



## Making the most of available monitoring data: A grid-summarization method to allow for the combined use of monitoring data collected at random and fixed sampling stations



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### ABSTRACT

Statistical habitat models, such as spatial generalized linear mixed models (GLMMs) and spatial generalized additive models (GAMs), provide valuable products to habitat assessments and ecosystem-based fisheries management (EBFM) efforts. In particular, derived spatial distribution maps and quantitative relationships of marine organisms to environmental variables (e.g., suitability indices) can be employed to develop or validate ecosystem simulation models. Recent studies fitted spatial GLMMs and spatial GAMs to encounter/non-encounter data collected by different regional monitoring programs that use random sampling designs, so as to enable the production of distribution maps and suitability indices in bulk. However, despite these large efforts, it was not possible to obtain distribution maps for a number of species and life stage combinations, including the juvenile stages of coastal fish species such as croaker (*Micropogonias undulatus*). In this study, we introduce a grid-summarization method that allows for the combined use of encounter/non-encounter data collected by multiple monitoring programs at random and fixed sampling stations. We demonstrate our grid-summarization method for contrasting species of the western U.S. Gulf of Mexico: red snapper (*Lutjanus campechanus*), for which data delivered by monitoring programs employing random sampling designs have a satisfactory spatial coverage and the use of monitoring data collected at fixed sampling stations is not necessary; and croaker and brown shrimp (*Farfantepenaeus aztecus*), for which the combined use of monitoring data collected at random and fixed sampling stations enables or improves the generation of distribution maps. We compare spatial GLMMs and spatial GAMs that rely on the grid-summarization method (“new models”) to spatial GLMMs and spatial GAMs that do not rely on the grid-summarization method (“status-quo models”). We found that the grid-summarization method that allows for the combined use of monitoring data collected at random and fixed sampling stations results in reasonable seasonal distribution maps and suitability indices for the species and life stage combinations (e.g., croaker early juveniles, small brown shrimps) that are undersampled by the monitoring programs that employ random sampling schemes. We also found that the grid-summarization method provides reasonable seasonal distribution maps and suitability relationships for species and life stage combinations (e.g., red snapper adults) for which the status-quo method already provided reasonable results and the combined use of monitoring data collected at random and fixed sampling stations is not necessary. For these species and life stage combinations for which the status-quo method worked well, the choice of the grid-summarization method over the status-quo method depends on whether the fisheries analysts wish to produce smoother distribution maps and whether they target higher predictive accuracy at the expense of lower discrimination accuracy when working with spatial GAMs. Our results suggest that additional monitoring datasets that were previously excluded can be employed by statistical habitat models, thereby enabling generation of distribution maps and suitability indices for a wider range of species, life stage and season combinations.

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## 1. Introduction

Monitoring programs represent an invaluable source of data for stock, habitat and climate-vulnerability assessments, and ecosystem-based fisheries management (EBFM) efforts (Gunderson, 1993; Schneider, 2000; Grüss et al., 2017a; O'Farrell et al., 2017). Monitoring programs can be classified as fisheries-independent or fisheries-dependent. Fisheries-independent monitoring programs collect data through well-designed research surveys, while fisheries-dependent monitoring programs rely on fishing activities to obtain the data (Thompson, 2002; Grüss et al., 2018e). One can also distinguish between monitoring programs that visit the same sampling stations repeatedly across time (i.e., use a fixed sampling design) and monitoring programs that employ random sampling designs. Random sampling designs typically consist of dividing the region of interest into sampling units (e.g., based on predefined longitudinal, latitudinal and depth strata), and visiting only a random fraction of these sampling units for each sampling period. By enabling all sampling units a non-zero probability of selection, random sampling designs facilitate straightforward statistical analyses of monitoring data (Giuffre, 1997; Kitchenham and Pfeleger, 2002).

Statistical habitat models (also referred to as “species distribution models”) fitted to monitoring data can provide a diversity of products to habitat assessments and EBFM efforts (Grüss et al., 2018b; Thorson, 2019). Statistical habitat models are particularly useful to map the spatial distributions of marine organisms, notably their preferred nursery and spawning habitat (often referred to as “essential fish habitat”; Kai et al., 2017; Grüss et al., 2018a, 2019a; Laman et al., 2018). In the U.S., mapping essential fish habitat is one of the requirements of the Magnuson-Stevens Fishery Conservation and Management Act (MSRA (Magnuson-Stevens Fishery Conservation and Management Reauthorization Act), 2006). Distribution maps generated from the predictions of statistical habitat models are also critical inputs of many of the spatially-explicit ecosystem simulation modeling platforms that are instrumental to advancing EBFM efforts (e.g., Atlantis; Fulton et al., 2004, 2011; OSMOSE; Shin and Cury, 2001; Grüss et al., 2016). For spatially-explicit ecosystem modeling platforms like Ecospace (Walters et al., 1999, 2010) that do not rely on distribution maps as inputs, distribution maps can serve to validate model spatial predictions. Many of the spatially-explicit ecosystem modeling platforms that do not rely on distribution maps as inputs use some form of suitability indices to simulate the spatial distribution patterns of marine organisms (e.g., Ecospace; Christensen et al., 2014). A suitability index expresses the probability of encountering individuals of a given species group/species/life stage as a function of an environmental parameter, and suitability relationships have a long history of use in fisheries science (Secor, 2009; Grüss et al., 2018b; Runnebaum et al., 2018). Both distribution maps and suitability indices are often estimated by species and life stage, and when appropriate, further estimated specific to season.

One major issue with individual monitoring programs is that their spatial, temporal and/or taxonomic coverage is often too limited to produce satisfactory distribution maps and suitability indices in bulk for the many species typical of habitat assessments and EBFM efforts (Grüss et al., 2017b; Dolder et al., 2018; Pirtle et al., 2019). To remedy this issue, some recent studies have fitted statistical habitat models to encounter/non-encounter data (e.g., Grüss et al., 2017b, 2018b, 2018c, 2018e, 2018f), count data (e.g., Roberts et al., 2016; Mannocci et al., 2017; Runnebaum et al., 2018) or biomass data (e.g., Dolder et al., 2018; Perretti and Thorson, 2019; Weijerman et al., 2019) collected by multiple monitoring programs. In particular, in the U.S. Gulf of Mexico, spatial generalized linear mixed models (GLMMs) and spatial generalized additive models (GAMs) have been fitted to encounter/non-encounter data collected by the different regional monitoring programs that use random sampling designs, so as to enable the production of distribution maps and suitability indices for the numerous species

groups, species and life stages represented in regional ecosystem models (Grüss et al., 2018b, 2018c, 2018f). This endeavor resulted in the provision of hundreds of annual and seasonal distribution maps and suitability indices to ecosystem models. However, despite these large efforts, it was not possible to obtain distribution maps and suitability indices for several species and life stages, including the juvenile stages of some common coastal fish and invertebrate species such as Atlantic croaker (henceforth “croaker”; *Micropogonias undulatus*), common snook (*Centropomus undecimalis*), black drum (*Pogonias chromis*) sheepshead (*Archosargus probatocephalus*), and stone crab (*Menippe mercenaria*) (Grüss et al., 2018e).

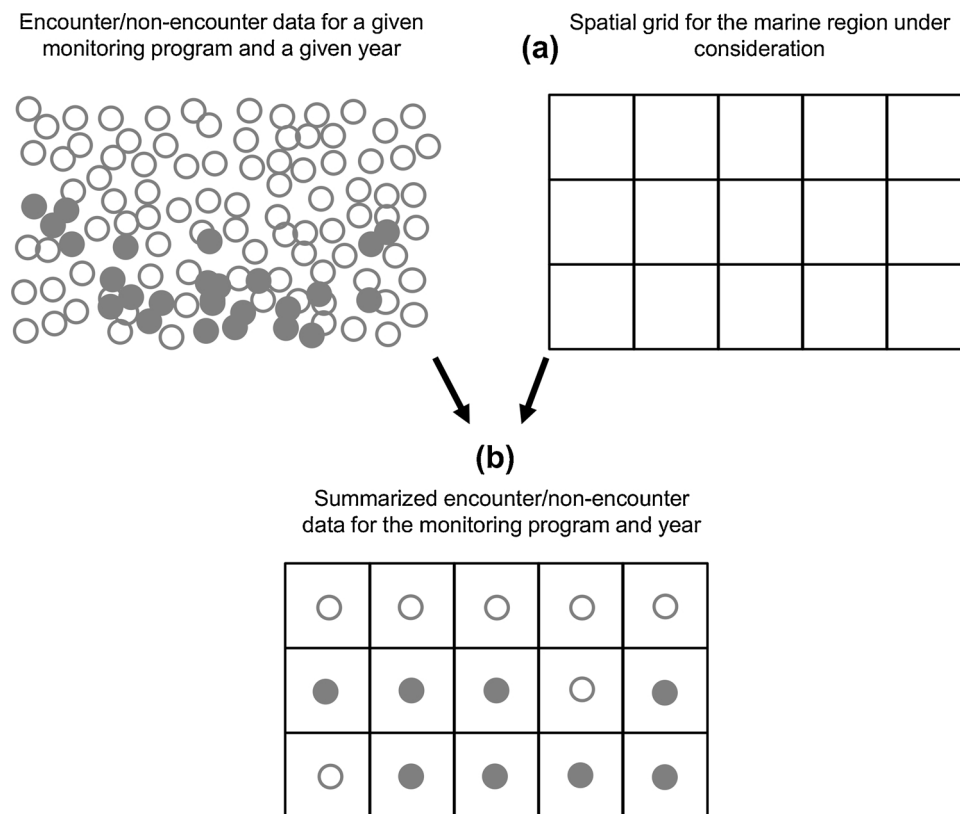
To date, the large efforts undertaken in the U.S. Gulf of Mexico relied on monitoring data collected only at random sampling stations. However, in the U.S. Gulf of Mexico, many fisheries-independent surveys are carried out at fixed sampling stations (Grüss et al., 2018e). In particular, all the fisheries-independent surveys conducted by the Louisiana Department of Wildlife and Fisheries (LDWF), except for one (the vertical line survey that operates on offshore petroleum platforms), employ fixed sampling designs in coastal areas (SEDAR, 2010; Brown et al., 2013). Developing a method that allows for the combined use of monitoring data collected at random and fixed sampling stations would enable the generation of distribution maps and suitability indices for species and life stages for which this is currently not possible, and may improve on the distribution maps and suitability indices presently feasible from monitoring data collected only at random sampling stations.

In this study, we introduce a grid-summarization method that allows for the combined use of encounter/non-encounter data collected by multiple monitoring programs at random and fixed sampling stations. Our grid-summarization method consists of producing a spatial grid for the marine region of interest, and assigning the encounter/non-encounter data collected by monitoring programs to the barycenter of the closest spatial grid cell. Statistical habitat models are then fitted to grid-summarized monitoring data and, ultimately, the predictions of the statistical habitat models are utilized to construct distribution maps and suitability indices. We demonstrate our grid-summarization method for contrasting species of the northwestern Gulf of Mexico (“NWGOM”): red snapper (*Lutjanus campechanus*), for which data delivered by monitoring programs employing random sampling designs have a satisfactory spatial coverage and the use of monitoring data collected at fixed sampling stations is not necessary for any life stage or season; and croaker and brown shrimp (*Farfantepenaeus aztecus*), for which the combined use of monitoring data collected at random and fixed sampling stations enables or improves the generation of distribution maps. We compare statistical habitat models fitted to grid-summarized monitoring data (“new models”) to statistical habitat models fitted to raw (not grid-summarized) monitoring data (“status-quo models”). We fit spatial GLMMs whose predictions are employed to construct seasonal distribution maps, and then spatial GAMs whose predictions are employed to produce suitability indices. In these two situations, we examine the predictions of the new models versus the status-quo models. The statistical habitat models developed for croaker and brown shrimp life stages allow us to explore the benefits of using monitoring data collected at both random and fixed sampling stations, while the statistical habitat models developed for red snapper life stages specifically allow us to evaluate the impacts of using the grid-summarization method rather than the status-quo method to generate distribution maps and suitability indices.

## 2. Material and methods

### 2.1. A grid-summarization method allowing for the combined use of monitoring data collected at random and fixed sampling stations

We developed a new grid-summarization method that enables the fitting of statistical habitat models to encounter/non-encounter data



**Fig. 1.** Key steps of the new grid-summarization method introduced in the present study. (a) Construction of a spatial grid for the marine region under consideration. (b) Use of the spatial grid to summarize encounter/non-encounter data (filled and empty dots, respectively) for each monitoring program and sampling year.

collected by multiple monitoring programs at random and fixed sampling stations. The first step of our new method consists of the definition of a spatial grid of cells for the marine region under consideration (Fig. 1a). This spatial grid is utilized to summarize the monitoring data collected at random and fixed sampling stations (see next paragraph), but also to generate a prediction grid that is employed to translate the predictions of statistical habitat models fitted to grid-summarized monitoring data into distribution maps and suitability indices (see Subsections 2.5 and 2.6).

For a given species/life stage/season, the grid-summarization of monitoring data consists, for each monitoring program and year, of: (i) assigning the encounter/non-encounter data to the closest spatial grid cell, and assigning to these data the geographical coordinates of the barycenter of the assigned spatial grid cell; and (ii) assuming encounter (i.e., a value of 1) within a given spatial grid cell if at least one of the data points falling within that spatial grid cell is an encounter data point, and non-encounter (i.e., a value of 0) otherwise (Fig. 1b). For example, looking at Fig. 1, as no encounter data point falls within the top left cell of the spatial grid, the top left cell is assigned a value of 0 (non-encounter); and, as four encounter data points fall within the middle left cell of the spatial grid, the middle left cell is assigned a value of 1 (encounter). Our grid-summarization of monitoring data is necessary for obtaining a dataset of independent data points for subsequent statistical analyses. This process is similar to the calculation of average predator stomachs in fish diet studies, which fisheries analysts implement because individual stomachs obtained from the same sampling event are in general non-independent samples (Nielsen et al., 1983; Moriarty et al., 2017; Binion-Rock et al., 2018; Grüss et al., 2020).

Next, statistical habitat models are fitted to the grid-summarized monitoring data. The probabilities of encounter predicted by the statistical habitat models (e.g., spatial GLMMs, spatial GAMs) can be used to construct distribution maps and suitability indices. The statistical habitat models fitted to grid-summarized monitoring data collected at

random and/or fixed sampling stations (i.e., employing the grid-summarizing method) are hereafter referred to as “new models”, while the statistical habitat models fitted to the raw (not grid-summarized) monitoring data collected only at random sampling stations are hereafter referred to as “status-quo models”. In the following, we compare the predictions of new spatial GLMMs to those of status-quo spatial GLMMs, and then the predictions of new spatial GAMs to those of status-quo spatial GAMs.

## 2.2. Study areas and study species

In addition to demonstrating our new grid-summarization method, this study aims to provide seasonal distribution maps and suitability indices to an ecosystem model of the NWGOM that is currently under development. This ecosystem model under development is an ESIBM (an extension of single-species individual based model (IBM), namely a single-species IBM that incorporates environmental considerations) that follows individuals of croaker within a coupled hydrodynamic-biogeochemical model (namely FVCOM-WASP, Justić and Wang, 2014); a precursor version of the ESIBM for croaker under development is described in Rose et al. (2018a). The ESIBM for croaker under development will use the results for croaker for formulation of bycatch mortality effects of the NWGOM shrimp fishery on croaker and to validate the predicted spatial distributions and habitat locations of croaker in multi-year simulations. Distribution maps and suitability indices are produced for brown shrimp and red snapper life stages in the present study only to further analyze the performance and implications of our new grid-summarization method.

