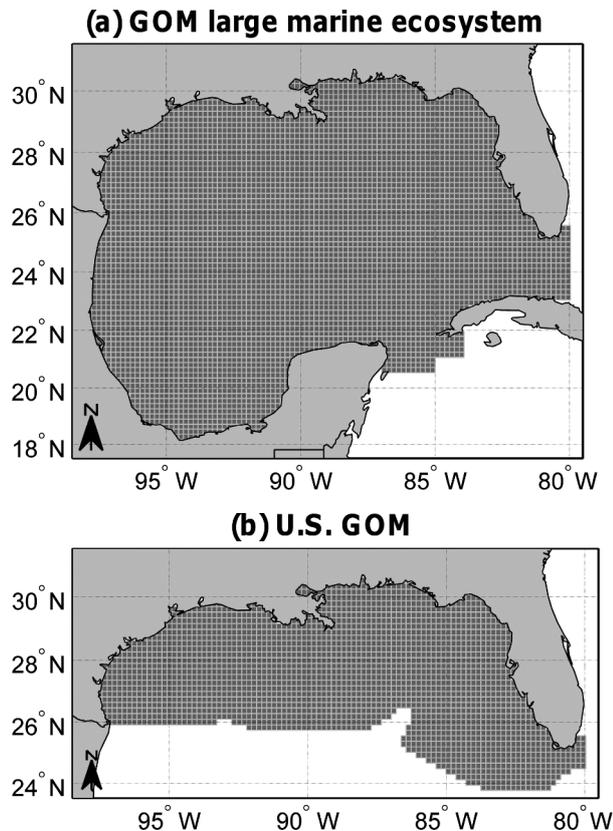
(a) GOM large marine ecosystem

(b) U.S. GOM

Fig. 4. Spatial grids used to produce distribution maps for the present study. (a) 20 × 20 km grid for the Gulf of Mexico (GOM) large marine ecosystem; (b) 20 × 20 km grid for the US GOM

toring programs were conducted (i.e. the US GOM), and the annual density surfaces predicted from Mannocci et al. (2017)'s models outside of the monitored area where extrapolation is required (i.e. the rest of the GOM LME). Second, we added together the annual density maps for the 22 individual cetacean species to obtain density maps for the 3 cetacean groups. For example, we added together the density maps for Bryde's whale *Balaenoptera edeni* and fin whale *Balaenoptera physalus* to arrive at a density map for Mysticeti. Third, to obtain distribution maps for dolphins, Odontoceti, and Mysticeti usable in Atlantis-GOM, we averaged the densities from the 20 × 20 km density maps over the extent of each Atlantis-GOM polygon and rescaled the resulting estimates into relative abundances such that the sum of relative abundances was equal to 1.0.

Manatee

In the US, manatees occur in greatest numbers year-round in Florida, but are also found in the other GOM States (Alabama, Mississippi, Louisiana, and Texas; Fertl et al. 2005, Deutsch et al. 2008, Pabody et al. 2009, Hieb et al. 2017). The manatee population of the Mexican and Cuban GOM is negligible compared to that of the US GOM (Deutsch et al. 2008, Alvarez-Alemán et al. 2010). During winter months, manatees aggregate in Florida waters where they typically remain within 30 km of warm-water refuges (e.g. warm-water natural springs, coastal power plants, boat basins; Irvine & Campbell 1978, Laist & Reynolds 2005, Laist et al. 2013). In this study, we relied on the 2 sources providing sighting data for manatees for the US GOM: (1) the Manatee Synoptic Surveys, an ensemble of aerial surveys which was initiated in 1991 and is conducted in Florida during winter months every year (Martin et al. 2015); and (2) the sighting records for all US GOM states compiled in Fertl et al. (2005), Carmichael et al. (2017) and Hieb et al. (2017), which come from many resources (other than the Manatee Synoptic Surveys) and date back to 1912.

To generate distribution maps for the manatee for each season (spring, summer, fall, and winter) that are usable in the Atlantis-GOM ecosystem model, we proceeded in 2 steps. Here, the northeastern GOM refers to the region of West Florida southeast of Panama City Beach and extending to the Florida Keys, and the northwestern GOM refers to the remainder of the US GOM to the west (Fig. 3a).

First, we used the georeferenced sighting records for the period 1991 to 2016 to determine the proportion of the manatee population of the GOM present in the northwestern GOM in each season. To estimate this proportion, we proceeded as follows: (1) for each year of the period 1991 to 2016, we divided the total number of sightings in the northwestern GOM per season by the total number of manatees sighted in West Florida through the Manatee Synoptic Surveys; and (2) computed the mean of the resulting estimates. These calculations are based on the assumption that almost the entire manatee population of the GOM is present in West Florida during the winter months (Martin et al. 2015). The other assumption we made is that each individual manatee sighted in the northwestern GOM represented a unique individual. This assumption is justified by the fact that manatee abundance is low in the northwestern GOM relative to the northeastern GOM all year round (Deutsch et al. 2008, Hieb et al. 2017). Moreover, although it is likely that some encounters in the northwestern GOM represent repeated sightings of the same individuals, this potential source of error is offset by individuals never detected in the northwestern GOM.

Second, we apportioned the manatee population into Atlantis-GOM polygons for each season (Fig. 3a). To do this, we made 2 assumptions: (1) a certain proportion of the manatee population of the GOM was present in the northwestern GOM, based on the estimates produced in Step 1; and (2) the remainder of the manatee population was homogeneously distributed in the 5 Atlantis-GOM polygons located in the coastal northeastern GOM. The second assumption is reasonable given the very low spatial resolution of Atlantis-GOM and the spatial distribution patterns of the manatee in West Florida suggested in previous studies (e.g. Deutsch et al. 2003, USFWS 2007, Martin et al. 2015). Then, for each season, we apportioned all georeferenced sightings for the northwestern GOM for the period 1991 to 2016 for that season to the Atlantis-GOM polygons that contained the data points, using a ray-casting algorithm (Shimrat 1962). Finally, we estimated relative manatee abundance in each Atlantis-GOM polygon, p, of the northwestern GOM in season s ($N_{p,s}$) as follows:

$$N_{p,s} = \frac{S_{p,s}}{\sum_p S_{p,s}} \cdot P_s \qquad (1)$$

where $S_{p,s}$ is the total number of sightings during the period 1991 to 2016 in polygon p and season s (determined by the ray-casting algorithm), and P_s is the proportion of the manatee population of the GOM that is present in the northwestern GOM in season s.

Sea turtles

To construct distribution maps for the 3 sea turtle groups represented in Atlantis-GOM, we developed a MaxEnt model (Phillips et al. 2006) for each of the 3 groups. MaxEnt takes as input presence-only (occurrence) data, as well as an environmental landscape defining the value of environmental predictions over a spatial grid (Phillips et al. 2006, 2017). From the environmental landscape, MaxEnt defines a set of 'background locations', which it then contrasts against the occurrence locations to estimate the spatial distribution of the species under consideration; the presence of the species under consideration is not known at the background locations (Merow et al. 2013, Phillips et al. 2017).

