Protecting juveniles, spawners or both: A practical statistical modelling approach for the design of marine protected areas

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Abstract

1. Fish populations undertaking ontogenetic or spawning migrations pose challenges to marine protected area (MPA) planning because of the large extent of their distribution areas. There is a need to identify the juvenile and spawner hotspots of these populations that could be set aside as MPAs. Species distribution models making comprehensive use of available monitoring data and predicting the realized juvenile and spawner hotspots of migratory fish populations will assist resource managers with MPA planning.

2. We developed a statistical modelling approach relying on multiple, regional monitoring datasets for assisting spatial protection efforts targeting the juveniles, spawners, or both life stages, of migratory fish species and species complexes. This approach predicts juvenile and spawner hotspot indices, and critical life stage (CLS) hotspot indices, which integrate both juvenile and spawner hotspot indices. We applied the approach to 11 vulnerable species of the grouper-snapper complex of the U.S. Gulf of Mexico, which all form fish spawning aggregations (FSAs).

3. The CLS hotspot index was predicted to be highest in the Pulley Ridge and Flower Garden Banks areas, followed by the West Florida Shelf, southwestern Florida waters and portions of the Louisiana-Mississippi-Alabama shelf.

4. The Pulley Ridge Habitat Area of Particular Concern and Flower Garden Banks National Marine Sanctuary are two important existing MPAs of the U.S. Gulf of Mexico, whose possible expansion is being considered. The predicted CLS hotspot indices suggest that expanding these MPAs or increasing harvest regulations within them would offer substantial protection to both the juveniles and spawners of many FSA-forming species of the grouper-snapper complex.

5. *Synthesis and applications*. As the number of marine protected areas (MPAs) continues to increase worldwide, statistical modelling approaches making comprehensive use of available data are urgently needed to support resource managers' abilities to establish sound and efficient spatial protection plans. The outputs of our statistical models can serve as inputs to conservation planning software packages seeking optimal MPA configurations or can be directly employed by resource managers for formulating spatial protection plans.

Keywords: fish habitat; geostatistical generalized linear mixed models; large monitoring database; marine conservation; marine protected areas; spatial generalized additive models; species complexes; Gulf of Mexico.

Introduction

Marine protected areas (MPAs), zones where fishing and other human uses are restricted seasonally or year-round, have become key tools for resource management and conservation (Lubchenco & Grorud-Colvert, 2015). MPAs can be partial-take (e.g., allow for longlining, but not for trawling) or no-take (i.e., “marine reserves”). The potential benefits of MPAs for fish populations are numerous and include the maintenance or enhancement of reproductive capacity (Claudet, 2011). MPAs may also increase fish exploitable biomass or fisheries catches over the long term, by subsidizing non-protected areas with larval and post-larval fish individuals (Gell & Roberts, 2003; Kerwath, Winker, Götz, & Attwood, 2013). In 2010, parties to the Convention on Biological Diversity (CBD) committed to set aside 10% of world’s marine areas as MPAs by 2020 (CBD, 2010). More recently, during an International Union for Conservation of Nature (IUCN) World Conservation Congress, it was proposed to protect 30% of world’s marine areas by 2030 (O’Leary et al., 2016). While the CBD and IUCN’s targets may or may not be achieved by 2020 and 2030, respectively, countries and regional organizations will very likely establish an increasing number of MPAs and MPA networks in the near and distant future (Boonzaier & Pauly, 2016).

Managing migratory fish populations using MPAs poses significant challenges. Many fish populations change habitats at sexual maturity (i.e., undertake ontogenetic migrations) or migrate as adults between normal residence and spawning areas (Botsford et al., 2009; Green et al., 2015). Therefore, the spatial distribution of these populations covers an extensive surface area, which presents the challenge of effectively protecting all life stages of these fish populations without implementing excessively large MPAs (Grüss, Kaplan, Guénette, Roberts, & Botsford, 2011). Preferentially protecting juveniles may result in increased spawning and exploitable biomasses, while preferentially protecting adults during the spawning season (i.e., spawners) may improve reproductive output and recruitment and, over the longer term, fisheries catches (Grüss, 2014). Thus, there is a need for tools for identifying the juvenile and spawner hotspots of migratory fish populations that could be set aside as individual MPAs or integrated within MPA networks.