The spatial domain of the ESIBM of croaker under development, which is the same as the FVCOM-WASP model domain, encompasses the NWGOM shelf from Mobile Bay, Alabama, to East Matagorda Bay, Texas (Fig. 2a). Depth ranges between 0 and 300 m within this spatial domain. The FVCOM-WASP model also provided environmental data

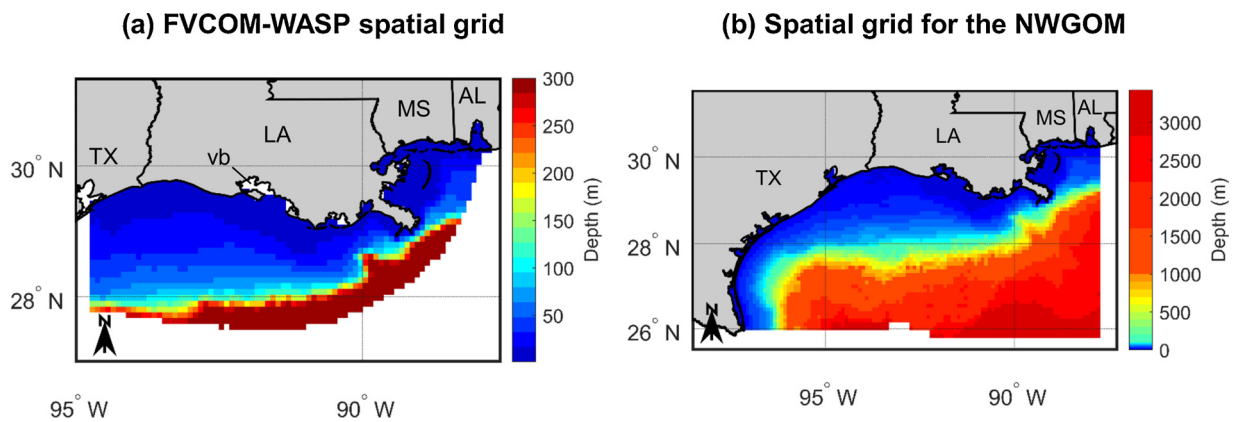


Fig. 2. Spatial grids developed for the present study. (a) The 10 km  $\times$  10 km FVCOM-WASP spatial grid developed for this study, showing the depth estimates used in the coupled hydrodynamic-biochemical model FVCOM-WASP. (b) The 10 km  $\times$  10 km spatial grid for the northwestern Gulf of Mexico developed for this study, and spatial patterns of depth in the region. The depth data used in (b) were derived from the 15 arc second ( $\sim$  500 m) resolution bathymetry grid predicted by the Coastal Relief Model for the U.S. Gulf of Mexico (<https://www.ngdc.noaa.gov/mgg/coastal/crm.html>). TX = Texas – LA = Louisiana – MS = Mississippi – AL = Alabama – vb = Vermilion Bay.

for the present study (see Subsection 2.4). We designed 10 km  $\times$  10 km (0.09°) spatial grid covering the FVCOM-WASP spatial domain (henceforth the “FVCOM-WASP spatial grid”; Fig. 2a). We employed the 10 km  $\times$  10 km FVCOM-WASP spatial grid for developing spatial GAMs for croaker, brown shrimp and red snapper life stages to then generate suitability indices (Subsection 2.6). The suitability indices for croaker life stages will serve to calibrate the ESIBM currently under development.

For developing spatial GLMMs to then construct seasonal distribution maps (Subsection 2.5), we did not utilize the 10 km  $\times$  10 km FVCOM-WASP spatial grid, but rather a larger 10 km  $\times$  10 km (0.09°) spatial grid covering the entire NWGOM, namely the U.S. Gulf of Mexico exclusive economic zone from Mobile Bay to the Mexican border (Fig. 2b). As the spatial GLMMs do not include environmental covariates, the spatial grid for the spatial GLMMs could be expanded beyond the FVCOM-WASP grid to include additional sampling locations. The distribution maps that were produced for croaker life stages from the predictions of the spatial GLMMs in this study will serve to validate the spatial distributions predicted by the ESIBM of croaker currently under development.

Our first study species is croaker, one of the dominant demersal fish species by biomass in the waters of Louisiana, particularly those impacted by large hypoxic events (Monk et al., 2015). Thus, croaker is one of the focal species of studies interested in the potential effects of nutrient loading and hypoxia (Rose et al., 2018a, 2018b). Croaker undertakes several ontogenetic migrations, i.e., moves offshore and into deeper waters with age. Croaker larvae ( $<$  32 mm TL) settle in shallow coastal waters (Rooker et al., 1998). Croaker early juveniles migrate to slightly deeper waters as they reach around 97.5 mm TL (Yakupzack et al., 1977). Croaker transition from the late juvenile to the adult stage when they reach around 180 mm TL, and, as adults, they occupy primarily a large band of the NWGOM shelf (Sheridan et al., 1984; Darnell, 1990; Diamond et al., 1999). Therefore, while croaker adults are caught by many monitoring programs using random sampling designs, a large fraction of croaker juveniles can only be sampled by the coastal LDWF surveys that use fixed sampling designs (Grüss et al., 2018e). In this study, we consider the early juvenile (32–97.5 mm TL), late juvenile (97.5–180 mm TL) and adult ( $\geq$  180 mm TL) stages of croaker.

Our second study species is brown shrimp, which is one of the most economically valuable living resources in the U.S. Gulf of Mexico (National Marine Fisheries Service (NMFS), 2017). Shrimps account for 60 % of landings revenue in the U.S. Gulf of Mexico (National Marine Fisheries Service (NMFS), 2017), and shrimp landings in the U.S. Gulf of Mexico represent around 73 % of the total shrimp landings in the U.S. (Iverson and Martin, 2009; Purcell et al., 2017). Like white shrimp

(*Litopenaeus setiferus*) and contrary to pink shrimp (*Farfantepenaeus duorarum*), brown shrimp is much more abundant in the NWGOM than in the northeastern Gulf of Mexico (Grüss et al., 2018e). Small brown shrimps ( $<$  100 mm TL) are in general encountered in shallow areas where depth ranges between 0 and 20 m (e.g., marshes, inshore estuaries; Fry, 2008; Lassuy, 1983; Craig et al., 2005; Grüss et al., 2018e). Therefore, like croaker juveniles, in Louisiana waters, small brown shrimps are only sampled by the coastal LDWF surveys that employ fixed sampling designs. Large brown shrimps ( $\geq$  100 mm TL) are encountered in deeper waters (primarily at depths ranging between 20 and 110 m) that are well covered by the monitoring programs that use random sampling designs (Darnell et al., 1983; Lassuy, 1983; Grüss et al., 2018e). Brown shrimp is particularly abundant in Texas territorial waters, where a combination of management measures, including spatial and temporal closures, have been imposed for several decades (Caillouet et al., 2008; Matlock, 2010; Grüss et al., 2018e). In particular, since 1960, spatial closures have been implemented in Texas territorial waters from the shore to 9 nautical miles during small brown shrimp peak emigration period (from late May to early July), so as to delay the harvest of the small brown shrimps that are migrating from inshore to offshore areas (Cody et al., 1989; Matlock, 2010). In this study, we consider small ( $<$  100 mm TL) and large ( $\geq$  100 mm TL) brown shrimps.

Finally, our third study species is red snapper, which also undertakes ontogenetic migrations and is one of the most socio-economically important fish species in the U.S. Gulf of Mexico (Gallaway et al., 2009). The red snapper commercial fishery has been historically one of the fisheries with the largest landings in the U.S. Gulf of Mexico, while the red snapper recreational fishery is a multi-billion-dollar industry (National Marine Fisheries Service (NMFS), 2017). The ecology of red snapper has been extensively studied, and relying only on monitoring programs using random sampling designs is sufficient to map the spatial distributions of all red snapper life stages, including the younger juveniles (Grüss et al., 2018e). Red snapper is much more abundant in the NWGOM than in the eastern U.S. Gulf of Mexico (Karnauskas et al., 2017; Grüss et al., 2018e; Dance and Rooker, 2019). Red snapper younger juveniles (50–230 mm TL) are primarily found at depths of 20–60 m (Gallaway et al., 1999; Szedlmayer and Conti, 1999; Monk et al., 2015), red snapper older juveniles (230–300 mm TL) at depths of 40–60 m (Szedlmayer and Lee, 2004; Wells, 2007; Gallaway et al., 2009), and red snapper adults ( $\geq$  300 mm TL) at depths of 80–200 m (Patterson et al., 2001; Mitchell et al., 2004; Gallaway et al., 2009). In this study, we consider the juvenile (50–300 mm TL) and adult ( $\geq$  300 mm TL) stages of red snapper.



**Table 1**

Monitoring programs operating in the northwestern Gulf of Mexico that were considered in this study. Details about the monitoring programs can be found in Table A1.

Monitoring program	Fisheries-independent or fisheries-dependent program?	Sampling design	Total number of stations-years
Alabama Marine Resources Division (AMRD) Fisheries Assessment and Monitoring Program (FAMP) Gillnet Survey (Alias: ALGILL)	Fisheries-independent	Random	2291
AMRD FAMP Trawl Survey (Alias: ALTRAWL)	Fisheries-independent	Fixed	4954
National Marine Fisheries Service (NMFS) Bottom Longline Survey (Alias: BLL)	Fisheries-independent	Random	2542
Southeast Area Monitoring and Assessment Program (SEAMAP) Gulf of Mexico Inshore Bottom Longline Survey (Alias: INBLL)	Fisheries-independent	Random	1054
Louisiana Department of Wildlife and Fisheries (LDWF) Gillnet Survey (Alias: LAGILL)	Fisheries-independent	Fixed	16,670
LDWF Seine Survey (Alias: LASEINE)	Fisheries-independent	Fixed	11,766
LDWF Trammel Survey (Alias: LATRAM)	Fisheries-independent	Fixed	4650
LDWF Trawl Survey (Alias: LATRAWL)	Fisheries-independent	Fixed	1087
LDWF Vertical Line Survey (Alias: LAVL)	Fisheries-independent	Random	859
Gulf Coast Research Laboratory (GCRL) Trawl Survey (Alias: MSTRAWL)	Fisheries-independent	Random	642
NMFS Southeast Gillnet Observer Program (Alias: OBSGILL)	Fisheries-dependent	Random	489
Reef Fish Bottom Longline Observer Program (Alias: OBSLL)	Fisheries-dependent	Random	9017
Southeastern Shrimp Fisheries Observer Coverage Program (Alias: OBSSHIMP)	Fisheries-dependent	Random	44,783
Reef Fish Vertical Line Observer Program (Alias: OBSVL)	Fisheries-dependent	Random	39,696
SEAMAP Groundfish Trawl Survey (Alias: TRAWL)	Fisheries-independent	Random	1593
Texas Parks and Wildlife Department (TPWD) Bottom Longline Survey (Alias: TXBLL)	Fisheries-independent	Random	141
TPWD Gillnet Survey (Alias: TXGILL)	Fisheries-independent	Random	12,480
TPWD Seine Survey (Alias: TXSEINE)	Fisheries-independent	Random	34,476
TPWD Trawl Survey (Alias: TXTRAWL)	Fisheries-independent	Random	42,106
SEAMAP Reef Fish Video Survey (Alias: VIDEO)	Fisheries-independent	Random	5284
SEAMAP Gulf of Mexico Vertical Longline Survey (Alias: VL)	Fisheries-independent	Random	1807

### 2.3. Monitoring data used in this study

We compiled a large monitoring database that gathered the encounter/non-encounter data collected between 2000 and 2015 by almost all the monitoring programs that operate in the NWGOM and collect fish length information. The datasets incorporated in the large monitoring database came from a total of 21 monitoring programs, including 12 fisheries-independent programs using random sampling schemes, 4 fisheries-dependent programs using random sampling schemes, and 5 fisheries-independent programs using fixed sampling schemes (Table 1 and A1). From each monitoring dataset, we extracted the following information: (i) the latitude and longitude of sampling events; (ii) the year and season (spring: April-June; summer: July-September; fall: October-December; winter: January-March) of the sampling events; and (iii) whether the sampling events encountered or not the life stages of interest (croaker early juveniles, late juveniles and adults, small and large brown shrimps, and red snapper juveniles and adults). One of the five fixed-station programs considered in this study is conducted in coastal Alabama waters, while the four others are carried out in coastal Louisiana waters (Fig. A2). Out of the 238,387 stations-years sampled by the 21 monitoring programs considered in this study, a total of 39,127 stations-years was sampled by the fixed-station programs (Table 1). In other words, using a combination of random-station and fixed-station monitoring data instead of only random-station monitoring data in this study increased the amount of monitoring data potentially available for statistical analyses by 20 %. Note that we did not employ the encounter/non-encounter data collected by the Texas marine sport-harvest monitoring program survey, a fisheries-dependent program using a fixed sampling scheme (Matter, 2012). The reason for this is that the fisheries-independent programs collecting monitoring data at random sampling stations in Texas waters that were considered in this study already provided us with an extremely large amount of encounter/non-encounter data for the entirety of the Texas coast.

For each croaker, brown shrimp and red snapper life stage and each season, we determined which of the monitoring datasets and years should be considered to fit spatial GLMMs and spatial GAMs. Specifically, we excluded: (i) monitoring datasets with fewer than 50 encounters (Leathwick et al., 2006; Austin, 2007; Laman et al., 2018);

and (ii) years with fewer than 5 encounters (Grüss et al., 2018b, 2018c, 2018e).

### 2.4. Environmental data used in this study

To generate suitability indices for each study life stage and season, we fitted spatial GAMs to encounter/non-encounter data, as well as to environmental data that came from the FVCOM-WASP simulations of 2002, 2005, and 2012. The FVCOM-WASP environmental data used as predictor variables in the spatial GAMs were depth and bottom salinity. Depth and bottom salinity have been found to influence the spatial distribution patterns of croaker (Moore et al., 1970; Chittenden and Moore, 1977; Craig and Crowder, 2005; Carassou et al., 2011), brown shrimp (Zein-Eldin and Aldrich, 1965; Clark et al., 2004; Montero et al., 2016; Hijuelos et al., 2017), and red snapper (Galloway et al., 1999; Szedlmayer and Conti, 1999; Karnauskas et al., 2017; Grüss et al., 2018e; Dance and Rooker, 2019). Other environmental parameters are also thought to influence croaker, brown shrimp and red snapper spatial distribution patterns, such as temperature, low dissolved oxygen concentration, seafloor substrate type, and the presence of artificial reefs (Migliarese et al., 1982; Diaz and Onuf, 1985; Craig and Crowder, 2005; Li and Clarke, 2005; Karnauskas et al., 2017; Dance and Rooker, 2019). These other environmental parameters were not included as predictors in the spatial GAMs, because they were related to depth or bottom salinity, they had incomplete spatial coverage, or because their expected effects were a threshold or another relationship (e.g., avoidance of low dissolved oxygen concentration) requiring more precise temporal and spatial matching of encounter/non-encounter data with environmental data than was possible between the monitoring data and the FVCOM-WASP output.