We downloaded occurrence data for loggerhead, Kemp's ridley, and leatherback sea turtles from OBIS (OBIS 2017). OBIS data are primarily based on atlases, aerial surveys, vessel surveys, and satellite telemetry (typically aggregated in 1 × 1° grids). Before fitting MaxEnt models, we cleaned OBIS data;

occurrence data were discarded if they were located entirely over land or outside the GOM LME. After having cleaned the OBIS data, we had a total of 866 data points for the loggerhead sea turtle, 197 data points for Kemp's ridley sea turtle, and 883 data points for the leatherback sea turtle. The sea turtle occurrence data associated with a year of observation span the period 1758 to 2015 for loggerhead, 1913 to 2015 for Kemp's ridley, and 1766 to 2015 for leatherback sea turtles, though the years during which sea turtles were observed are often not provided.

Loggerhead, Kemp's ridley, and leatherback sea turtles are found throughout the GOM LME, and their spatial distribution patterns are influenced by bottom depth, sea surface temperature (SST), surface salinity, and oceanic current speed (Thompson 1984, Ogren 1989, Griffin & Griffin 2003, Luschi et al. 2003, Plotkin 2003, Gaspar et al. 2006, Hawkes et al. 2007, Lambardi et al. 2008, Casale et al. 2009, Howell et al. 2015). Therefore, we provided a 20 × 20 km gridded map of environmental parameters (bottom depth, SST metrics, surface salinity metrics, and oceanic current speed metrics) for the entire GOM LME to MaxEnt.

We produced an annual raster of bottom depth and monthly rasters of SST, surface salinity, and oceanic current speed with a resolution of 20 km for the GOM LME. Regarding bottom depth, we accessed the SRTM30 PLUS global bathymetry grid from the Gulf of Mexico Coastal Observing System (http://gcoos.tamu.edu/), from which we constructed a continuous raster of bathymetry for the GOM LME at a resolution of 20 km. We downloaded Ocean Surface Current Analyses Real-time (OSCAR) third degree resolution ocean surface current data for the period 2005 to 2015 from https://podaac.jpl.nasa.gov/dataset/OSCAR_L4_OC_third-deg and Aqua MODIS monthly 0.0125° SST composites (daytime; 11 microns) for the period 2002 to 2011 from http://coastwatch.pfeg.noaa.gov/erddap/griddap/, from which we estimated, respectively, oceanic current speed and SST in each of the cells of a 20 × 20 km grid covering the entire GOM LME for the different months of the year. For each month, measurements of salinity at the surface for the period 2006 to 2009 for each grid point can be extracted from the National Oceanographic Data Center regional climatology database (Boyer et al. 2009). These measurements are incomplete. Therefore, we subjected surface salinity data to spline interpolation on a 20 × 20 km grid using ArcGIS 10.4 (ESRI) to provide a continuous surface with which to fit MaxEnt models and make predictions with the fitted models. Following Hattab et al. (2014), we

derived 4 metrics from the monthly SST, surface salinity, and oceanic current speed climatologies: annual maximum, annual minimum, annual mean, and annual range (i.e. the difference between annual maximum and annual minimum, which is a proxy for seasonal variation in the parameter of interest).

We fitted MaxEnt models for loggerhead, Kemp's ridley, and leatherback sea turtles using the R package 'dismo' (Hijmans et al. 2015). The MaxEnt models of the 3 sea turtle groups were initially fitted to 13 environmental parameters: bottom depth, the 4 SST metrics, the 4 surface salinity metrics, and the 4 oceanic current speed metrics. If, for a given sea turtle group, some environmental predictors contributed less than 1% of the model fit, those environmental predictors were removed from the MaxEnt model of the group and the model was re-fitted (Maunder & Punt 2004, Lynch et al. 2012); this procedure was repeated until all the environmental parameters integrated in a MaxEnt model contributed to at least 1% of the model fit.

After the individual MaxEnt models for the 3 sea turtle groups were fitted, we validated them using the leave-group-out cross validation procedure (Hastie et al. 2001, Kuhn & Johnson 2013), as implemented in the R package 'dismo' (Hijmans et al. 2015). In this procedure, occurrence data for each sea turtle species were randomly split into training and test data sets, with 80% of the data going to the training data set and the rest of the data to the test data set. MaxEnt models were fitted to the training data set and then evaluated using the test data set. The procedure was repeated 10 times, i.e. 10 MaxEnt models were fitted to training data sets and then evaluated using the test data sets corresponding to the training data sets. The metric employed to evaluate the MaxEnt model of each sea turtle group was the area under the receiver operating characteristic (ROC) curve (the AUC metric), which assesses the ability of MaxEnt to rank a randomly chosen occurrence location higher than a randomly chosen background location (Merow et al. 2013). Following Hanley & McNeil (1982), Swets (1988), and Pearce & Ferrier (2000), we considered that the MaxEnt model fitted for a given sea turtle group passed the validation test if its median AUC value was greater than 0.7. While implementing cross validation, the R package 'dismo' also runs an analysis of parameter contribution to the MaxEnt model (Hijmans et al. 2015); we took advantage of this to estimate the median relative contributions of environmental parameters to the individual MaxEnt models for each sea turtle group.

After the MaxEnt models for sea turtle species were fitted and validated, we used the probabilities of encounter predicted by the models to generate distribution maps for the Atlantis-GOM ecosystem model. To make final distribution maps usable in Atlantis-GOM, MaxEnt predictions were averaged over the extent of each of the Atlantis-GOM polygons (Fig. 3a), and the resulting estimates were normalized across Atlantis-GOM polygons so that their sum was 1.0.

Preference functions

We employed the method that Grüss et al. (2018a) developed for fish and invertebrates to produce preference functions for dolphin for the WFS Reef fish Ecospace ecosystem model. In brief, this method relies on GAMs integrating environmental covariates and consists of 2 steps. First, for each individual environmental covariate, x_i, integrated in the GAM, densities, y'_i, are predicted (in the original scale, i.e. not in the link scale) with the fitted GAM (i.e. from estimated GAM parameters) over a vector of values ranging between $\min\{x_i\}$ and $\max\{x_i\}$, while keeping the other environmental covariates constant at their mean value from the GAM modeled dataset; $\min\{x_i\}$ and $\max\{x_i\}$ are, respectively, the minimum and maximum value of environmental covariate x_i in the study region. Second, for each environmental covariate x_i, where $i \in 1,...,n$, a preference function y_i is determined from $y'_i, ..., y'_n$, as follows:

$$y_i = \frac{y'_i - \min\{y'_1,...,y'_n\}}{\max\{y'_1,...,y'_n\} - \min\{y'_1,...,y'_n\}} \qquad (2)$$

Eq. (2) entails that all the preference functions of the species of interest range between 0 and 1, but also accounts for the relative effect of each environmental covariate on the density of the species of interest. For example, if the GAM estimates that environmental covariate x_2 has a less pronounced effect on the density of the species of interest than environmental covariate x_3, then the range of the preferences associated with environmental covariate x_2 will be smaller than that associated with environmental covariate x_3 (e.g. 0–0.5 vs. 0–1 in the example provided in Fig. 2). When Ecospace is running, spatial estimates of environmental variables are read from data layers for each monthly time step, and the habitat capacity, C, in each cell of the Ecospace model is computed as the product of preferences for the environmental conditions (e.g. $C = y_1 \cdot y_2 \cdot y_3$ in the example provided in Fig. 2). Then, if at a given