Many mechanistic modelling studies have examined the potential conservation and fisheries effects of MPAs preferentially protecting the juveniles or the spawners of migratory fish populations (e.g., Pelletier & Magal, 1996; Edwards & Plagányi, 2011; Hussein et al., 2011; Ellis & Powers, 2012; Grüss & Robinson, 2015). Overall, these studies suggest that, in the case of most temperate migratory fishes, it would be more beneficial to set aside juvenile hotspots rather than spawner hotspots as MPAs to let most individuals grow larger and rebuild biomasses (e.g., Pelletier & Magal, 1996; Edwards & Plagányi, 2011; Hussein et al., 2011). In the case of fishes with vulnerable life history traits (e.g., slow growth, protogyny) whose populations migrate to form fish spawning aggregations (FSAs), mechanistic models that estimate changes in reproductive capacity and exploitable biomass as a function of the fraction of FSA habitat set aside as MPAs support the implementation of MPAs at spawning sites to optimize reproductive outcomes (e.g., Ellis & Powers, 2012; Grüss & Robinson, 2015). However, regardless of the specific ecology of the migratory species of interest, it can be argued that creating MPAs or MPA networks to protect both juvenile and spawner hotspots would be a good "portfolio" strategy. We define such areas as "critical life stage hotspots."

The mechanistic models that have evaluated the potential effects of MPAs for migratory fish populations can provide useful insights on their potential conservation or fisheries benefits (Grüss, 2014). Yet, these models are often general and rely on assumed functional relationships and on limited or no data (e.g., Pelletier & Magal, 1996; Hussein et al., 2011; Grüss & Robinson, 2015). Models that rely strongly on data generally garner far more confidence and buy-in from resource managers and stakeholders. Thus, species distribution models (SDMs) fitted to monitoring data that can predict juvenile and spawner hotspots for migratory fish populations are a valuable alternative to mechanistic models for assisting resource managers with MPA planning. For example, SDMs are typically employed in the U.S. for mapping juvenile and spawner hotspots, as mandated by the Magnuson-Stevens Fishery Conservation and Management Act (Rosenberg, Bigford, Leathery, Hill, & Bickers, 2000; Laman et al., 2018). However, in large marine regions like the U.S. Gulf of Mexico (U.S. GOM), the spatial footprint of individual monitoring programs does not cover the entire distribution range of many fish populations (Grüss et al., 2018). Therefore, in such regions, it is not possible to predict the juvenile and spawner hotspots of many fish populations when relying on only one source of monitoring data.

Resource managers are increasingly interested in the management of groups of species with similar spatial distribution patterns and life history traits (often called "species complexes") rather than individual fish populations (USOFR, 2009). This is mainly because, in multispecies fisheries (the most common fisheries), it is impossible to target some fish populations independently of one another, and fishers often cannot distinguish between individual fish populations (Farmer, Malinowski, McGovern, & Rubec, 2016). Furthermore, when some fish populations are data-limited compared to others, it is more efficient to manage species complexes rather than individual fish populations (Kruse et al., 2005). For instance, fisheries management is greatly streamlined when harvest catch limits can be established for species complexes rather than individual fish populations (Farmer, Malinowski, McGovern, & Rubec, 2016). In this context, SDMs predicting the juvenile and spawner hotspots of species complexes would be beneficial to resource managers.

Here, we present a statistical modelling approach for assisting spatial protection efforts targeting the juvenile or spawner life stages of migratory fish populations or both. Our approach relies on multiple, regional monitoring datasets rather than a unique monitoring data source. We first outline our approach and then apply it to FSA-forming species of the grouper-snapper complex of the U.S. GOM.

Materials and methods

OUTLINE OF THE APPROACH

Our statistical modelling approach consists of four steps: (1) compiling a large monitoring database storing the encounter/non-encounter data collected in the region of interest for the species of interest, over multiple years, by different monitoring programs using random sampling methods; (2) fitting SDMs that account for spatial variation in fish encounter probability ("spatial SDMs") to the large monitoring database; (3) predicting juvenile and spawner hotspots for individual species from fitted spatial SDMs; and (4) combining predictions to map the juvenile and spawner hotspots of species complexes. Thus, our approach makes comprehensive use of the monitoring data available for the region of interest and is, therefore, very practical to resource managers.