The depth field was time-invariant, and the temporal and spatial aggregation of FVCOM-WASP predictions provided seasonal fields of bottom salinity for our spatial GAM efforts (Appendix A3). The final seasonal fields of bottom salinity produced for this study resulted from the averaging of the seasonal fields of bottom salinity for years of low spring (2012), intermediate spring (2005), and high spring (2002) freshwater inflows from the Mississippi River. The spatial resolution of the coupled hydrodynamic-biogeochemical model FVCOM-WASP is finer than that of the 10 km × 10 km FVCOM-WASP spatial grid used in

the present study; FVCOM-WASP employs a 1–10 km unstructured grid. Therefore, we first averaged the bottom salinity over the cells of the 10 km × 10 km FVCOM-WASP spatial grid developed for this study for all hours within spring, summer, fall and winter for each of 2002, 2005 and 2012. We then averaged over the three years to obtain single 10 km × 10 km maps of bottom salinity for spring, summer, fall and winter (Appendix A3). We averaged the seasonal fields of bottom salinity for 2002, 2005 and 2012 (i.e., we provided “climatologies” to the spatial GAMs), because we wanted general relationships not subject to variation within specific years. “Contemporaneous” environmental estimates (Mannocci et al., 2017a), rather than climatological environmental estimates, could be provided to the spatial GAMs to generate possibly more refined and year-specific suitability indices, but we leave this for future research.

## 2.5. Development of spatial GLMMs and production of distribution maps

Spatial binomial GLMMs were developed for croaker, brown shrimp and red snapper life stages for the different seasons of the year with R package “VAST” Version 3.0.0 (Thorson, 2019), which can be accessed freely online (<https://github.com/James-Thorson-NOAA/VAST>). We only briefly detail the spatial binomial GLMMs here, as they were extensively described in many previous studies (e.g., Grüss et al., 2017b, 2018e). Additional details on spatial binomial GLMMs can also be found in Appendix A4.

For each life stage and season, a spatial binomial GLMM approximates probability of encounter  $p_i$  at a sampled location  $s(i)$ , using a logit link function and linear predictors, including a Gaussian Markov random field representing spatial variation in probability of encounter at a fine scale (i.e., spatial autocorrelation at a fine scale):

$$p_i = \text{logit}^{-1} \left( \sum_{t=1}^{n_t} \beta_t Y_{i,t} + \sum_{m=1}^{n_m} \gamma_m G_{i,m} + \varepsilon_{s(i)} \right) \quad (1)$$

where: (i)  $\beta_t$  is an intercept that varies among years;  $Y_{i,t}$  is a design matrix such that  $Y_{i,t}$  is 1 for the year  $t$  during which sample  $i$  was collected and 0 otherwise;  $n_t$  is the total number of years for which monitoring data are available for the life stage and season under consideration; and, therefore, the first term,  $\sum_{t=1}^{n_t} \beta_t Y_{i,t}$  is the fixed year effect on  $p_i$  on the logit scale; (ii)  $G_{i,m}$  is a design matrix such that  $G_{i,m}$  is 1 for the monitoring program  $m$  that obtained sample  $i$  and 0 otherwise;  $\gamma_m$  is a coefficient such  $\gamma_m = 0$  for the program  $m$  associated with the largest sample size for the life stage and season under consideration, so as to allow for the identifiability of all year intercepts  $\beta_t$ ;  $n_m$  is the total number of monitoring programs retained for the life stage and season under consideration; and, therefore, the second term,  $\sum_{m=1}^{n_m} \gamma_m G_{i,m}$  is the monitoring program effect on  $p_i$ , which is treated as a random effect via the implementation of restricted maximum-likelihood (REML); and (iii)  $\varepsilon_{s(i)}$  are the random effects of the spatial residuals in probability of encounter on the logit scale.

For the sake of computational efficiency, the random effects  $\varepsilon$  are approximated using 4000 “knots”, which are defined through the application of a  $k$ -means algorithm to the locations of the monitoring data (raw (not grid-summarized) monitoring data collected only at random sampling stations in the case of the status-quo models, and grid-summarized monitoring data collected at random and/or fixed sampling stations in the case of new models). The  $k$ -means algorithm allocates knots over space with a density proportional to monitoring intensity (Shelton et al., 2014; Thorson et al., 2015).

Template Model Builder (TMB) is called within R to estimate the parameters of the spatial binomial GLMMs (Kristensen et al., 2016). After fitting to monitoring data, the spatial GLMMs pass a validation test, where standard convergence diagnostics and Pearson residuals are employed (Appendix A4; Thorson et al., 2015; Grüss et al., 2017b, 2018e).

Once fitted and validated spatial binomial GLMMs are obtained, the

next step is to make predictions with the GLMMs. This step necessitates, for each life stage and season, the construction of a prediction grid from the spatial grid defined for the marine region of interest (the 10 km × 10 km spatial grid for the NWGOM shown in Fig. 2b in our case), based on the ranges of longitude, latitude and depth at which the life stage was encountered by monitoring programs during the season under consideration. In other words, for each life stage and season, the spatial grid defined for the marine region of interest is subsetted to obtain a prediction grid. The depth data that we used for generating prediction grids were derived from the 15 arc second (~ 500 m) re-solution bathymetry grid predicted by the Coastal Relief Model for the U.S. Gulf of Mexico (<https://www.ngdc.noaa.gov/mgg/coastal/crm.html>). We made predictions of probability of encounter with the fitted and validated GLMMs for the 10 km × 10 km prediction grids, while assuming, for the life stage and season under consideration, that the Gaussian Markov random field in each prediction grid cell is given by the value of the Gaussian Markov random field at the closest knot.

Ultimately, it is possible to produce distribution maps from the predictions made with fitted and validated GLMMs. First, for each life stage and season, the fitted and validated GLMM is employed to construct a map of probability of encounter for each sampling year. Then, the maps of probability of encounter for each sampling year are averaged to yield one average map of probability of encounter for each life stage and season (Grüss et al., 2017b, 2018e).

We compared the results of the validation test and distribution maps for the new versus the status-quo spatial GLMMs. As mentioned earlier, the only difference between the new and the status-quo spatial GLMMs is that, to define the 4000 knots, the  $k$ -means algorithm is applied to the locations of the grid-summarized monitoring data collected at random and/or fixed sampling stations in the case of the new spatial GLMMs, and to the locations of raw monitoring data collected only at random sampling stations in the case of the status-quo spatial GLMMs.

## 2.6. Development of spatial GAMs and production of suitability indices

For the life stage and season combinations analyzed for croaker, brown shrimp and red snapper, spatial binomial GAMs were developed with R package “mgcv” (Wood, 2017). These spatial binomial GAMs included the fixed effects of depth and bottom salinity, an interaction term between eastings and northings (i.e., longitude and latitude expressed in UTM coordinates), and the effects of year and monitoring program. The interaction term between eastings and northings accounted for spatial autocorrelation at a broad scale (Wood, 2017; Grüss et al., 2018b, 2019b). Year and monitoring program were “nuisance” variables treated as fixed effect factors (Farmer and Karnauskas, 2013; Grüss et al., 2018b). Here, we used the depth estimates from the coupled hydrodynamic-biogeochemical model FVCOM-WASP (averaged for our 10 km × 10 km FVCOM-WASP spatial grid) to match with the bottom salinities obtained from FVCOM-WASP (averaged for our 10 km × 10 km FVCOM-WASP spatial grid). Suitability indices could only be predicted for the domain of the FVCOM-WASP spatial grid where depth and bottom salinity are available.

For each life stage and season, prior to fitting spatial GAMs to monitoring data, we conducted a collinearity analysis, which was necessary as regression methods like GAMs may be sensitive to correlated predictors (Guisan et al., 2002; Dormann et al., 2013). This collinearity analysis consisted of: (i) calculating Pearson’s correlation coefficients between depth and bottom salinity, and between depth and bottom salinity and eastings and northings; and (ii) removing depth and/or bottom salinity if we found Pearson’s correlation coefficients greater than 0.7 in absolute value (Leathwick et al., 2006; Dormann et al., 2013).

For each life stage and season, a spatial binomial GAM of the following form was fitted to monitoring data (raw (not grid-summarized) monitoring data collected only at random sampling sites in the case of the status-quo models, and grid-summarized monitoring data collected

at random and/or fixed sampling sites in the case of the new models):

$$g(\eta) = te(X, Y) + s(\text{depth}) + s(\text{bottom salinity}) + \text{factor}(\text{year}) + \text{factor}(\text{monitoring program}) \quad (2)$$

where  $\eta$  is the probability of encounter;  $g$  is the logit link function between  $\eta$  and each term on the right side of the equation;  $te(X, Y)$  is a tensor product smooth fitted to eastings and northings;  $s$  is a thin plate regression spline with shrinkage fitted to depth or bottom salinity, which is limited to four degrees of freedom to help preserve the ecological interpretability of the suitability indices generated from GAM predictions (Roberts et al., 2016; Mannocci et al., 2017; Grüss et al., 2018b, 2019b). The REML optimization method was utilized (Wood, 2011).

We implemented a shrinkage approach to select environmental predictors (depth and bottom salinity) for the spatial binomial GAMs (Roberts et al., 2016; Mannocci et al., 2017b). Additionally, we applied an extra penalty to each environmental predictor, as the smoothing parameter approached zero, which allowed for the complete removal of depth and/or bottom salinity from a spatial GAM when the smoothing parameter was equal to zero (Marra and Wood, 2012). Moreover, after GAM fitting, if the  $p$ -value of depth or bottom salinity exceeded 0.05, depth or bottom salinity was removed from the spatial GAM and the spatial GAM was refitted (Koubbi et al., 2006; Grüss et al., 2014; Chagaris et al., 2015). Thus, it was possible to obtain final spatial GAMs that included the effect of depth, the effect of bottom salinity, both of these effects or none of these effects.

The fitted spatial binomial GAMs were evaluated using a 10-fold cross validation procedure called “Leave Group Out Cross Validation” (Hastie et al., 2001; Kuhn and Johnson, 2013). Briefly, for each life stage and season, this 10-fold cross validation procedure consists of: (i) randomly splitting the monitoring dataset into a training dataset (60 % of the data) and a test dataset (40 % of the data); (ii) repeating Step 1 ten times and, therefore, producing 10 training datasets and 10 test datasets; (iii) fitting a binomial GAM to each of the 10 training datasets; (iv) evaluating the 10 fitted binomial GAMs using the test datasets, by means of two performance metrics: the area under the receiver operating characteristic curve (AUC), which describes how well a binomial GAM discriminates between non-encounters and encounters (i.e., is indicative of discrimination accuracy); and the adjusted coefficient of determination (adjusted  $R^2$ ), which quantifies how much of the variance of the probability of encounter is explained by the GAM under consideration (i.e., is indicative of predictive accuracy); and (v) considering a GAM acceptable if both the median AUC value over the 10 folds is greater than 0.7 (Hanley and McNeil, 1982; Pearce and Ferrier, 2000) and the median adjusted  $R^2$  over the 10 folds is above 0.1 (Legendre and Legendre, 1998).

After the spatial binomial GAM for each life stage and season was fitted and validated, probabilities of encounter were predicted. For each life stage and season, we constructed a 10 km  $\times$  10 km prediction grid from the 10 km  $\times$  10 km FVCOM spatial grid (Fig. 2a), based on the ranges of longitude, latitude and depth at which the life stage was encountered by monitoring programs during the season under consideration. Here, the depth data that we employed for generating prediction grids were the depth estimates used in FVCOM-WASP (Fig. 2a). For each environmental predictor  $i$  included in the spatial GAM for a given life stage and season (depth or bottom salinity), predictions were made over a vector of values ranging between the minimum and maximum values of environmental predictor  $i$  over the prediction grid for the life stage and season under consideration. This was done while: (i) setting eastings and northings to their values at the barycenter of the prediction grid; (ii) keeping the other environmental predictor integrated in the GAM constant at their mean value from the modeled dataset; and (iii) setting the year and monitoring program factors to their most frequent levels from the modeled dataset (Grüss et al., 2018d, 2018b, 2019b). Let us denote the  $j$ th value of environmental

variable  $i$  by  $x_{i,j}$ , where  $x_{i,j}$  ranges between the minimum and maximum values of environmental variable  $i$  over the prediction grid for the life stage and season under consideration. The predictions we made with spatial GAMs resulted in probabilities of encounter  $p_{i,j}$  for each value of  $x_{i,j}$ .

Ultimately, it was possible to compute suitability indices ( $y_{i,j}$ ), which express the suitability of environmental conditions  $x_{i,j}$  for a given life stage in a given season, as follows:

$$y_{i,j} = \frac{p_{i,j} - \min\{p_{i,j}\}}{\max\{p_{i,j}\} - \min\{p_{i,j}\}} \quad (3)$$

This computation ensures that suitability indices range between 0 and 1; the higher a given suitability index  $y_{i,j}$ , the more suitable the environmental conditions  $x_{i,j}$  are for the life stage and season under consideration (Grüss et al., 2018b, 2018d, 2019b).

We compared the results of the validation test and predicted suitability indices for the new versus the status-quo spatial GAMs. Again, the difference between the new and the status-quo spatial GAMs is that the new spatial GAMs were fitted to grid-summarized monitoring data collected at random and/or fixed sampling stations, while the status-quo spatial GAMs were fitted to raw (not grid-summarized) monitoring data collected only at random sampling stations.

To facilitate the interpretation of the suitability indices, we also produced maps of probability of encounter from spatial GAM predictions. For each life stage and season, maps of probability of encounter were constructed using (i) the spatial GAMs fitted for those life stage and season; (ii) the 10 km  $\times$  10 km prediction grid generated for those life stage and season from the 10 km  $\times$  10 km FVCOM-WASP spatial grid; and (iii) the most frequent year and monitoring program factor levels in the modeled dataset for those life stage and season (Punt et al., 2000; Ono et al., 2015; Grüss et al., 2018d, 2018b, 2019b).

### 3. Results

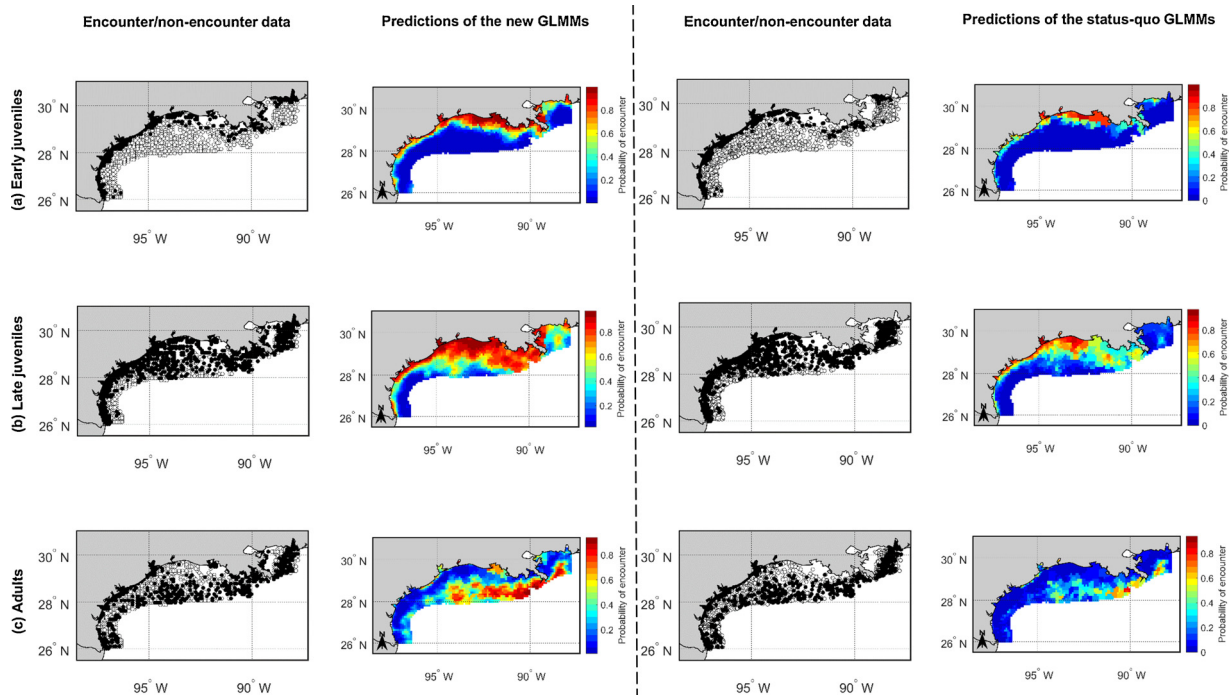
#### 3.1. Monitoring data available for statistical habitat modeling

The monitoring data available for statistical habitat modeling varied widely in terms of their coverage of life stages and seasons (Figs. 3–7 and A5 and Tables A6 and A7). In the cases of croaker and brown shrimp, monitoring data collected at random sampling stations were generally supplemented by a reasonable amount of monitoring data collected at fixed sampling stations in Louisiana and Alabama coastal waters (Figs. 3–5 and A5 and Tables A6 and A7). Exceptions to this general pattern included croaker early juveniles in fall and winter, croaker late juveniles in winter, croaker adults in winter, small brown shrimps in fall and winter, and large brown shrimps in winter (Fig. A5); therefore, statistical habitat models were not developed for these particular life stage and season combinations. By contrast, in the case of red snapper, monitoring data collected at random sampling stations were never supplemented by monitoring data collected at fixed sampling stations, and the monitoring data collected at random sampling stations were sufficient for developing statistical habitat models for all our target life stages and seasons (Figs. 6 and 7 and A5 and Tables A6 and A7). Therefore, for each red snapper life stage and season, we fitted the new and the status-quo statistical habitat models to the exact same monitoring dataset. Thus, differences between the new and the status-quo statistical habitat models for red snapper life stages can only be attributed to the fact that monitoring data were grid-summarized in the case of new statistical habitat models versus not grid-summarized in the case of status-quo statistical habitat models.