Table 2. Environmental covariates integrated in the generalized additive model of the common bottlenose dolphin *Tursiops truncatus* developed in Roberts et al. (2016)

Environmental covariate	Range values in the West Florida Shelf region
Bottom depth	2–363 m
Bottom slope	0–1.5 degrees
Distance to shore	$2 \times 10^3 – 251 \times 10^3$ m
Distance to fronts	$0–1.7 \times 10^6$ m
Sea surface temperature	13–31°C
Zooplankton biomass	0–27 g m^{-2}
Eddy kinetic energy	0–0.1 cm^2 s^{-2}

monthly time step, say, the value of environmental variable x_2 is optimal and that of environmental variable x_3 is entirely suboptimal in Ecospace cell 1 (such that y_1, y_2 and y_3), while the value of environmental variable x_3 is optimal and that of environmental variable x_2 is entirely suboptimal in Ecospace cell 2 (such that y_1, y_2 and $y_3 = 1$), then habitat capacity in Ecospace cell 1 (C_1) will be lower than habitat capacity in Ecospace cell 2 ($C_2 = 0.5$).

To generate preference functions for dolphin, we used the Tweedie GAM of the common bottlenose dolphin developed and validated in Roberts et al. (2016). This GAM integrates 7 environmental covariates: bottom depth, bottom slope, distance to shore, distance to fronts, SST, zooplankton biomass, and eddy kinetic energy. The spatio-temporal patterns of these 7 environmental covariates in the WFS Reef fish Ecospace model are described in Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m602 p255_supp.pdf, and their range values in the WFS region are provided in Table 2.

Estimation of the percentage spatial overlap between animal hotspots and their areas of bycatch in the US pelagic longline fishery

We took advantage of inferring the spatial distributions of cetaceans and sea turtles in the GOM in this study to estimate the percentage of spatial overlap between the hotspots of these marine organisms in the US GOM and their areas of bycatch in the US pelagic longline fishery. This analysis provided an estimation of the degree of exposure of cetaceans and sea turtles to bycatch in the US pelagic longline fishery. Mysticeti and Kemp's ridley sea turtles were not considered in this analysis, because they have not been observed as bycatch in the US pelagic longline fishery (Beerkircher et al. 2002).

To conduct the analysis, we proceeded in 3 steps. First, we determined the hotspots of cetaceans and sea turtles in the US GOM. To determine the hotspots of cetaceans, we added together the density maps of dolphins and Odontoceti generated previously and retained only the resulting density estimates for the US GOM (Fig. 4b). Then, we identified the hotspots of cetaceans in the US GOM as those cells where the density of cetaceans was equal to or greater than their mean density over the entire US GOM (Brodeur et al. 2008, 2014, Grüss et al. 2018a). To determine the hotspots of sea turtles, we produced a map of relative abundance (such that the sum of relative abundances was equal to 1.0) for loggerhead and leatherback sea turtles for the US GOM from the probability of encounter maps generated previously for the 2 sea turtle species for the GOM LME. Then, we added together the maps of relative abundance for loggerhead and leatherback sea turtles, and we normalized the resulting spatial estimates so that they summed to 1.0; we thus obtained a map of relative abundance for sea turtles for the US GOM. Finally, we identified the hotspots of sea turtles in the US GOM as those cells where the relative abundance of sea turtles was equal to or greater than their mean relative abundance over the entire US GOM (Brodeur et al. 2008, 2014, Grüss et al. 2018a).

Second, we determined the areas of bycatch of cetaceans and sea turtles in the US pelagic longline fishery. To do so, we relied on the bycatch data collected by the pelagic observer program (POP). POP places trained observers randomly on US pelagic longline vessels throughout the GOM all year round (Beerkircher et al. 2002). NOAA's Southeast Fisheries Science Center provided us with POP data for the period 2000 to 2015. From this data set, we extracted the geographic coordinates of the areas where cetaceans and sea turtles were caught as bycatch. These data allowed us to map the areas of bycatch of cetaceans and sea turtles in the US GOM.

Third, we estimated the percentage of spatial overlap between hotspots of cetaceans and sea turtles in the US GOM and the areas of bycatch of these marine organisms in the US pelagic longline fishery (PO, in %). For cetaceans, this percentage was obtained as follows (Drapeau et al. 2004, Brodeur et al. 2008, Grüss et al. 2018c):

$$PO_{cetaceans} = \frac{N_{cetaceans, bycatch}}{N_{cetaceans}} \cdot 100 \qquad (3)$$

where $N_{cetaceans, bycatch}$ is the number of cells of the spatial grid for the US GOM (Fig. 4b) that are both hotspots of cetaceans and areas of bycatch of

cetaceans in the US pelagic longline fishery, and $N_{ceataceans}$ is the number of cells of the spatial grid for the US GOM that are hotspots of cetaceans. For sea turtles, PO was estimated in a similar way:

$$PO_{sea\ turtles} = \frac{N_{sea\ turtles,\ bycatch}}{N_{sea\ turtles}} \cdot 100 \qquad (4)$$

where $N_{seaturtles,\ bycatch}$ is the number of cells of the spatial grid for the US GOM that are both hotspots of sea turtles and areas of bycatch of sea turtles in the US pelagic longline fishery, and $N_{sea\ turtles}$ is the number of cells of the spatial grid for the US GOM that are hotspots of sea turtles.