The spatial SDMs employed in our approach include geostatistical binomial generalized linear mixed models (GLMMs) implemented with R package "VAST" (Thorson, 2019) and spatial binomial generalized additive models (GAMs) implemented with R package "mgcv" (Wood, 2006). Our approach primarily uses geostatistical GLMMs, which account for spatial structure at a fine scale (Thorson, Shelton, Ward, & Skaug, 2015). If geostatistical GLMMs do not converge due to a scarcity of encounter estimates, GAMs accounting for spatial structure at a broad scale through the inclusion of a tensor product between eastings and northings (Grüss, Chagaris, Babcock, & Tarnecki, 2018) are employed. Since our approach relies on encounter/non-encounter data collected by different programs over multiple years, both geostatistical GLMMs and spatial GAMs integrate a monitoring program effect and a year effect (Appendix S1 in Supporting Information).

Separate spatial SDMs are fitted for the two life stages, i.e., juveniles and spawners, of each species of interest. Spawners refer to adult individuals during the spawning season. To distinguish between the monitoring data for juveniles and those for spawners, the monitoring programs included in the large monitoring database need to collect length information, and the length at sexual maturity of the species of interest needs to be known or estimated. Based on previous research (e.g., Leathwick, Elith, & Hastie, 2006; Austin, 2007; Grüss, Chagaris, Babcock, & Tarnecki, 2018), for each life stage of each species of interest, one should ideally consider: (1) only monitoring programs providing at least 20-50 encounter estimates; and (2) only years associated with at least four encounter estimates.

Once spatial SDMs have been fitted and validated (see Appendix S1 for the description of the evaluation process), their outputs can be used to predict the spatial patterns of encounter probability of the juveniles and spawners of the species of interest. Next, the juvenile and spawner hotspots of the species of interest are defined as the areas where the encounter probability of the life stage under consideration is equal to or greater than the average encounter probability of the life stage over its entire distribution range (Grüss, Chagaris, Babcock, & Tarnecki, 2018). Then, for each location l of the study region (e.g., each cell of a spatial grid for the region of interest), hotspot indices, $H_{a,l}$, are estimated for the juveniles ($a = 1$) and spawners ($a = 2$) of a species complex of interest as (Grüss, Chagaris, Babcock, & Tarnecki, 2018):

$$H_{a,l} = \frac{\sum_{s=1}^{ns} H_{s,a,l} - \min_{l=1,\ldots,n_l} \left\{ \sum_{s=1}^{ns} H_{s,a,l} \right\}}{\max_{l=1,\ldots,n_l} \left\{ \sum_{s=1}^{ns} H_{s,a,l} \right\} - \min_{l=1,\ldots,n_l} \left\{ \sum_{s=1}^{ns} H_{s,a,l} \right\}} \qquad \text{eqn 1}$$

where $H_{s,a,l}$ is the hotspot index of life stage a of species s at location l, which is equal to 1 if location l is a hotspot for life stage a of species s and 0 otherwise; n_s is the number of species comprising the species complex; n_l is the number of locations in the region of interest; and

$H_{a,l}$ ranges between 0 and 1. Finally, critical life stage (CLS) hotspot indices, which integrate both juvenile and spawner hotspots, are calculated for each location *l*:

$$CLS_l = \frac{\sum_{a=1}^{2} H_{a,l} - \min_{l=1,\ldots,n_l} \left\{ \sum_{a=1}^{2} H_{a,l} \right\}}{\max_{l=1,\ldots,n_l} \left\{ \sum_{a=1}^{2} H_{a,l} \right\} - \min_{l=1,\ldots,n_l} \left\{ \sum_{a=1}^{2} H_{a,l} \right\}} \qquad \text{eqn 2}$$

such that CLS_l ranges between 0 and 1. The $H_{s,a,l}$ terms in eqn 1 and the $H_{a,l}$ terms in eqn 2 could be weighted based on the importance (e.g., socio-economic or conservation importance) given to individual species and life stages, respectively, but we do not consider this option here and leave it for future research (see Discussion).

APPLICATION

We apply our approach to FSA-forming species of the grouper-snapper complex of the U.S. GOM (Fig. 1). Groupers (Epinephelidae) and snappers (Lutjanidae) are some of the most economically important species of the U.S. GOM (NMFS, 2017). The grouper and snapper species that form FSAs at a few locations outside of their normal residence areas within a limited time window are particularly vulnerable to fishing and should be primary targets of MPA efforts (Erisman et al., 2017). A previous study identified 11 FSA-forming grouper and snapper species of the U.S. GOM that show high extrinsic vulnerability to fishing pressure during their spawning seasons (Biggs et al., 2018a, 2018b), which form the set of species considered in this study (Table 1).