#### 3.2. Development of spatial GLMMs and production of distribution maps

For the present study, we fitted a total of 42 spatial GLMMs, including 21 spatial GLMMs that were fitted to grid-summarized

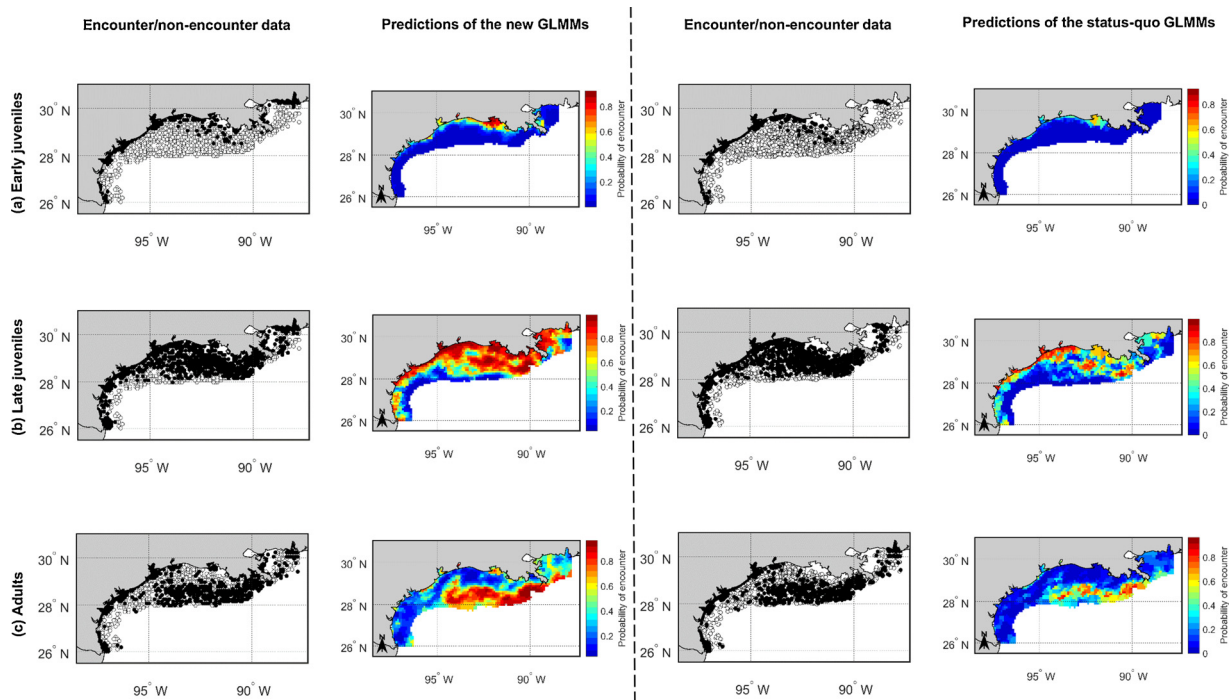




**Fig. 3.** Encounter/non-encounter data (full circles: encounters; empty circles: non-encounters) and predictions of the new and status-quo spatial generalized linear mixed models (GLMMs) for (a) early juveniles, (b) late juveniles and (c) adults of croaker (*Micropogonias undulatus*) in spring. The new spatial GLMMs use grid-summarized monitoring data collected at random and fixed sampling stations, while the status-quo spatial GLMMs use raw (not grid-summarized) monitoring data collected only at random sampling stations.

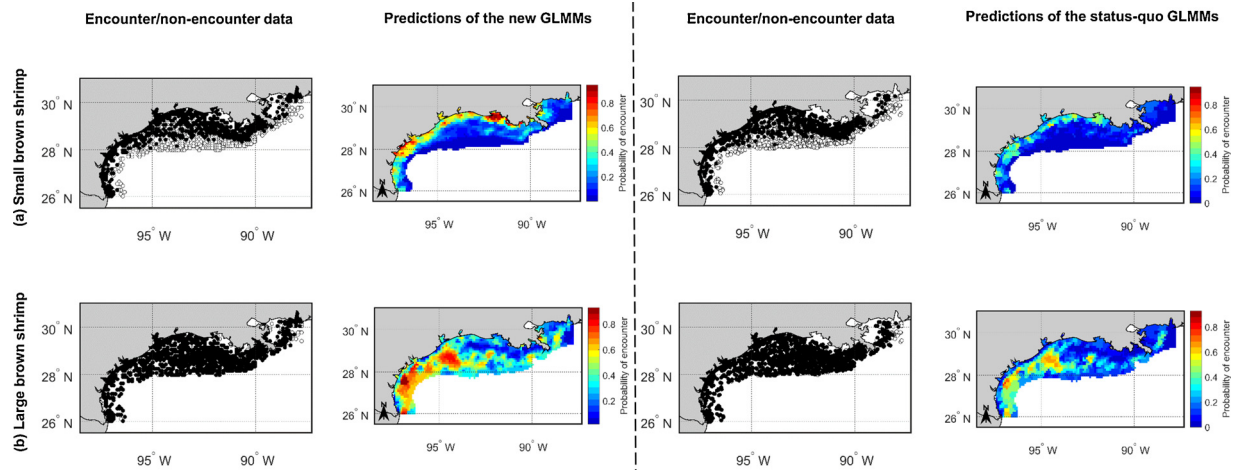
monitoring data collected at random and/or fixed sampling stations (i.e., 21 “new” spatial GLMMs), and 21 spatial GLMMs that were fitted to raw (not grid-summarized) monitoring data collected only at random sampling stations (i.e., 21 “status-quo” spatial GLMMs). Specifically, we fitted 2 \* 2 spatial GLMMs for croaker early juveniles, 3 \* 2 spatial

GLMMs for croaker late juveniles, 3 \* 2 spatial GLMMs for croaker adults, 2 \* 2 spatial GLMMs for small brown shrimps, 3 \* 2 spatial GLMMs for large brown shrimps, 4 \* 2 spatial GLMMs for red snapper juveniles, and 4 \* 2 spatial GLMMs for red snapper adults (Table A6). For all croaker, brown shrimp and red snapper life stages and seasons,



**Fig. 4.** Encounter/non-encounter data (full circles: encounters; empty circles: non-encounters) and predictions of the new and status-quo spatial generalized linear mixed models (GLMMs) for (a) early juveniles, (b) late juveniles and (c) adults of croaker (*Micropogonias undulatus*) in summer. The new spatial GLMMs use grid-summarized monitoring data collected at random and fixed sampling stations, while the status-quo spatial GLMMs use raw (not grid-summarized) monitoring data collected only at random sampling stations.





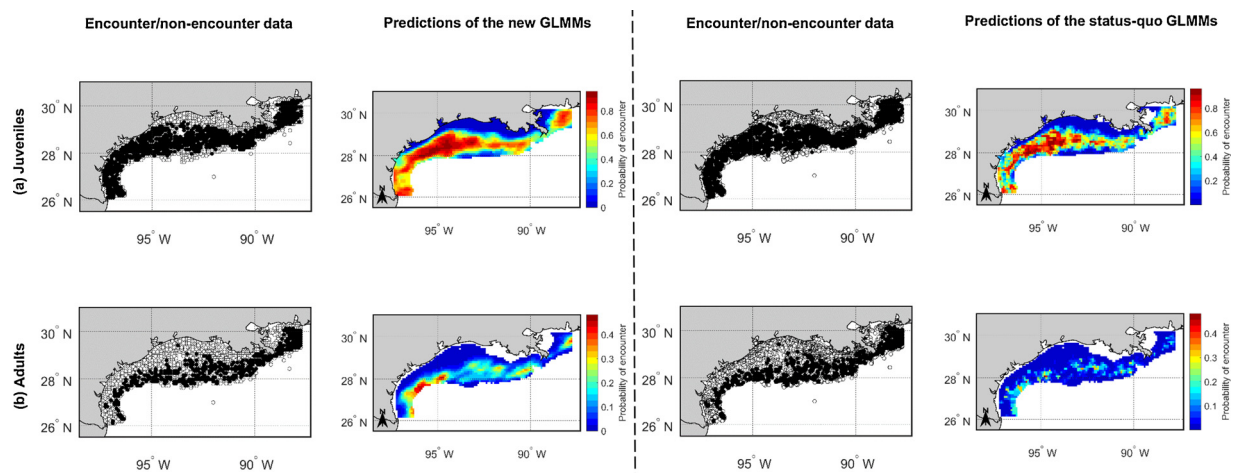
**Fig. 5.** Encounter/non-encounter data (full circles: encounters; empty circles: non-encounters) and predictions of the new and status-quo spatial generalized linear mixed models (GLMMs) for (a) small brown shrimp (*Farfantepenaeus aztecus*) and (b) large brown shrimps in summer. The new spatial GLMMs use grid-summarized monitoring data collected at random and fixed sampling stations, while the status-quo spatial GLMMs use raw (not grid-summarized) monitoring data collected at random sampling stations.

none of the estimated fixed parameters hit an upper or lower bound, the final gradient for each fixed parameter was close to zero, and the Hessian matrix was positive definite (Table A8). Therefore, for all study life stages and seasons, we found no evidence of non-convergence. Moreover, for all study life stages and seasons, Pearson residual plots showed that observed encounter frequencies for either low or high probability samples were within or extremely close to the 95 % confidence interval for predicted probability of encounter (Fig. A9). Pearson residual plots were usually similar for the new and the status-quo spatial GLMMs. The only exception to this usual pattern was croaker early juveniles in summer. In that case, the status-quo spatial GLMM slightly underestimated probability of encounter for the highest probability samples (Fig. A9).

Overall, the new and the status-quo spatial GLMMs predicted roughly similar spatial distribution patterns for all croaker life stages and seasons (Figs. 3 and 4 and A10 and Table A11). Both the new and the status-quo spatial GLMMs predicted that: (i) croaker early juveniles occupy relatively shallow coastal waters (mean depth  $\leq 10$  m), croaker late juveniles generally occupy deeper areas of the NWGOM (mean depth of 18 – 24 m), and croaker adults are usually encountered on the continental shelf of the NWGOM rather than in coastal areas (mean

depth of 35 – 53 m); and (ii) in summer, croaker early juveniles tend to be found at shallower depths and croaker adults at deeper depths, compared to the other seasons of the year.

However, the status-quo spatial GLMMs predicted very low probabilities of encounter in some of the coastal areas where the new spatial GLMMs predicted high probabilities of encounter, as the status-quo models relied on monitoring data collected only at random sampling stations, while new models relied on monitoring data collected at both random and fixed sampling stations (Figs. 3 and 4 and A10). For example, the probabilities of encounter of croaker early and late juveniles in the coastal waters of eastern Louisiana, Mississippi and Alabama in spring were predicted to be high by the new spatial GLMMs, but low by the status-quo spatial GLMMs (Fig. 3). We can also note that, while the new spatial GLMMs developed for croaker life stages did not use additional fixed-station monitoring data for Texas coastal waters, these new spatial GLMMs predicted higher probabilities of encounter for croaker life stages in Texas nearshore areas than the status-quo spatial GLMMs (Figs. 3 and 4 and A10). These predictions of the new spatial GLMMs are due to the spatial autocorrelation terms (i.e., the random effects  $\epsilon$ ) that the new spatial GLMMs estimated from a combination of random-station and fixed-station monitoring data, which suggested a



**Fig. 6.** Encounter/non-encounter data (full circles: encounters; empty circles: non-encounters) and predictions of the new and status-quo spatial generalized linear mixed models (GLMMs) for (a) juveniles and (b) adults of red snapper (*Lutjanus campechanus*) in spring. The new spatial GLMMs use grid-summarized monitoring data collected at random sampling stations, while the status-quo spatial GLMMs use raw (not grid-summarized) monitoring data collected at random sampling stations.

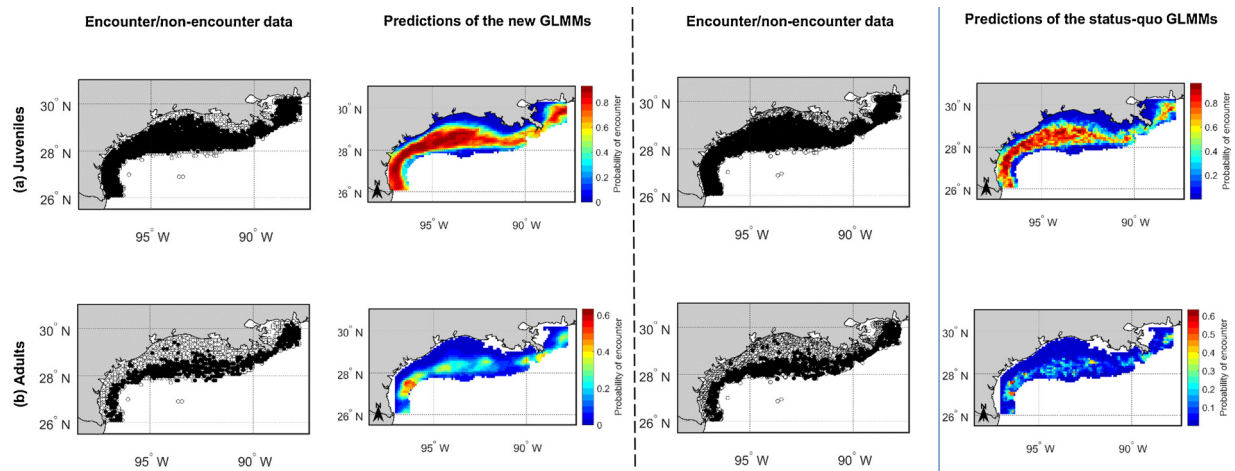


Fig. 7. Encounter/non-encounter data (full circles: encounters; empty circles: non-encounters) and predictions of the new and status-quo spatial generalized linear mixed models (GLMMs) for (a) juveniles and (b) adults of red snapper (*Lutjanus campechanus*) in fall. The new spatial GLMMs use grid-summarized monitoring data collected at random sampling stations, while the status-quo spatial GLMMs use raw (not grid-summarized) monitoring data collected at random sampling stations.

higher probability of encounter in Texas coastal areas based on the very high probabilities of encounter estimated in nearby Louisiana coastal areas from the encounter/non-encounter data collected at fixed sampling stations by the LDWF. Another example is that croaker adults, whose probability of encounter in the Vermilion Bay area (labelled as “vb” on Fig. 2a) in all seasons was predicted to be high by the new spatial GLMMs, but close to zero by the status-quo spatial GLMMs (Figs. 3 and 4 and A10). Finally, for all croaker life stages and seasons, the spatial distributions predicted by the new spatial GLMMs were smoother, with somewhat wider areas of encounters, compared to the spatial distributions predicted by the status-quo spatial GLMMs (Figs. 3 and 4 and A10).