RESULTS

Distribution maps

Cetaceans

The dolphin group represented in the Atlantis-GOM ecosystem model is predicted to be present across the entire GOM LME (Fig. 5a,b). The spatial distribution patterns predicted for the dolphin group primarily reflect those of the common bottlenose dolphin, because of the very high densities predicted for that species in coastal areas, especially those of the
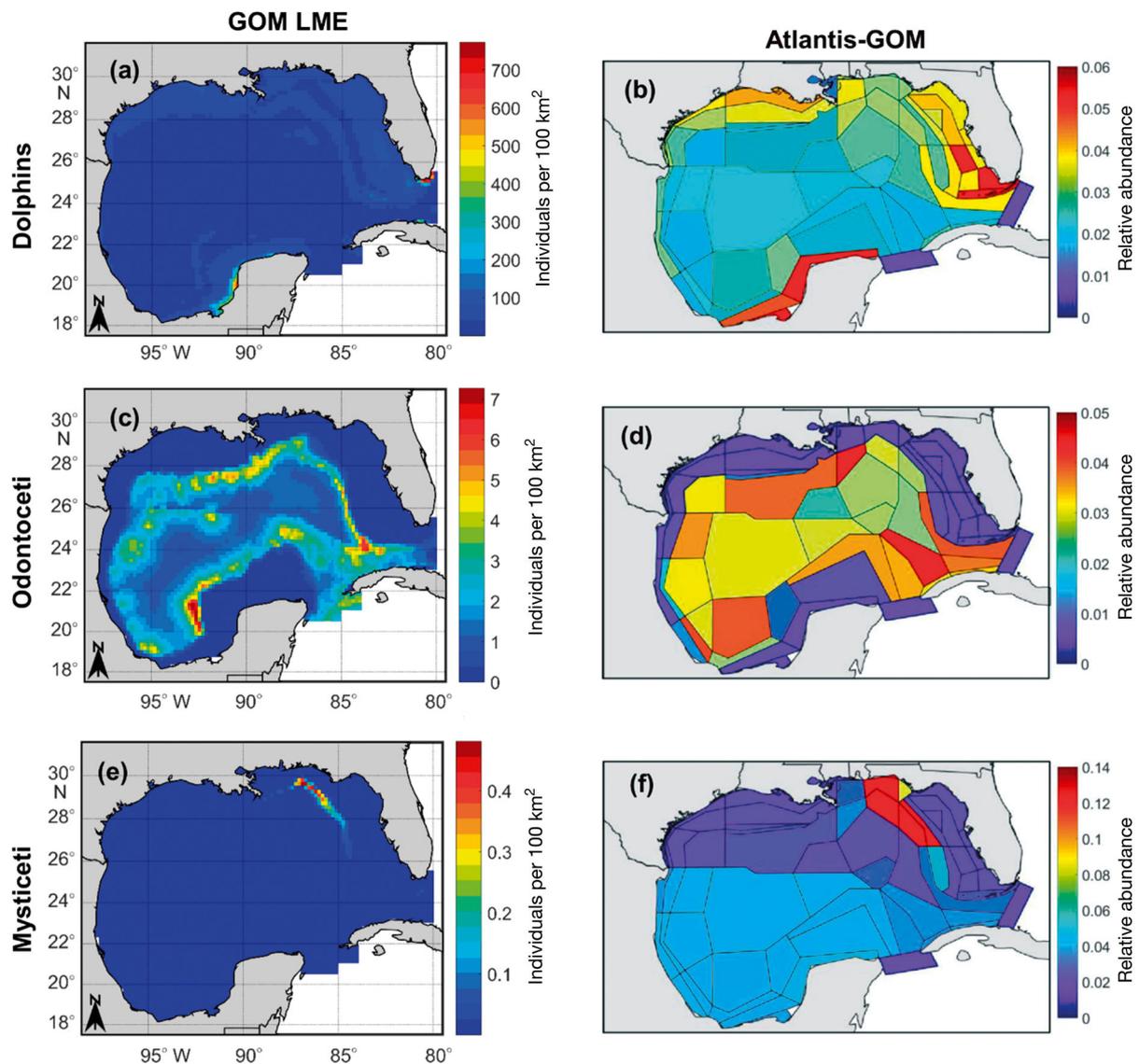

Fig. 5. Maps produced for the (a,b) dolphin group, (c,d) Odontoceti group, and (e,f) Mysticeti group represented in the Atlantis-Gulf of Mexico (GOM) ecosystem model; (a,c,e) are density maps for the entire GOM large marine ecosystem generated from the predictions of habitat-based density models; (b,d,f) are maps of relative abundance usable in Atlantis-GOM (such that the sum of relative abundances for each map is equal to 1.0)

southern WFS and the Campeche Bank (Figs. 5a,b & Fig. S2 in the Supplement). The other areas of the GOM LME where the density of the dolphin group is predicted to be relatively high are the mid- and outer-shelf areas of the GOM LME, which are dominated by Atlantic spotted dolphin *Stenella frontalis*, and the moderately deep slopes of the northeastern and north-central GOM, which are dominated by pantropical spotted dolphin *Stenella attenuata* (Fig. S2).

The Odontoceti group represented in Atlantis-GOM is predicted to be present all along the continental slope of the GOM LME and in the deep waters of the LME (Fig. 5c,d). The species making up the Odontoceti group have similar spatial distribution patterns and densities in the GOM LME (see Fig. S3 in the Supplement). Consequently, the spatial distribution patterns predicted for the Odontoceti group are not primarily dictated by a given species. The density of Odontoceti tends to be higher along the continental slope than in the deeper areas of their distribution area (Figs. 5c,d & S3).

The Mysticeti group represented in Atlantis-GOM is predicted to have much lower densities in the GOM LME than dolphins and deep-diving Odontocetae (compare Fig. 5e vs. a & c). The spatial distribution patterns predicted for the Mysticeti group prima-

rily reflect those of Bryde's whale; this species is essentially concentrated in the area of the WFS edge northwest of Tampa, Florida (Figs. 5e,f & Fig. S4 in the Supplement).

Manatee

The proportion of the manatee population of the GOM present in the northwestern GOM (i.e. in the region west of Panama City Beach) was estimated to be 0.09% in winter, 1.91% in spring, 4.19% in summer, and 1.48% in fall. Consequently, the relative number of manatees in the northwestern GOM is relatively low in all seasons and is easier to visualize with a transformation (e.g. a root-root transformation, as in Fig. 6). Hotspots of relative abundance for the manatee in the northwestern GOM are located in the region between Panama City Beach and Apalachicola, Florida in winter (Fig. 6a), in the Florida Panhandle and in Alabama and Mississippi coastal waters in spring (Fig. 6b), in the Florida Panhandle and in Alabama, Mississippi, and eastern Louisiana coastal waters in summer (Fig. 6c), and in the region between Panama City Beach and Apalachicola and in Alabama and Mississippi coastal waters in fall (Fig. 6d).
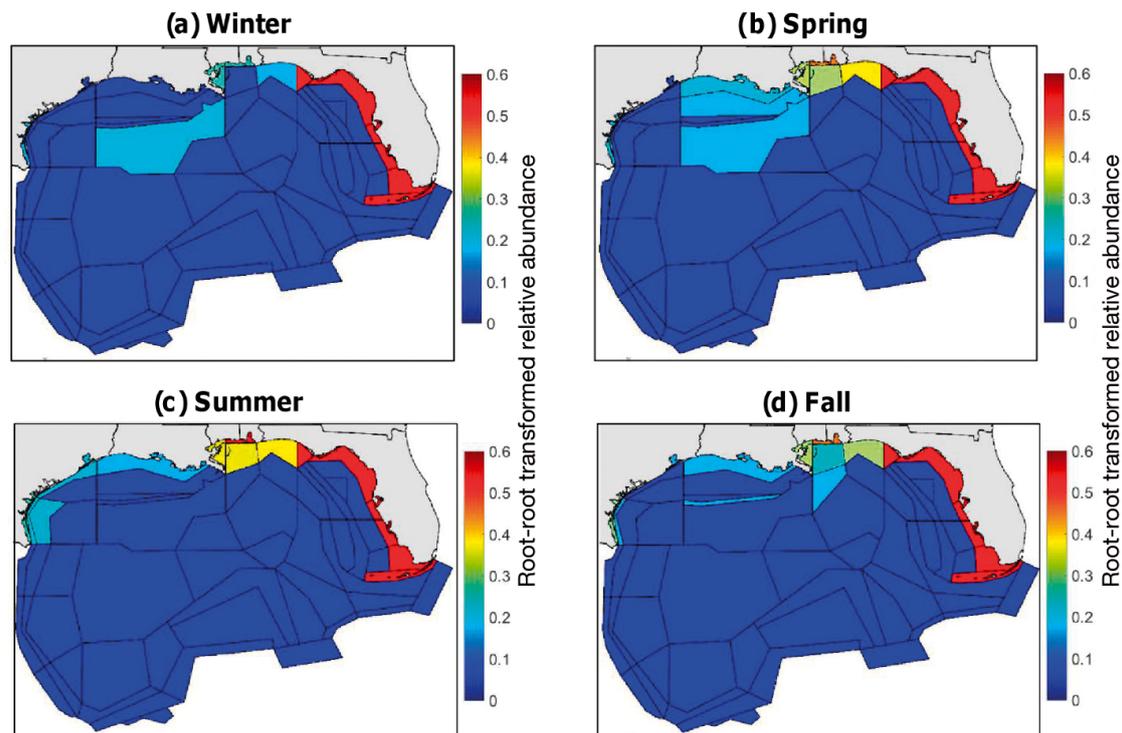