The new and the status-quo spatial GLMMs tended to predict similar spatial distribution patterns for the small and large brown shrimp for the summer season (Fig. 5 and Table A11) and other seasons (Fig. A12 and Table A11). As with croaker, the spatial distributions predicted by the new spatial GLMMs were broader, although similarly centered, as the spatial distributions predicted by the status-quo spatial GLMMs. Both the new and the status-quo spatial GLMMs predicted that small brown shrimps are found in relatively shallow coastal waters (mean depth of 12–17 m), while large brown shrimps generally occupy deeper areas on the NWGOM shelf (mean depth of 41–54 m) (Table A11). Both the new and the status-quo spatial GLMMs predicted that the bulk of small shrimps in spring and the bulk of large shrimps in spring and summer are encountered west of Vermilion Bay, particularly in Texas waters, yet the probabilities of encounter in Louisiana, Mississippi and Alabama waters predicted by the new GLMM were higher than those predicted by the status-quo spatial GLMM (Figs. 5 and A12). Both the new and the status-quo spatial GLMMs predicted that, in summer, small brown shrimps are primarily encountered in the coastal waters of western Louisiana and Texas (Fig. 5). Predictions were not available for small brown shrimps in the fall. The probability of encounter of large brown shrimps in fall was predicted to be high all over the NWGOM shelf by the new spatial GLMM, but high only on the western Louisiana and Texas shelves by the status-quo spatial GLMM (Fig. A12).

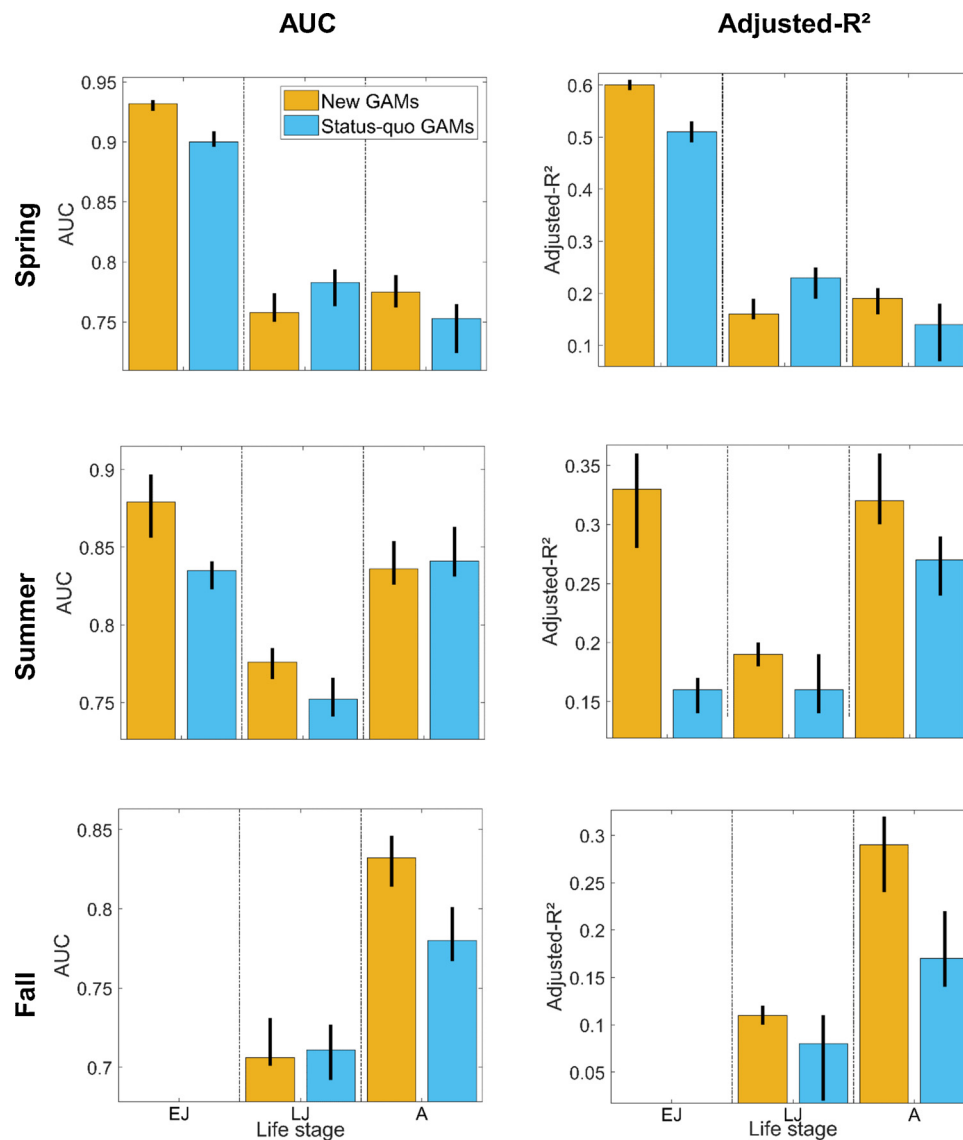
The new and the status-quo spatial GLMMs predicted very similar spatial distribution patterns for all red snapper life stages and seasons, as the two types of spatial GLMMs relied on the exact same monitoring datasets (Figs. 6 and 7 and A13 and Table A11). In all seasons, both the new and the status-quo spatial GLMMs predicted that: (i) red snapper juvenile hotspots are mainly located off Texas, Mississippi and Alabama; (ii) the probability of encounter of red snapper adults tends to be higher in Texas waters than in Louisiana, Mississippi and Alabama waters; and

(iii) red snapper adults are usually found in deeper waters than red snapper juveniles (mean depth of 70–88 m versus 43–58 m). However, the new spatial GLMMs resulted in much smoother distribution maps (although similar extent and location of the distributions) than the status-quo spatial GLMMs for all red snapper life stages and seasons (Figs. 6 and 7 and A13). In other words, using our new grid-summarization method rather than the status-quo method does not affect spatial GLMM predictions qualitatively, and simply results in smoother predicted spatial patterns of probability of encounter.

### 3.3. Development of spatial GAMs and production of suitability indices

We fitted 42 spatial GAMs that matched the spatial GLMMs. Thus, 21 spatial GAMs were fitted to grid-summarized monitoring data collected at random and/or fixed sampling stations (i.e., 21 “new” spatial GAMs), and 21 spatial GAMs were fitted to raw monitoring data collected only at random sampling stations (i.e., 21 “status-quo” spatial GAMs) (see Table A7 for details). The selection of environmental covariates (depth and/or bottom salinity) based on the collinearity analysis and the  $p$ -values of the environmental predictors sometimes resulted in final new and status-quo spatial GAMs that included only depth, only bottom salinity, both predictors, or none of the two predictors (Table A7). For example, in the case of red snapper juveniles in winter, the final new spatial GAM included the effects of depth and bottom salinity, while the final status-quo spatial GAM included only the effect of bottom salinity.

The spatial GAMs fitted in the present study usually had a median AUC value greater than 0.7 and a median adjusted  $R^2$  greater than 0.1 (Figs. 8–10 and Table A14). Therefore, the spatial GAMs fitted in this study usually passed the validation test. The only exceptions to this usual pattern were (i) the status-quo spatial GAM for croaker late juveniles in fall, for which we found a median adjusted  $R^2$  of 0.08; and (ii) the status-quo spatial GAM for small brown shrimps in summer, for which we found a median AUC of 0.682 and a median adjusted  $R^2$  of 0.08. Even though these two status-quo spatial GAMs did not pass the validation test, we used their predictions to produce suitability indices for comparison to the suitability indices from the new spatial GAMs. However, our results for the status-quo spatial GAM for croaker late juveniles in fall and small brown shrimp in summer should not be interpreted ecologically. We also caution about the interpretation of the suitability index for the status-quo spatial GAM for croaker adults in spring, which had a lower bound of the 95 % confidence interval of the AUC lower than 0.7 and a lower bound of the 95 % confidence interval of the adjusted- $R^2$  lower than 0.1 (Fig. 8 and Table A14). In the case of



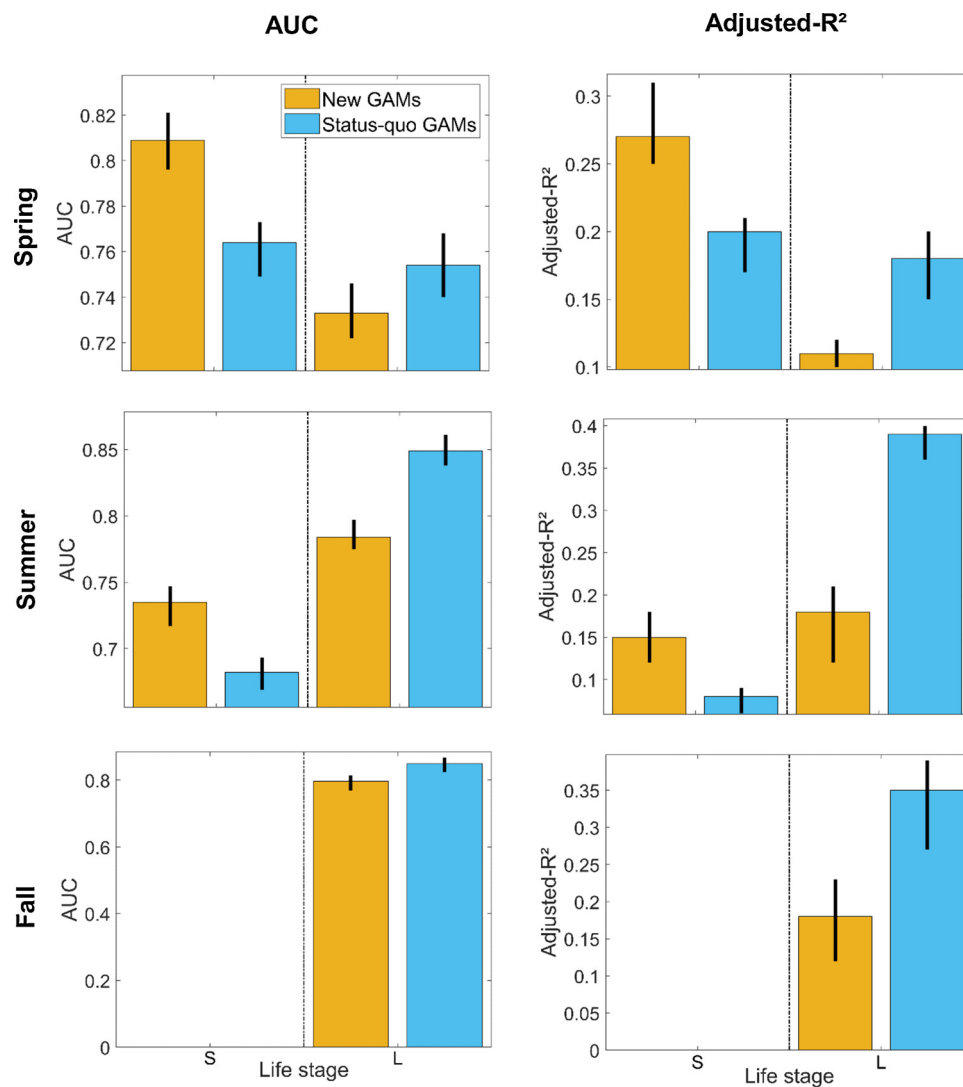
**Fig. 8.** Results of the validation test for the spatial generalized additive models (GAMs) of croaker (*Micropogonias undulatus*) life stages (EJ: early juveniles; LJ: late juveniles; A: adults). Results are provided for the new and the status-quo spatial GAMs. The new spatial GAMs use grid-summarized monitoring data collected at random and fixed sampling stations, while the status-quo spatial GAMs use raw (not grid-summarized) monitoring data collected only at random sampling stations. AUC = Area under the receiver operating characteristic curve.

croaker, the AUCs of the new and status-quo spatial GAMs were similar, while the adjusted-R<sup>2</sup> of the new spatial GAMs was usually higher than that of the status-quo spatial GAMs (Fig. 8 and Table A14). For small brown shrimps, the AUC and adjusted-R<sup>2</sup> of the new spatial GAMs were higher than those of the status-quo spatial GAMs (Fig. 9 and Table A14). By contrast, for large brown shrimps, the AUC and adjusted-R<sup>2</sup> of the status-quo spatial GAMs were higher than those of the new spatial GAMs (Fig. 9 and Table A14). Finally, in the case of red snapper, the AUC of the new spatial GAMs was lower than that of the status-quo spatial GAMs, but the adjusted-R<sup>2</sup> of the new spatial GAMs was generally higher than that of the status-quo spatial GAMs (Fig. 10 and Table A14).

The suitability indices expressing the probability of encountering croaker life stages as a function of depth predicted by the new and, to a lesser extent, by the status-quo spatial GAMs showed the expected general usage of progressively deeper waters for early juveniles, late juveniles, and adults (Figs. 11 and 12 and A15). Depth was not included as an environmental predictor for many of the status-quo models; we, therefore, focus on spring where both the new and status-quo spatial GAMs generated results related to depth. Both the new and status-quo

spatial GAMs for spring showed that suitability decreased rapidly with depth for early juveniles, and the new spatial GAM further showed the progression towards deeper waters with late juveniles and adults (Fig. 11). The increasing suitability with depth for adults was also predicted by the status-quo spatial GAM (Fig. 11). The results were more complete (more life stages and seasons covered) for the new spatial GAMs compared to the status-quo spatial GAMs (Figs. 11 and 12), with neither type of spatial GAMs generating suitability results for depth in fall (Fig. A15).

The suitability indices expressing the probability of encountering croaker life stages as a function of bottom salinity predicted by the new and the status-quo spatial GAMs were qualitatively similar but with some differences (Figs. 11 and 12 and A15). Bottom salinity has a complicated relationship with depth in the NWGOM region (Appendix A3). In general, in the NWGOM region, bottom salinity rapidly increases with depth reaching 35 ppt by about 75 m depth, which results in rapid changes (steep gradients) and relatively high variability in bottom salinity for the nearshore (0–50 m depth) coastal areas. There are also localized pockets of low bottom salinity waters (e.g., at river mouths) that protrude into the coastal zone and get advected along



**Fig. 9.** Results of the validation test for the spatial generalized additive models (GAMs) of brown shrimp (*Farfantepenaeus aztecus*) life stages (S: small individuals; L: large individuals). Results are provided for the new and the status-quo spatial GAMs. The new spatial GAMs use grid-summarized monitoring data collected at random and fixed sampling stations, while the status-quo spatial GAMs use raw (not grid-summarized) monitoring data collected at random sampling stations. AUC = Area under the receiver operating characteristic curve.

shore (Appendix A3).

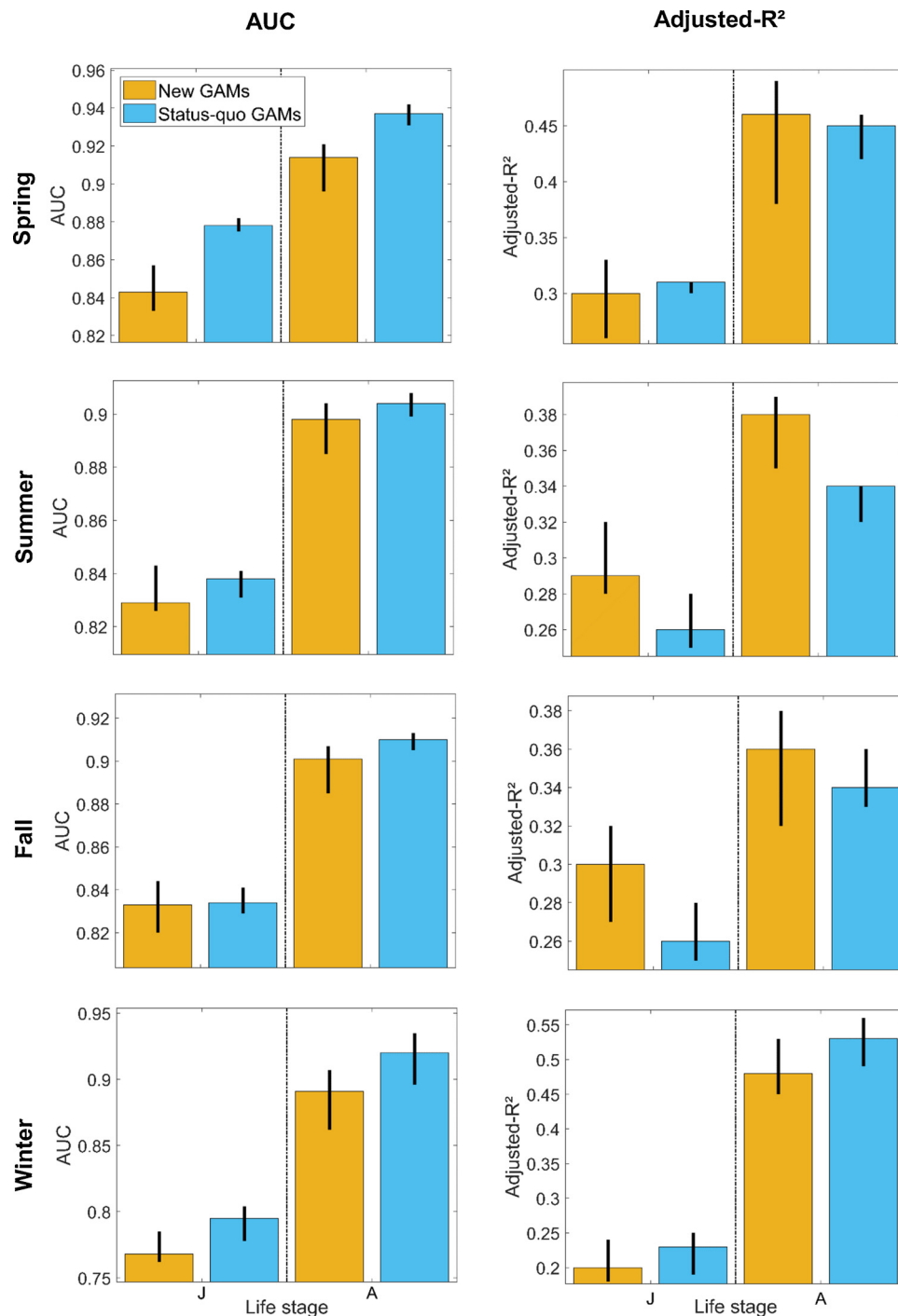
First, both the new and status-quo spatial GAMs showed that the dependence of early juveniles and late juveniles of croaker on shallow coastal waters results in high suitability for low bottom salinity. Suitabilities of croaker early juveniles in spring and summer generated from the predictions of the new spatial GAMs showed decreasing suitability with increasing depth and with increasing bottom salinity (Figs. 11 and 12); when available (early juveniles and adults in spring; late juveniles and adults in fall), these were similar to those for the status-quo spatial GAMs. Suitability of late juveniles showed a similar, although sometimes not simple, decrease of suitability with increasing bottom salinity. For the new spatial GAMs, suitability of bottom salinity steadily declined in spring (bottom right of Fig. 11) and declined with a slight up-turn at high bottom salinities in fall (Fig. A15). The suitability for bottom salinity for the status-quo spatial GAMs for fall also showed an upturn at high salinities.

Second, the new spatial GAMs predicted more complicated suitability relationships with bottom salinity for croaker adults compared to the status-quo spatial GAMs, due to influence of including the nearshore samples from fixed sampling. Both the new and status-quo spatial GAMs resulted in suitabilities of adult for bottom salinity in all

three seasons (green lines in bottom of Figs. 11 and 12 and A15). For both new and status-quo spatial GAMs, the suitability of depth for adults in spring showed them to be more offshore than juveniles and dispersed over a wide range (50–150 m) of depths (top of Fig. 11). However, because of a complicated relationship between depth and bottom salinity, the suitabilities for bottom salinity showed more complicated relationships than the expected increasing suitability with increasing bottom salinity (if bottom salinity simply increased with depth). The predicted probability of encountering croaker adults in spring, summer and fall using the new spatial GAMs started at very high suitability at low bottom salinity and decreased with increasing bottom salinity, showing an upturn or secondary peak after about 30 ppt (Figs. 11 and 12 and A15). This is in contrast to the status-quo spatial GAMs that showed low suitability at low bottom salinity in spring (Fig. 11), summer (Fig. 12), and fall (Fig. A15).

The differences in bottom salinity suitability between the new and status-quo spatial GAMs for croaker adults reflected the influence of nearshore monitoring data that was included with the fixed sampling (Fig. A16). Croaker adults are found over many depths so that the random and fixed sampling included adult use of nearshore habitat not represented in the random-only sampling. The complicated relationship

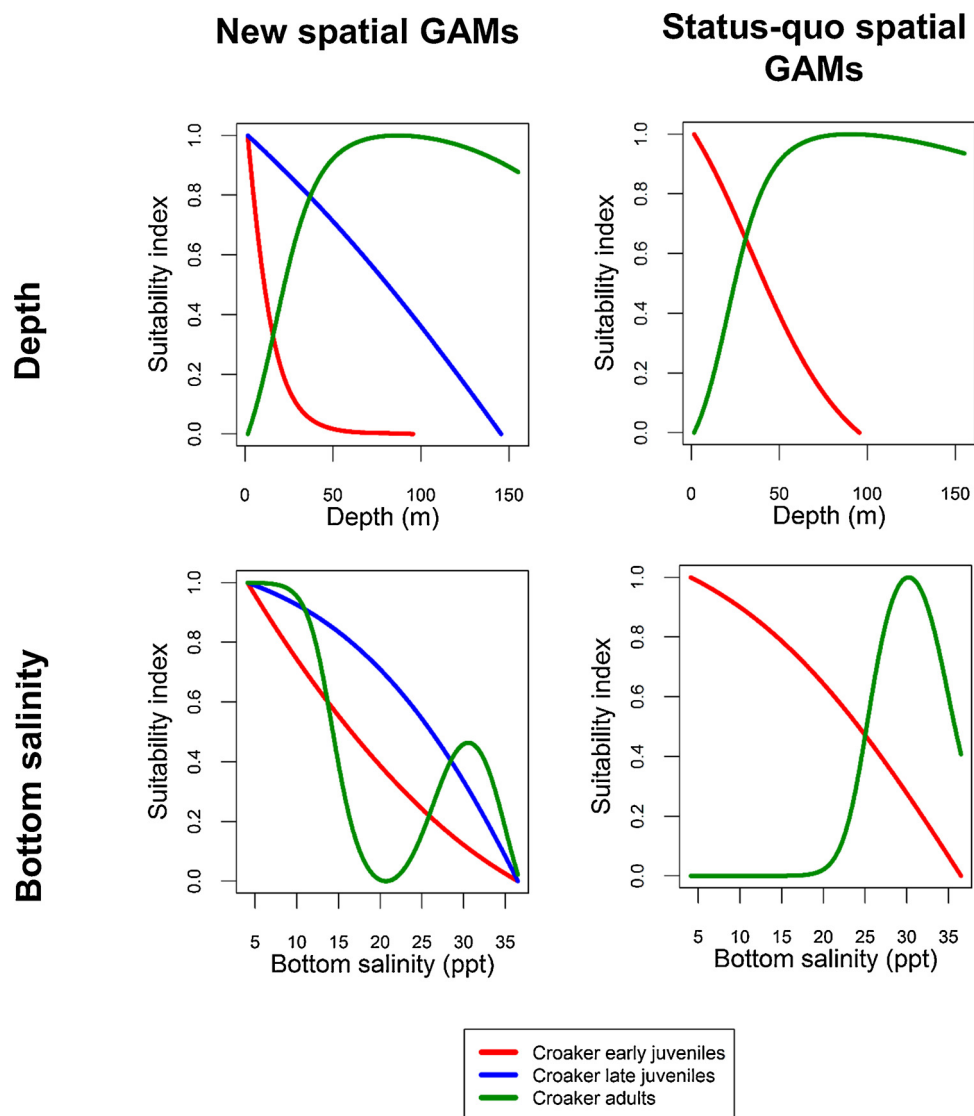




**Fig. 10.** Results of the validation test for the spatial generalized additive models (GAMs) of red snapper (*Lutjanus campechanus*) life stages (J: juveniles; A: adults). Results are provided for the new and the status-quo spatial GAMs. The new spatial GAMs use grid-summarized monitoring data collected at random sampling stations, while the status-quo spatial GAMs use raw (not grid-summarized) monitoring data collected at random sampling stations. AUC = Area under the receiver operating characteristic curve.

of suitability to bottom salinity for the new spatial GAMs suggests that some croaker adults are more inshore than random sampling suggests and are located in coastal waters that have low bottom salinities. The nearshore habitat having croaker present, such the Vermilion Bay area and other nearshore areas, have a range of bottom salinities at moderate depths due to influence by circulation and the freshwater inputs of estuaries and the Mississippi River plume (Fig. A16). However, the highest suitability occurring for bottom salinity less than 5 ppt for the new models is questionable and needs further evaluation (Figs. 11 and 12 and A15).

Third, while both the new and status-quo methods generated similar shaped suitability relationships to bottom salinity in fall (Fig. A15), the differences provided illustrate potentially important interpretation differences on the suitability of mid-range bottom salinities. The new spatial GAMs predicted that the probability of encountering croaker late juveniles as a function of bottom salinity in fall decreases until bottom salinity reaches around 32 ppt. The status-quo spatial GAMs predicted that suitability remained very high until about 25 ppt and then generally decreased (Fig. A15). These results create differences in suitability of bottom salinity from 10 to 20 ppt (much higher suitability



**Fig. 11.** Suitability indices generated for croaker (*Micropogonias undulatus*) life stages and the spring season from the predictions of spatial generalized additive models (GAMs). Results are provided for the new and the status-quo spatial GAMs. The new spatial GAMs use grid-summarized monitoring data collected at random and fixed sampling stations, while the status-quo spatial GAMs use raw (not grid-summarized) monitoring data collected only at random sampling stations.

for the status-quo spatial GAMs with its sudden drop-off) that involves a substantial portion of the habitat for croaker late juveniles. The inclusion of more nearshore samples with the fixed sampling stations has, perhaps, allowed for refinement of the almost step-wise suitability of bottom salinity obtained with the status-quo spatial GAMs of late juvenile croaker (Fig. A16).

The suitability indices expressing the probability of encountering brown shrimp life stages as a function of depth were often unavailable, as depth was often excluded from the new and status-quo spatial GAMs (Fig. 13 and A17). When available, the suitability indices expressing the probability of encountering brown shrimp life stages as a function of depth showed the expected general usage of deeper waters for large brown shrimps compared to small brown shrimps (Fig. 13). Both the new and the status-quo spatial GAMs predicted that, in spring, the probability of encountering small brown shrimps decreased with depth (Fig. 13). Regarding the summer season, depth was retained only in the new spatial GAM of small brown shrimps, and a dome-shaped relationship peaking at a depth of 30 m was predicted (Fig. A17). No suitability indices expressing the probability of encountering brown shrimp life stages as a function of depth were available for the fall season (Fig. A17).

The suitability indices expressing the probability of encountering brown shrimp life stages as a function of bottom salinity differed between life stages and among seasons (Fig. 13 and A17). We focus here on the spring and fall seasons, for which suitability indices related to bottom salinity were provided by both the new and status-quo methods. The suitability indices expressing the probability of encountering brown shrimp life stages as a function of bottom salinity predicted by the new and the status-quo spatial GAMs were similar. Both the new and the status-quo spatial GAMs predicted that the probability of encountering large brown shrimps in spring increased with bottom salinity (Fig. 13). Moreover, both the new and the status-quo spatial GAMs predicted that the probability of encountering small brown shrimps in spring and large brown shrimps in fall declined with bottom salinity with an up-turn at high bottom salinities (25–30 ppt) (Fig. 13 and A17). These more complex relationships stem from the fact that the highest probabilities of encounter predicted by the new and status-quo spatial GAMs are either for areas where bottom salinity is very low (5–10 ppt; e.g., Vermilion Bay) or for areas where bottom salinity is high (greater than 25–30 ppt; e.g., eastern Texas waters) (Fig. A18). We can note that the preference of small brown shrimps for bottom salinities less than 25 ppt in spring predicted by the new method is

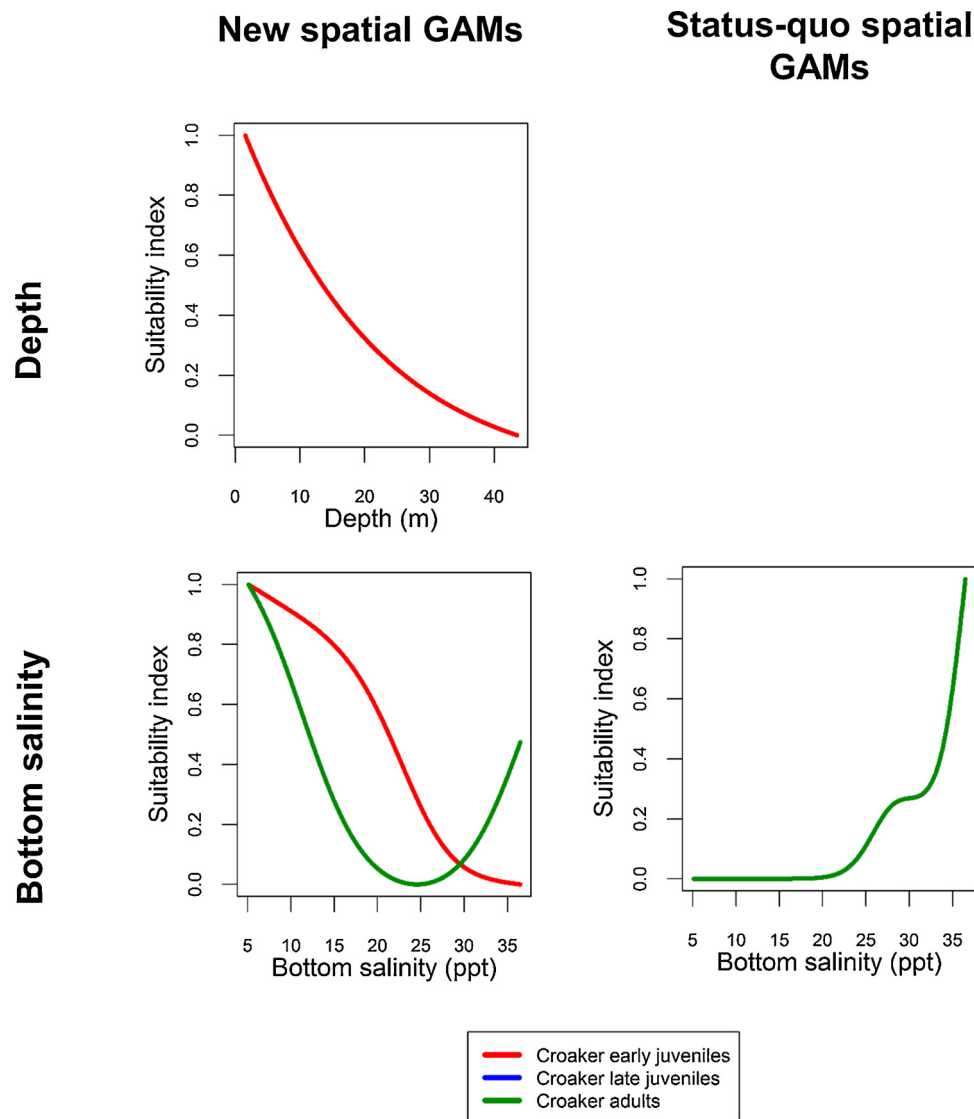


Fig. 12. Suitability indices generated for croaker (*Micropogonias undulatus*) life stages and the summer season from the predictions of spatial generalized additive models (GAMs). Results are provided for the new and the status-quo spatial GAMs. The new spatial GAMs use grid-summarized monitoring data collected at random and fixed sampling stations, while the status-quo spatial GAMs use raw (not grid-summarized) monitoring data collected only at random sampling stations.

much higher than that predicted by the status-quo method (Fig. 13). This is due to the new method relying on the additional, fixed-station encounter data covering nearshore areas of Louisiana and Alabama where bottom salinity is relatively low (Table A7 and Fig. A18).