Fig. 6. (a–d) Seasonal maps of root-root transformed relative abundance for the Florida manatee *Trichechus manatus latirostris* for the Atlantis-Gulf of Mexico (GOM) ecosystem model. Root-root transformation was used here to emphasize the areas of the GOM with low Florida manatee abundance

Table 3. Median area under the receiver operating characteristic curve (AUC) of the MaxEnt models of loggerhead sea turtle *Caretta caretta,* Kemp's ridley sea turtle *Lepidochelys kempii*, and leatherback sea turtle *Dermochelys coriacea*, and median relative contributions of environmental parameters to the 3 models. The estimates reported here were obtained using 10 cross validation runs implemented with the R package 'dismo' (Hijmans et al. 2015). SST: sea surface temperature

Sea turtle species	Median AUC value	Median relative contributions of environmental parameters to the MaxEnt model of the species (%)
Loggerhead sea turtle	0.869	Maximum annual oceanic current speed (23.6) Oceanic current speed annual range (23.3) Maximum annual surface salinity (13.9) SST annual range (7) Mean annual SST (5.6) Mean annual surface salinity (5.6) Depth (5.5) Minimum annual oceanic current speed (4.8) Mean annual surface salinity (4.5) Mean annual oceanic current speed (3.8) Maximum annual SST (3)
Kemp's ridley sea turtle	0.914	Oceanic current speed annual range (36.3) Mean annual SST (30.7) Minimum annual surface salinity (15.9) Depth (15.3) Maximum annual oceanic current speed (3.3)
Leatherback sea turtle	0.928	SST annual range (28) Depth (16.5) Mean annual surface salinity (12.2) Minimum annual surface salinity (10.1) Mean annual oceanic current speed (7.7) Mean annual SST (6.4) Minimum annual oceanic current speed (5.2) Maximum annual surface salinity (4.8) Maximum annual SST (3.5) Oceanic current speed annual range (3) Minimum annual SST (2.8)

Sea turtles

Because they contributed less than 1 % of the model fit, 2 of the environmental parameters initially integrated in the MaxEnt models of loggerhead and leatherback sea turtles were excluded (Table 3). For the same reason, 8 of the 13 parameters initially integrated in the MaxEnt model of Kemp's ridley sea turtle were excluded. The median AUC values of the MaxEnt models of loggerhead sea turtle (0.869), Kemp's ridley sea turtle (0.914), and leatherback sea turtle (0.928) were all greater than 0.7 and thus passed the validation test. The environmental parameters that made the largest contribution to the MaxEnt models were maximum annual oceanic current speed and oceanic current speed annual range in the case of loggerhead sea turtle, oceanic current speed annual range and mean annual SST in the case of Kemp's ridley sea turtle, and SST annual range in the case of leatherback sea turtle (Table 3).

Loggerhead sea turtles were predicted to occur throughout the GOM LME, except in the nearshore areas of Louisiana and Mississippi (Fig. 7a,b). The highest probabilities of encounter of loggerhead turtles were predicted on the WFS and in the Florida Panhandle.

Kemp's ridley sea turtles were predicted to occur quasi-exclusively on the GOM shelf (Fig. 7c,d). The highest probabilities of encounter of Kemp's ridley sea turtle were predicted along the northern GOM shelf, between the Sarasota region and Tamaulipas waters.

Leatherback turtles were predicted to be encountered over the entire GOM LME (Fig. 7e,f). However, the probability of encounter of leatherback turtles was predicted to be highest in the Florida Panhandle, all along the continental slope of the US GOM and, to a lesser extent, in the deep regions of the US and Mexican and Cuban GOM.

Preference functions

We produced 7 preference functions for the common bottlenose dolphin for the WFS Reef fish Ecospace ecosystem model, which are all easily interpretable (Fig. 8). Some of these preference functions have a more pronounced effect on dolphin density than others. Depth has a much larger effect on dolphin density than all the other environmental parameters integrated in the GAM of dolphin; dolphin density on the WFS is predicted to peak at depths ranging between 5 and 45 m (Fig. 8; note the different scales on the *y*-axes).

Estimation of the percentage spatial overlap between animal hotspots and their areas of bycatch in the US pelagic longline fishery