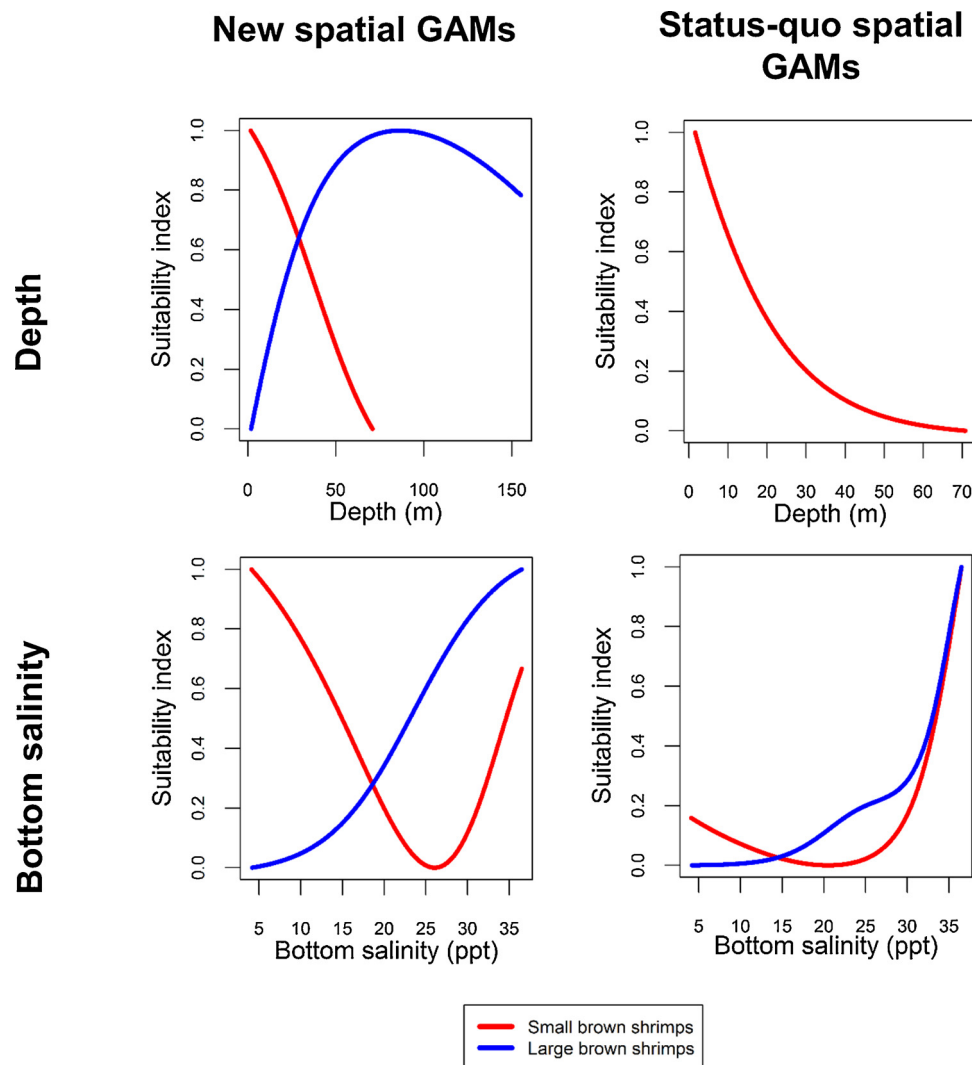
The suitability indices expressing the probability of encountering red snapper life stages as a function of depth predicted by the new and the status-quo spatial GAMs were generally very similar (Figs. 14 and 15 and A19). Both the new and the status-quo spatial GAMs predicted that the probability of encountering red snapper juveniles and adults decreases with depth in all seasons, and that the decrease is generally slower for red snapper adults (blue line to the right of red line in Figs. 14 and 15 and A19). One difference was the peak in suitability sometimes predicted for intermediate depths: 30 m for red snapper juveniles and 70 m for red snapper adults with the status-quo spatial GAM in spring, and about 70 m for adults with the new spatial GAM in winter (Fig. 14 and A19).

The suitability indices for red snapper and bottom salinity predicted by the new and the status-quo spatial GAMs were, like for depth, very similar (Figs. 14–15 and A19). Both the new and the status-quo spatial GAMs predicted that the probabilities of encountering red snapper juveniles and adults increased with bottom salinity (tracking the

suitability for depth; blue line to the right of red line in Figs. 14 and 15 and A19) and reached a maximum at 35 ppt, and that the ranges of bottom salinity over which red snapper juveniles and adults were encountered are constrained to 25–35 ppt in all seasons (Figs. 14 and 15 and A19 and A20).

#### 4. Discussion

We developed and demonstrated a new grid-summarization method that allows for the combined use of monitoring data collected at random and fixed sampling stations. By making a comprehensive use of the monitoring data available for a given marine region, our new method allows for the generation of distribution maps and suitability indices that are not attainable when relying on monitoring data collected only at random sampling stations. For example, Grüss et al. (2018c) fitted status-quo spatial GLMMs to a blending of monitoring data collected only at random sampling stations to then construct distribution maps for the life stages of many fish and invertebrate species of the U.S. Gulf of Mexico, with the ultimate goal to parameterize an Atlantis ecosystem model. However, due to a lack of monitoring data collected using random sampling designs in Louisiana, Mississippi and



**Fig. 13.** Suitability indices generated for brown shrimp (*Farfantepenaeus aztecus*) life stages and the spring season from the predictions of spatial generalized additive models (GAMs). Results are provided for the new and the status-quo spatial GAMs. The new spatial GAMs use grid-summarized monitoring data collected at random and fixed sampling stations, while the status-quo spatial GAMs use raw (not grid-summarized) monitoring data collected only at random sampling stations.

Alabama coastal waters, Grüss et al. (2018c) were unable to develop spatial GLMMs for several key fish and invertebrate life stages. Our new grid-summarization method will allow for the development of spatial GLMMs and the construction of annual distribution maps and, in some cases, seasonal distribution maps for these key fish and invertebrate life stages (see also the discussion on seasonal distribution maps below). In addition, for species, life stages and seasons that have substantial data available from fixed sampling stations, improved (more confidence, better resolved location and extent used habitat) distribution maps and suitability indices can be produced than with just random-station data.

The spatial distribution maps and suitability indices predicted for croaker, brown shrimp and red snapper life stages using our new grid-summarization method concurred with insights from the literature (Table 2). In the cases of croaker and brown shrimp, we found some differences between the predictions of our new method (that is capable of employing monitoring data collected at both random and fixed sampling stations) and the status-quo method (that can only employ monitoring data collected at random sampling stations). By contrast, in the case of red snapper, for which the data delivered by monitoring programs collected only at random sampling sites have a satisfactory spatial coverage and the new and status-quo statistical habitat models only differed by the use of the summarization using a 10 km by 10 km spatial grid in the case of the new models, the predictions of the new

and the status-quo models were generally very similar. The high similarity of results between status-quo and new models for red snapper demonstrates that the results are robust to the use of the new gridding step described in Fig. 1.

For croaker and brown shrimp life stages, the major differences between the new and the status-quo statistical habitat models were the predicted seasonal spatial distributions. Specifically, because they use monitoring data collected only at random sampling stations, the status-quo spatial GLMMs largely underpredicted the probabilities of encounter of croaker and brown shrimp life stages in some nearshore areas. This also affected the suitability indices, especially for croaker adults, that use a broad area of the shelf; some differences between new and status-quo spatial GAMs suggested different importance of shallower waters (environmental predictor of depth) and low and mid-range bottom salinities. These results can have implications for habitat assessments, as spatial protection efforts targeting critical life stages would miss some juvenile or spawner hotspots if they relied only on status-quo statistical habitat models (Grüss et al., 2019a). Moreover, in the case of croaker, the validation procedure suggested that new spatial GAMs generally had higher predictive accuracy (higher adjusted- $R^2$ s) than status-quo spatial GAMs. Also, one status-quo spatial GAM (croaker late juveniles in fall) did not pass the validation test, and we observed one case (croaker adults in spring) where the lower bound of



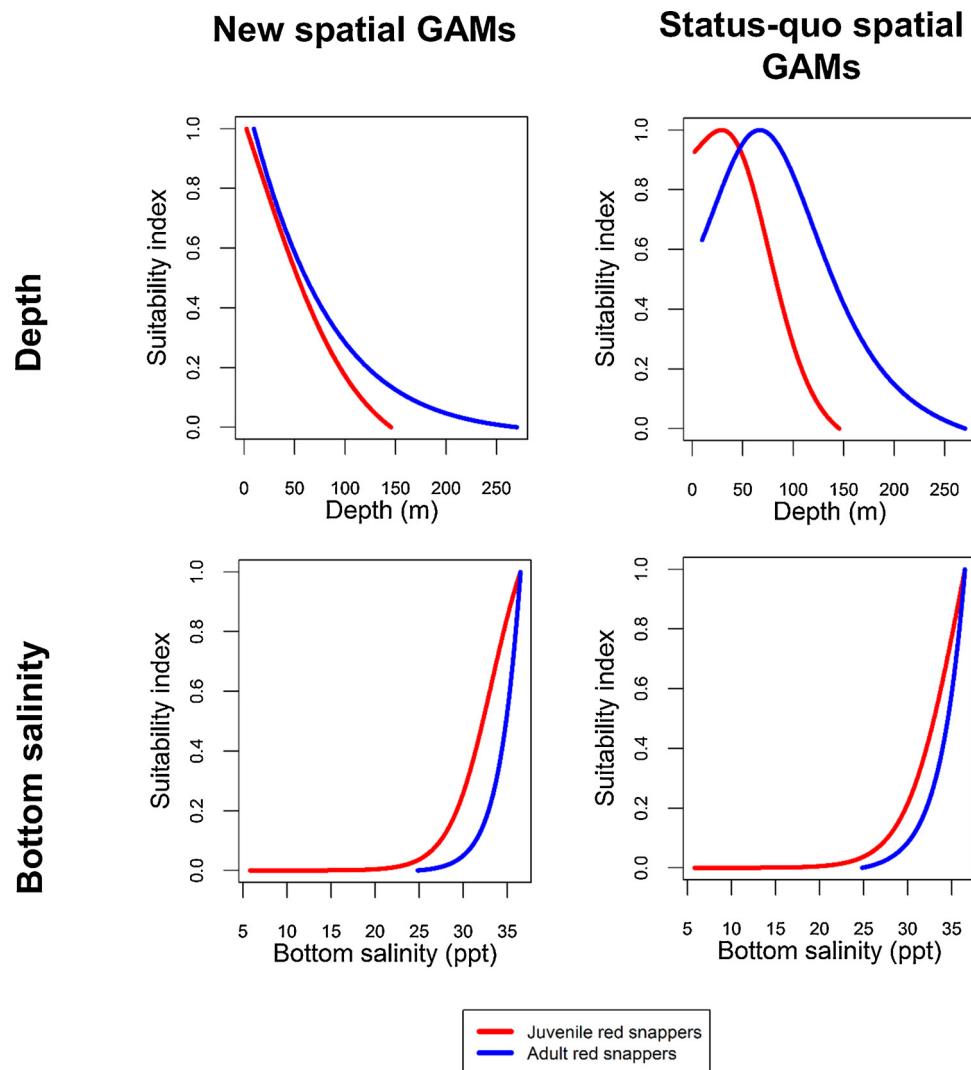


Fig. 14. Suitability indices generated for red snapper (*Lutjanus campechanus*) life stages and the spring season from the predictions of spatial generalized additive models (GAMs). Results are provided for the new and the status-quo spatial GAMs. The new spatial GAMs use grid-summarized monitoring data collected at random sampling stations, while the status-quo spatial GAMs use raw (not grid-summarized) monitoring data collected at random sampling stations.

the 95 % confidence interval of the adjusted- $R^2$  was lower than 0.1. In the case of brown shrimp, the new spatial GAMs of small brown shrimps had higher predictive accuracy (higher adjusted- $R^2$ 's) and higher discrimination accuracy (lower AUCs) than status-quo GAMs, but the opposite was true for large brown shrimps. The reason for this result is that monitoring data collected at random sampling stations do not have a satisfactory spatial coverage in the case of small brown shrimps, but are adequate for large brown shrimps (Fig. A5). In conclusion, for species/life stages like croaker life stages and small brown shrimps for which monitoring data collected at random sampling stations do not have a satisfactory spatial coverage, the use of status-quo statistical habitat models is discouraged; fisheries analysts should instead seek to obtain monitoring data collected at both random and fixed sampling stations and employ our new grid-summarization method.

The predictions of our new method and the status-quo method were very similar for the red snapper life stages. Some minor differences between the new and status-quo spatial GLMMs were that the spatial distribution maps from the new models were smoother, and that the new spatial GAMs of red snapper life stages had higher predictive accuracy (higher adjusted- $R^2$ 's) than the status-quo spatial GAMs, but lower discrimination accuracy (lower AUCs). The smoother distribution maps obtained with the new spatial GLMMs for red snapper life stages are due to the fact that the grid-summarization step described in Fig. 1

results in slightly different encounter/non-encounter datasets. More precisely, the geographic coordinates of the encounter/non-encounter datasets provided to the new and the status-quo spatial GLMMs are different, so that the spatial variation terms (i.e., the random effects  $\epsilon$ ) estimated by the new and the status-quo spatial GLMMs are different and do not result in identical distribution maps. We conclude that, for species/stages like red snapper for which monitoring data collected at random sampling stations have a satisfactory spatial coverage: (i) spatial GLMMs implemented using our new approach do not offer advantages over status-quo spatial GLMMs; and (ii) choosing new spatial GAMs versus status-quo modeling spatial GAMs may, for specific species, stage and season combinations, be a tradeoff between predictive accuracy and discrimination accuracy.