We found 29 records of bycatch for cetaceans (dolphins and Odontoceti) in the POP dataset (Fig. 9a). Consequently, as hotspots of cetaceans were predicted to cover a relatively large fraction of the US GOM (Fig. 9b), the percentage of spatial overlap between hotspots of cetaceans in the US GOM and the areas of bycatch of cetaceans in the US pelagic longline fishery (i.e. PO) was predicted to be very low (1.5 %).
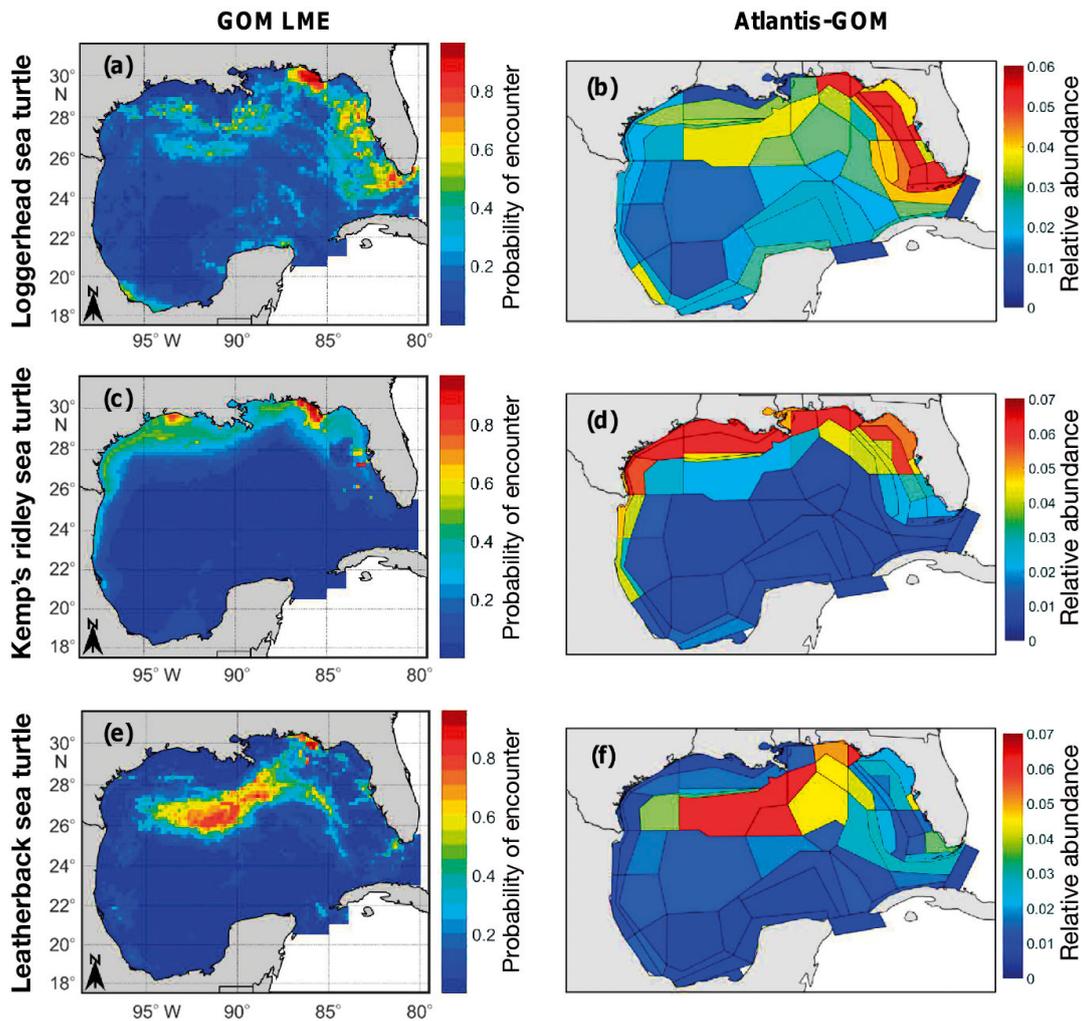
Fig. 7. Maps produced for (a,b) loggerhead sea turtle *Caretta caretta*, (c,d) Kemp's ridley sea turtle *Lepidochelys kempii*, and (e,f) leatherback sea turtle *Dermochelys coriacea* for the Atlantis-Gulf of Mexico (GOM) ecosystem model; (a,c,e) are probability of encounter maps for the entire GOM large marine ecosystem generated from the predictions of MaxEnt models; (b,d,f) are maps of relative abundance usable in Atlantis-GOM (such that the sum of relative abundances for each map is equal to 1.0)

In contrast, we found about 10 times more records (268) of bycatch for sea turtles (loggerhead and leatherback sea turtles) than for cetaceans in the POP dataset (Fig. 9c), while hotspots of sea turtles were predicted to cover a large fraction of the US GOM (Fig. 9d). The PO estimated for sea turtles was moderately high (37.9%).

DISCUSSION

The spatial allocation of species biomasses in spatially explicit ecosystem models has usually relied on simplistic methods (see Grüss et al. 2016 for a review). For example, the biomasses of marine mammals and sea turtles were previously allocated over

the Atlantis-GOM spatial domain based on the known depth preferences of these animals rather than using distribution maps (Ainsworth et al. 2015). To provide ecosystem models with better inputs and, therefore, allow these models to make more reliable predictions, new methods have recently been designed; these methods made the most comprehensive possible use of monitoring and environmental data to produce preference functions (Grüss et al. 2018a) and distribution maps (Grüss et al. 2018b,c) for fish and invertebrates. In this study, we developed new methods to generate distribution maps for marine mammals and sea turtles. We also employed Grüss et al. (2018a)'s method to produce preference functions for the common bottlenose dolphin. The methods we developed for constructing distribution
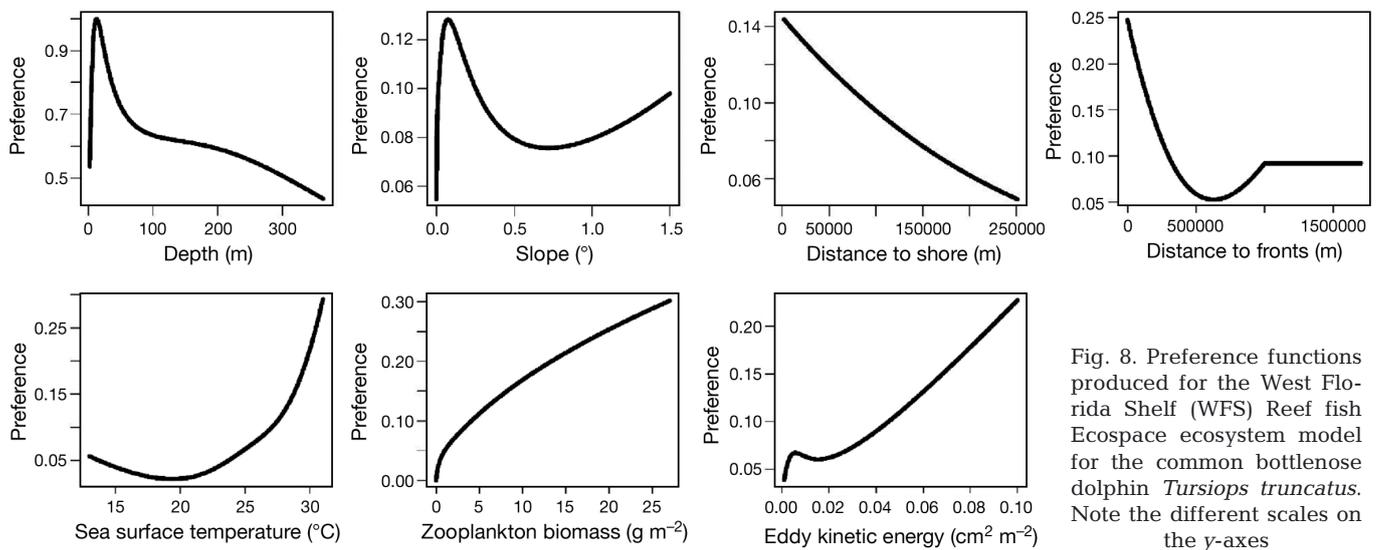
Fig. 8. Preference functions produced for the West Florida Shelf (WFS) Reef fish Ecospace ecosystem model for the common bottlenose dolphin *Tursiops truncatus*. Note the different scales on the *y*-axes

maps in this study relied on statistical habitat models (GAMs or MaxEnt models) fitted to density or occurrence estimates and environmental data, or on the treatment of sighting data and results from previous studies. In the case of dolphins, Odontoceti, and Mysticeti, we also demonstrated the benefits of combining the predictions of different statistical habitat models for obtaining distributions for a LME which is not entirely covered by monitoring programs. This approach allowed us to rely on more elaborate statistical habitat models when inferring spatial distributions where robust monitoring data were available (the US GOM) and to fall back to more parsimonious statistical habitat models when extrapolating spatial distributions in unsurveyed areas (the GOM LME outside US waters).