One of the major results reported for brown shrimp in this study is that brown shrimp probabilities of encounter are very high in Texas waters in all seasons. This result was already reported in previous studies (Matlock, 2010; Grüss et al., 2018e). The higher predicted probabilities of encounter of brown shrimp in Texas waters compared to the rest of the NWGOM likely do not reflect that Texas waters offer better habitat for brown shrimp than Louisiana waters, but is primarily the consequence of the more complex management measures that have been implemented in Texas for decades, including fishing gear restrictions, size and bag limits, and temporal and spatial closures (Cody et al.,

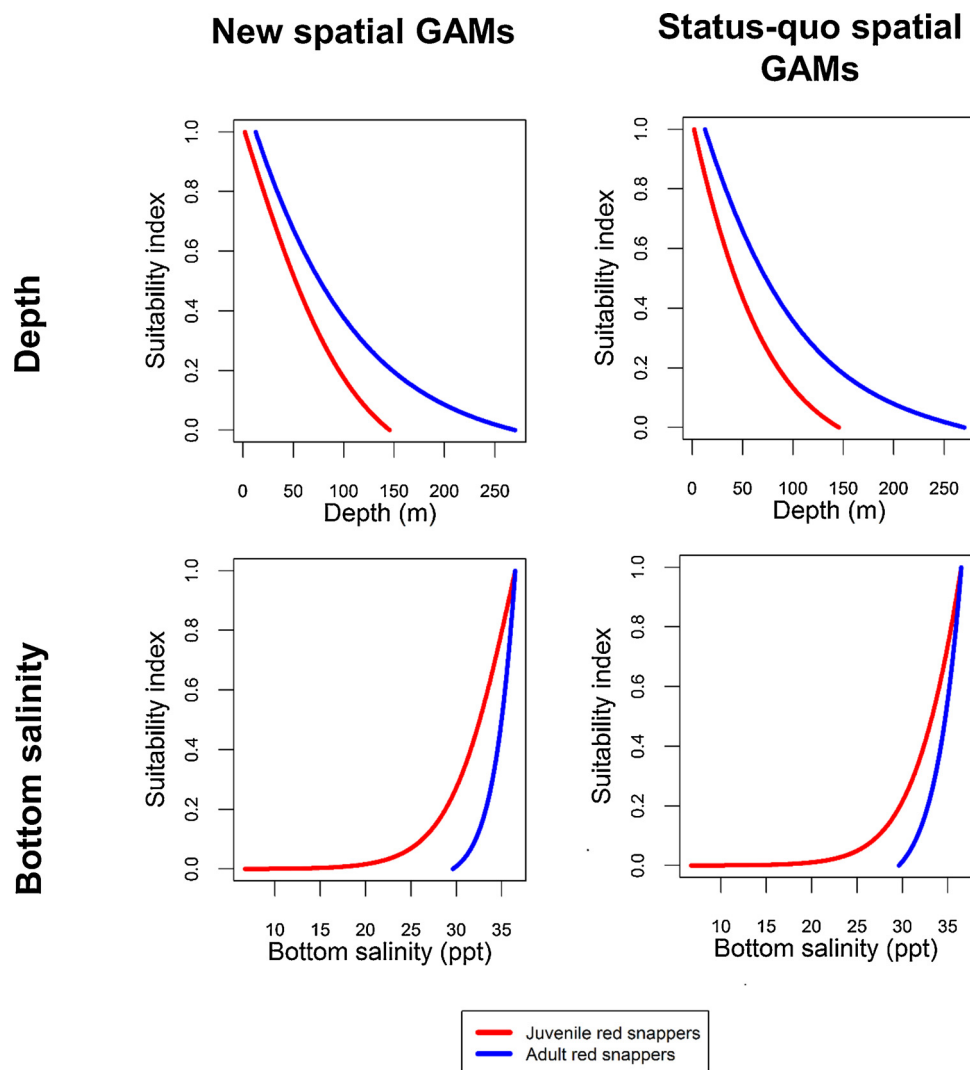


Fig. 15. Suitability indices generated for red snapper (*Lutjanus campechanus*) life stages and the fall season from the predictions of spatial generalized additive models (GAMs). Results are provided for the new and the status-quo spatial GAMs. The new spatial GAMs use grid-summarized monitoring data collected at random sampling stations, while the status-quo spatial GAMs use raw (not grid-summarized) monitoring data collected at random sampling stations.

1989; Caillouet et al., 2008; Matlock, 2010). Importantly, the high predicted probabilities of encounter of small and brown shrimps in spring west of Vermilion Bay, particularly in Texas waters, may be in great part due to the spatial closures that have been enforced from the shore to 9 nautical miles in Texas territorial waters from late May to early July since 1960 (Cody et al., 1989; Matlock, 2010). Note that, very recently, federal spatial closures that mimic the Texas closures have also been implemented in the exclusive economic zone adjoining to Texas state waters (<https://gulfcouncil.org/press/2017/noaa-texas-shrimp-closure-2017/>).

Even with the use of monitoring data collected at both random and fixed sampling stations, it is possible not to have enough information for certain stage and season combinations for some species. In our analysis, the dataset combining monitoring data collected at random and fixed sampling stations did not have a satisfactory spatial coverage for croaker early juveniles in fall, croaker late juveniles and adults in winter, small brown shrimps in fall, and small and large brown shrimps in winter. We suspect that there will be other instances where data availability will not allow for the implementation of our new grid-summarization method for some seasons of the year (e.g., some coastal fish and invertebrate species/life stages, wide-ranging large pelagic fishes like Bluefin tuna (*Thunnus thynnus*) and swordfish (*Xiphias gladius*); Grüss et al., 2018c, 2018e). To remedy this issue, we envision two

options: (i) improving existing monitoring programs or, ideally, creating new monitoring programs to allow for a satisfactory spatial coverage of monitoring data for the species, life stages and seasons of interest; and (ii) developing a new method enabling one to fit statistical habitat models not only to monitoring data collected at both random and fixed sampling stations, but also to opportunistic survey data.

The first option of improving the monitoring would be potentially useful for croaker and other similar NWGOM fish and invertebrate species that use nearshore habitats. Two monitoring programs conducted in Louisiana coastal waters (the LDWF groundfish survey and the LDWF shrimp trawl survey) have a good spatial coverage, but do not collect the length information that would allow us to easily distinguish between life stages. The second option of employing opportunistic survey data will not work for croaker life stages, as none of the opportunistic surveys that operate in the NWGOM collect length information (Grüss et al., 2018e). The data collected during opportunistic surveys are typically presence-only data. However, presence-only data are challenging to analyze, because the detection of species/life stages during opportunistic surveys is usually dependent upon sampling characteristics such as the distance to the coast or the distance to populated areas (Renner et al., 2015). Therefore, if a method capable of handling monitoring data collected using random, fixed and opportunistic sampling designs was developed, this method should take into

**Table 2**  
 Comparison of the insights from the present study and from the literature into the spatial distribution patterns and environmental preferences of croaker (*Micropogonias undulatus*), brown shrimp (*Farfantepenaeus aztecus*) and red snapper (*Lutjanus campechanus*) life stages in the northwestern Gulf of Mexico (NWGOM). Only the new statistical habitat models are considered here. The new statistical habitat models use grid-summarized monitoring data collected at random and/or fixed sampling stations.

Species	Insights from the present study	Insights from the literature
Croaker	<ul style="list-style-type: none"> <li>● Early juveniles occupy relatively shallow coastal waters (mean depth <math>\leq 10</math> m).</li> <li>● Late juveniles generally occupy deeper areas of the NWGOM (mean depth of 21 – 24 m).</li> <li>● Adults are usually encountered on the continental shelf of the NWGOM rather than in coastal areas (mean depth of 35 – 46 m).</li> <li>● In summer, early juveniles tend to be found at shallower depths and adults at deeper depths, compared to the other seasons of the year.</li> <li>● Overall, in all seasons, the probabilities of encounter of all life stages decrease with increasing bottom salinity.</li> </ul>	<ul style="list-style-type: none"> <li>● Early juveniles occupy shallow coastal waters where depth is typically less than 5 m (Rooker et al., 1998).</li> <li>● Late juveniles occupy slightly deeper waters than early juveniles (Yakupzack et al., 1977).</li> <li>● Adults occupy primarily a large band of the NWGOM shelf (Sheridan et al., 1984; Darnell, 1990; Diamond et al., 1999).</li> <li>● Adults undertake seasonal migrations and occupy deeper waters in summer, where bottom temperatures are cooler and dissolved oxygen concentrations are more tolerable than in shallower waters (Craig and Crowder, 2005; Craig, 2012).</li> <li>● Using generalized additive models (GAMs), Craig and Crowder (2005) found that the probability of encounter of croaker in summer decreased overall with increasing bottom salinity.</li> </ul>
Brown shrimp	<ul style="list-style-type: none"> <li>● Small brown shrimp are found in relatively shallow coastal waters (mean depth of 12 – 17 m).</li> <li>● Large brown shrimps generally occupy deeper areas than small brown shrimps (mean depth of 41 – 54 m).</li> <li>● Texas waters are brown shrimp hotspots in all seasons.</li> </ul>	<ul style="list-style-type: none"> <li>● Small brown shrimps are in general encountered in shallow areas where depth ranges between 0 and 20 m (e.g., marshes, inshore estuaries; Fry, 2008; Lassuy, 1983; Craig et al., 2005).</li> <li>● Large brown shrimps are generally encountered in deeper waters than small brown shrimps, at depths up to 110 m (Darnell et al., 1983; Lassuy, 1983; Grüss et al., 2018e), and large brown shrimps hotspots are typically found where depth ranges between 20 and 40 m (Matthews, 1982; Darnell et al., 1983; Sheridan et al., 1989; Montero et al., 2016).</li> <li>● Brown shrimp are abundant in Texas territorial waters, where a complex combination of management measures, including spatial and temporal closures, have been imposed for decades (Matlock, 2010; Grüss et al., 2018e).</li> </ul>
Red snapper	<ul style="list-style-type: none"> <li>● The probability of encountering large brown shrimps in spring increases with bottom salinity. Moreover, the probability of encountering small brown shrimps in spring and large brown shrimps in fall declines with bottom salinity with an up-turn at high bottom salinities (25 – 30 ppt).</li> <li>● Red snapper juvenile hotspots are mainly located off Texas, Mississippi and Alabama, in all seasons.</li> <li>● The probability of encounter of adults tend to be higher in Texas waters than in Louisiana, Mississippi and Alabama waters, in all seasons.</li> <li>● Adults are usually found in deeper waters than juveniles in all seasons (mean depth of 70 – 88 m versus 43 – 58 m).</li> <li>● The probabilities of encountering juveniles and adults increase with bottom salinity and reach a maximum at 35 ppt.</li> </ul>	<ul style="list-style-type: none"> <li>● Rozas and Minello (2011) found that brown shrimp grows more quickly in the high than in the intermediate bottom salinity areas. Barrett and Gillespie (1973) reported that a bottom salinity of around 19 ppt is required for brown shrimp production to be optimal in Louisiana estuaries. Using boosted regression trees, Montero et al. (2016) found that brown shrimp densities were high both where bottom salinities ranged between 10 and 20 ppt and where bottom salinity ranged between 30 and 40 ppt; high density areas with bottom salinities ranging between 10 and 20 ppt were located along eastern Texas and western Louisiana close to major rivers and estuaries, while high density areas with bottom salinities ranging between 30 and 40 ppt were observed further offshore.</li> <li>● High quality habitat for juveniles is greater on the inner Texas Shelf and in a small area off Alabama and Mississippi than elsewhere in the NWGOM (Dance and Rooker, 2019). The large hypoxic zone off Louisiana during the summer and the fall seasons may limit red snapper recruitment over the inner shelf, which may explain the higher abundance of red snapper juveniles on the inner Texas Shelf and in the small area off Alabama and Mississippi (Galloway et al., 1999).</li> <li>● Using GAMs, Dance and Rooker (2019) found that high quality habitat for red snapper adults is greater in Texas waters than elsewhere in the NWGOM.</li> <li>● Red snapper is primarily found in the areas of the NWGOM shelf where depth ranges between 40 m and 60 m as juveniles (Galloway et al., 1999; Szedlmayer and Conti, 1999; Szedlmayer and Lee, 2004; Wells, 2007; Galloway et al., 2009; Monk et al., 2015; Dance and Rooker, 2019), and where depth ranges between 80 m and 200 m as adults (Patterson et al., 2001; Mitchell et al., 2004; Galloway et al., 2009; Dance and Rooker, 2019).</li> <li>● Galloway et al. (1999) found that habitat suitability for red snapper juveniles increased when bottom salinity increased from 29 – 31 to 35 ppt and decreased afterwards.</li> </ul>

account sampling intensity and the covariates that influence sampling intensity for the presence-only data collected during opportunistic surveys (Fithian et al., 2015).

Recently, Grüss and Thorson (2019) designed a spatio-temporal GLMM approach that relies on an approximation to a compound Poisson-Gamma process to handle a combination of encounter/non-encounter, count and biomass data. One major advantage of these recent developments is that they not only allow for the production of distribution maps for informing habitat assessments and EBFM efforts, but also for the reconstruction of biomass trends and the description of patterns of distribution shifts and range expansion/contraction, which are valuable products for stock and habitat assessments (Grüss and Thorson, 2019). Therefore, we recommend future studies to build upon the present study and expand Grüss and Thorson (2019)'s spatio-temporal GLMM approach so that it can handle encounter/non-encounter, count and biomass data collected at random and/or fixed sampling stations. This endeavor would be particularly useful to construct accurate distribution maps and biomass time series with spatio-temporal GLMMs for ecologically and socio-economically important coastal species that are currently undersampled by the monitoring programs using random sampling schemes, such as red drum and spotted seatrout (*Cynoscion nebulosus*) (Grüss et al., 2018e).

In summary, we developed and demonstrated a new grid-summarization method that allows for expanded use of monitoring data by allowing for the combined statistical analysis of data collected at random and fixed sampling stations. Our new grid-summarization method allows for the generation of spatial distribution maps and suitability indices for those species and life stages that are under-sampled by the monitoring programs that employ random sampling schemes. We also showed that our new grid-summarization method generates similar results when the monitoring data collected at random sampling stations alone are sufficient, so that there is no loss of information in using our new method when monitoring data collected at random sampling stations are extensive. For these species and life stages for which previous (status-quo) methods based only on monitoring data collected at random sampling stations worked well, the choice of our new method depends on whether there are benefits to producing smoother distribution maps (new method), or whether the fisheries analysts target higher predictive accuracy (new method) or higher discrimination accuracy (status-quo method) when working with spatial GAMs to generate suitability indices. Our new grid-summarization method can be added to the statistical toolbox in the ever important drive towards using the best available science in fisheries management (MSRA (Magnuson-Stevens Fishery Conservation and Management Reauthorization Act), 2006; Sullivan et al., 2006).

#### Authorship statement

AG and KAR designed and analyzed the statistical models; AG conceived the statistical models; DJ and LW generated the environmental data; AG, KAR, DJ and LW wrote the paper; all authors have approved the final article.

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#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### CRediT authorship contribution statement

**Arnaud Grüss:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Writing - original draft, Writing - review & editing. **Kenneth A. Rose:** Conceptualization, Methodology, Writing - review & editing. **Dubravko Justić:** Resources, Writing - review & editing. **Lixia Wang:** Resources, Writing - review & editing.

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#### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.fishres.2020.105623>.

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