The mapping efforts for dolphins, Odontoceti, and Mysticeti conducted in this study highlighted greatly differing spatial patterns for the 3 cetacean groups. The combination of the predictions made by the habitat-based density models of Roberts et al. (2016) and Mannocci et al. (2017) revealed that in the GOM (1) dolphin density is highest over the continental shelf, where common bottlenose dolphins predominate, and lower over the continental slope and deeper areas, where diversity is higher (Fig. 5a,b); (2) Odontoceti hotspots are found along the continental slope and in the deep waters (Fig. 5c,d); and (3) Mysticeti are primarily concentrated in the area of the WFS edge northwest of Tampa (Fig. 5e,f). The predictions made for dolphins, Odontoceti, and Mysticeti in the present study reflect absolute density (ind. km^{-2}), as the habitat-based density models of Roberts et al. (2016) and Mannocci et al. (2017) did not consist solely of GAMs fitted to environmental

parameters, but also integrated detection functions that correct for availability and perception biases. The distribution maps we constructed for cetaceans in this study are useful inputs for ecosystem models like Atlantis-GOM that simulate the dynamics of numerous species groups, each of which generally includes a large number of species for computational convenience. However, our distribution maps should ideally not be used in cetacean-focused studies, due to the large ecological and distributional differences among the species making up the dolphin, Odontoceti, and Mysticeti groups considered in this study (e.g. common bottlenose dolphin and killer whale *Orcinus orca*, both included in the dolphin group considered in this study; Roberts et al. 2016). Moreover, some of the species making up the cetacean groups represented in Atlantis-GOM are migratory, while the others are resident. For example, in the Mysticeti group represented in Atlantis-GOM, fin whales migrate to the GOM during the winter season (Gambell 1985), whereas the Bryde's whale population of the GOM is probably resident (LaBrecque et al. 2015). Thus, cetacean-focused studies mapping the spatial distributions of cetaceans in the GOM should produce annual or seasonal distribution maps for cetacean species depending on whether these species undertake seasonal migrations or not, rather than solely annual distribution maps as we did in the present study.

This study is the first to quantitatively map Florida manatee spatial distribution over the entire US GOM. This effort primarily highlighted that hotspots of this species in the northwestern GOM differ from one season to the next (Fig. 6); this is due to the aggregation of Florida manatees in West Florida waters dur-
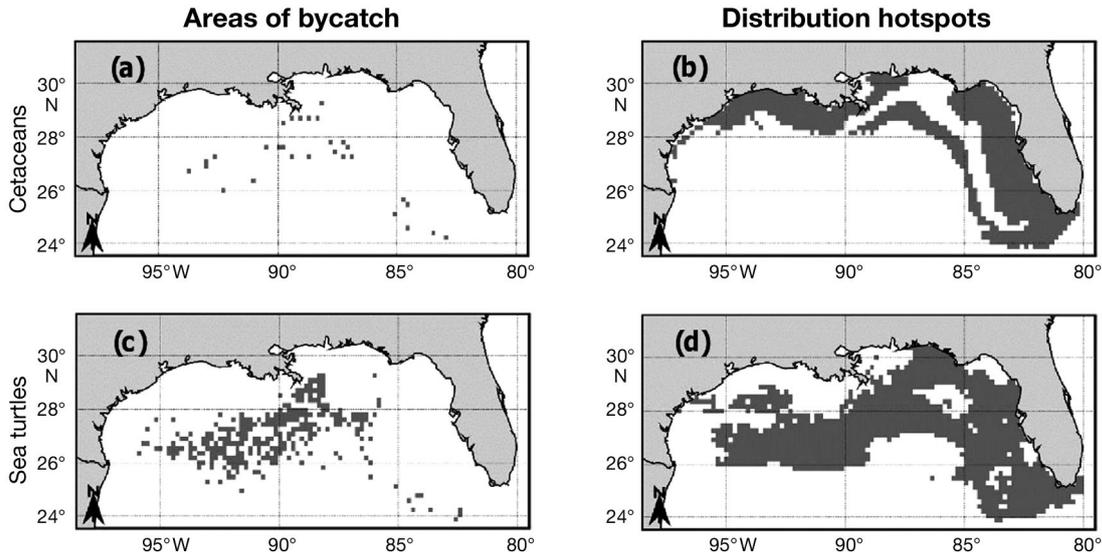
Fig. 9. (a,c) Areas of bycatch of cetaceans and sea turtles in the US pelagic longline fishery, and (b,d) distribution hotspots of cetaceans and sea turtles in the US Gulf of Mexico; (a,b) are for cetaceans (dolphins and Odontoceti), while (c,d) are for sea turtles (loggerhead turtle *Caretta caretta* and leatherback turtle *Dermochelys coriacea*); (a) and (c) were determined from the bycatch data collected by the pelagic observer program over the period 2000−2015, while (b) and (d) were obtained from the predictions of statistical habitat models

ing winter and the seasonal migrations that manatees undertake in spring and fall between warm-season residence and overwintering sites (Aven et al. 2016, Hieb et al. 2017). The main limitation of our approach is the assumption that the spatial distribution of the Florida manatee population of the GOM is homogeneous in the Atlantis-GOM polygons located in coastal northeastern GOM. While this assumption is reasonable for producing distribution maps for Atlantis-GOM, which has a very coarse spatial resolution, we recommend future studies try to infer detailed spatial distribution patterns for the Florida manatee in the entire US GOM including the WFS, using a spatial grid with a finer resolution than that of Atlantis-GOM. Future studies could also develop a statistical habitat model for the Florida manatee population of the GOM. Such an endeavor would require careful reflection on which data are most appropriate to use (e.g. sighting, focal survey, telemetry/GPS) and how to use them, given that different types of data exist at different quantities and qualities among different locations of the US GOM. A statistical habitat model for the Florida manatee population of the GOM may also benefit from integration of a detection function to correct for the availability and perception biases that can be associated with manatee sightings (Martin et al. 2015). The statistical model for the Florida manatee could be a binomial GAM, in which case (1) pseudo-absences should be generated by randomly sampling within the spatial grid defined

for the species, so as to obtain presence/absence estimates (Pearce & Boyce 2006, Aarts et al. 2012, Renner et al. 2015); and (2) since the likelihood of Florida manatees being reported as present is strongly related to sampling characteristics (e.g. the proximity to boat ramps; Aven et al. 2015), variables associated with sampling bias (e.g. distance to boat ramps) should be integrated in the binomial GAM (Renner & Warton 2013, Renner et al. 2015).

The distribution maps produced for sea turtles from MaxEnt predictions in this study highlighted different spatial distribution patterns for loggerhead, Kemp's ridley, and leatherback sea turtles. These mapping efforts are valuable for improving the spatial allocation of sea turtle biomasses in the Atlantis-GOM ecosystem model, which before simply relied on the known depth preferences of sea turtles (Ainsworth et al. 2015). For instance, the MaxEnt model for leatherback sea turtle predicted high probabilities of encounter near the Florida Panhandle, consistent with earlier reports (Collard 1990, Troëng et al. 2004). Likewise, our mapping concurred with previous studies that indicated that loggerhead sea turtle hotspots in the US GOM were located on the WFS and in the Florida Panhandle (Foley et al. 2014, Hardy et al. 2014) and that loggerhead sea turtle foraging areas primarily occured over the continental shelf of the GOM eastward of 90° W (from eastern Louisiana to the Florida Keys in the US, and on the Campeche Bank in Mexico) with relatively rare incursions west-

ward (Hart et al. 2014). In the US GOM, the MaxEnt model for Kemp's ridley sea turtles depicted the distribution of the species well (e.g. constrained to the continental shelf), but the model likely underestimated the probability of encounter of Kemp's ridley sea turtles in the Mexican GOM (Shaver et al. 2016). This issue highlights the need for more GOM-wide location data for future studies.

Another issue for sea turtles is that the spatial distribution patterns of smaller (younger) sea turtles differ from those of their larger counterparts (Carr 1980, Scott et al. 2014, Lamont et al. 2015). Direct observations of these small and cryptic animals by satellite telemetry or aerial surveys is not possible (Putman et al. 2013) and the distribution maps presented in this study probably best reflect the distributions of larger sea turtle life stages. One way forward may be the use of simulations with individual-based movement models (e.g. Ichthyop; Lett et al. 2008), in which the dispersal of young sea turtles from nesting areas to nursery habitat (Putman et al. 2013, 2015) and the seasonal and reproductive migrations of adult sea turtles (Painter & Hillen 2015) would be simulated. The spatial distribution patterns of young and adult sea turtles at different seasons of the year would then be inferred by considering the geographic location of individual sea turtles at a certain age.

Using the method developed in Grüss et al. (2018a), we additionally produced preference functions for the common bottlenose dolphin for an Ecospace model, which were easily interpretable and accounted for the relative effect of each environmental parameter on dolphin density (Fig. 8). These preference functions were readily interpretable due to the restriction of the thin-plate regression splines used in the GAM of the common bottlenose dolphin to 4 degrees of freedom (Roberts et al. 2016). GAMs are preferable to generalized linear models (GLMs) for generating preference functions because they allow for the estimation of non-linear relationships between environmental parameters and marine organisms, more realistically representing how the environment influences spatial distribution patterns (Grüss et al. 2018a). The predictions of MaxEnt models could also be employed for constructing preference functions. However, this endeavor should be pursued only if it is not possible to develop a GAM for the species or species group of interest, because the partial dependence plots derived from a MaxEnt models are generally very difficult to interpret (Phillips et al. 2006).

In the present study, we did not evaluate the impacts of the distribution maps and preference func-

tions we produced for Atlantis-GOM and WFS Reef fish Ecospace on the predictions and performance of these ecosystem models. The main reason for this is that, beforehand, it will be necessary to recalibrate the 2 ecosystem models enhanced by our products and those generated for fish, invertebrates, and seabirds in other studies (Grüss et al. 2018a,b, A. Grüss unpubl. data). It is important to note that the spatial distributions of marine mammals and sea turtles presented in this study will be used to initialize the Atlantis-GOM model, and the spatial distributions of marine mammals and sea turtles in Atlantis-GOM at run time will be relatively different; indeed, in Atlantis, the distribution of the biomass of a species group in the horizontal dimensional at each time step is also influenced by the migration rates specified for that species group (Fulton et al. 2004, 2007). With respect to Ecospace, the spatial allocation of species group biomasses is a complex process which does not rely solely on preference functions, but also on defined movement patterns as well as other factors (relative vulnerabilities to predation in non-preferred habitat, and relative feeding rates in non-preferred habitat) (Walters et al. 1999, Christensen & Walters 2004). It is also important to note that the simulation of spatio-temporal dynamics in Ecospace takes place in 2 parts: a 'spin-up' part to let the spatial distributions of biomasses reach an equilibrium, and an explanatory part where model results can be exploited (Chagaris 2013, Christensen et al. 2014).

In this study, we developed 3 different methods (a method based on GAMs, a method based on MaxEnt, and a non-statistical method) for each of our 3 study species groups (cetaceans, sea turtles, and manatee, respectively). However, we could have applied several methods to our study groups. For example, as mentioned earlier, we could have also generated pseudo-absences for the manatee to then fit a binomial GAM to the resulting presence/absence data set and pertinent predictors. Future studies could employ several of our methods and others to obtain products for marine mammals and sea turtles for spatially explicit ecosystem models; such a multi-method approach would allow gauging the uncertainty associated with the products delivered to ecosystem models. For instance, the niche distribution modeling approach BIOMOD (Thuiller et al. 2012), which fits several types of statistical models (GAMs, MaxEnt, and others) to the same presence/absence data set, could be used to generate products for marine mammals and sea turtles for ecosystem models. Although, for this study, we focused on employing the best method for each functional group using the available

data, future studies applying multiple methods to the same functional groups would be useful for understanding how the choice of a given statistical model influences the estimated distribution maps and preference functions.

To demonstrate the usefulness of distribution maps for marine mammals and sea turtles for EBFM efforts beyond ecosystem modeling, we compared distribution hotspots to areas of a known potential stressor for some species: commercial fishing bycatch. This analysis suggested that the degree of exposure of cetaceans to bycatch in the US pelagic longline fishery is very low (1.5%), while that of sea turtles is moderately high (37.9%). However, for cetaceans, we hasten to note that our distribution hotspot analysis (Fig. 9a,b) mainly reflects the density of pantropical spotted, common bottlenose, and Atlantic spotted dolphins, which together dominate total cetacean abundance in the US GOM, but not bycatch. While pantropical spotted dolphins are frequently bycaught in the US GOM pelagic longline fishery, the latter 2 species are not. The fishery generally operates along the continental slope and in deep offshore waters, but not in shelf waters where common bottlenose and Atlantic spotted dolphins are strongly concentrated. Other off-shelf, frequently-bycaught species, such as Risso's dolphin *Grampus griseus* and the short-finned pilot whale *Globicephala macrorhynchus*, occur in densities that are low relative to common bottlenose and Atlantic spotted dolphins, so that our analysis did not show many distribution hotspots off the shelf where these bycatch events actually occur. Also, our analysis should be considered preliminary, because it relied on raw bycatch data collected by POP rather than on statistical predictions of bycatch hotspots, while POP samples only a small fraction of US pelagic longline operations in most years (Beerkircher et al. 2002). The key outcomes of our preliminary analysis would probably not be dramatically altered had we employed a statistical model for predicting bycatch hotspots using the same data set, although a larger data set might yield new hotspots. Future studies could attempt to develop a statistical model for mapping the bycatch areas of sea turtles, for which a reasonable number of data points is available in the POP dataset. More generally, the distribution maps constructed using the methods developed in this study could be employed for assisting numerous EBFM efforts in the GOM, including, among others, ecosystem status reports (Karnauskas et al. 2013, 2017), studies evaluating the performance of MPA strategies (Brock 2015, O'Farrell et al. 2017), and efforts to mitigate sea turtle bycatch in the reef

fish and shrimp fisheries (Scott-Denton et al. 2012, Monk et al. 2015).

EBFM is increasingly being considered and used around the world, and it relies heavily on ecosystem modeling studies (FAO 2008, Christensen & Walters 2011, Collie et al. 2016). Thus, the methods developed in this study and other recent studies (Tarnecki et al. 2016, Grüss et al. 2018a,b,c) for improving the inputs provided to ecosystem models are timely. It is our hope that these efforts will continue to improve the reliability of ecosystem models, thereby facilitating their use in the fisheries management arena and beyond.

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