We contacted university laboratories, state and federal agencies and non-governmental organizations carrying out monitoring programs in the U.S. GOM that both employ random sampling methods and collate length information. We received eight fisheries-dependent and 26 fisheries-independent datasets for the period 2000-2016, which together form the large monitoring database for our application (Table S2). Encounter/non-encounters for the juveniles and spawners of our 11 study species were extracted from the 34 datasets based on the length estimates associated with data points and the lengths at sexual maturity gathered in Biggs et al. (2018a). The monitoring data used in this study that can be shared publicly are available via the Figshare Digital Repository https://doi.org/10.6084/m9.figshare.7439585.v1 (Grüss, 2018), and the contact persons to request the rest of the monitoring data (confidential fisheries-dependent data) are indicated in the "Data availability statement" section.

In addition to mapping the juvenile, spawner and CLS hotspot indices of species of the FSA-forming grouper-snapper complex, we examined the extent to which seven important existing MPAs of the U.S. GOM (Fig. 1 and Table 2) already protect the juveniles and spawners of the FSA-forming grouper-snapper complex. These seven MPAs are either partial-take or no-take and implemented either year-round or seasonally, and four of them were primarily established to conserve grouper or snapper FSAs: the Madison-Swanson MPA, Steamboat Lumps, The Edges, and the Dry Tortugas Marine Reserve (Table 2). The Madison-Swanson MPA and the Dry Tortugas Marine Reserve were found to effectively protect FSAs (Grüss, Robinson, Heppell, Heppell, & Semmens, 2014).

Results

We were able to fit a spatial SDM for 13 life stages of 7 species, including nine geostatistical GLMMs (juveniles: 6; spawners: 3) and four spatial GAMs (juveniles: 1; spawners: 3). It was not possible to develop a spatial SDM for the other nine study life stages due to a lack of sufficient monitoring data (Table 1 and Table S3). After the 13 fitted spatial SDMs were validated (Appendix S4), their predictions were used to produce maps of encounter probability and hotspot maps (Fig. 2 and Fig. S5). In general, maps for the individual species showed a strong spatial separation between juveniles and spawners, with spawners usually found in deeper waters.

The juvenile and spawner hotspots predicted for the FSA-forming grouper-snapper complex were also distinct (Figs. 3A and 3B). Juvenile hotspots included portions of the Louisiana-Mississippi-Alabama shelf and the southwestern Florida waters south of Naples, while spawner hotspots covered the entire West Florida Shelf. However, some areas of the U.S. GOM were both juvenile and spawner hotspots, including the Pulley Ridge area and the Flower Garden Banks area (Figs. 3A and 3B). Consequently, the CLS hotspot index, which integrates both juvenile and spawner hotspot indices, was highest in the Pulley Ridge and Flower Garden Banks areas, followed by the West Florida Shelf, southwestern Florida waters and portions of the Louisiana-Mississippi-Alabama shelf (Fig. 3C).

The seven existing MPAs considered in this study were predicted to have varying juvenile, spawner and CLS hotspot indices, although the CLS hotspot indices of all MPAs were usually higher than the CLS hotspot indices in surrounding non-protected areas (Table 3 and Figs. 3 and 4). The Pulley Ridge Habitat Area of Particular Concern (HAPC) had the highest spawner and CLS hotspot indices of all MPAs considered. The Flower Garden Banks National Marine Sanctuary (FGBNMS) had the highest juvenile hotspot index and the second largest CLS hotspot index. The Madison-Swanson Marine Reserve, located in the northern West Florida Shelf, had the second highest juvenile hotspot index and the third greatest CLS hotspot index. The large Florida Keys National Marine Sanctuary (FKNMS) had the third largest juvenile hotpot index, but the smallest spawner hotspot index. Steamboat Lumps and The Edges both had the smallest juvenile hotspot index and the second largest spawner hotspot index. Finally, the Dry Tortugas Marine Reserve had some of the smallest juvenile, spawner and CLS hotspot indices of the seven MPAs considered (Table 3 and Figs. 3 and 4).

Discussion

We developed a statistical modelling approach to assist MPA planning for fish populations undergoing ontogenetic migrations or migrations between normal residence and spawning areas. MPAs targeting juveniles or spawners are practical for effectively protecting these populations (Grüss, 2014); yet, MPA strategies attempting to protect both juveniles and spawners may provide higher, long-term conservation and fisheries benefits. We found that MPAs aimed at protecting both the juveniles and spawners of the FSA-forming grouper-snapper complex of the U.S. GOM should preferentially be implemented in the Pulley Ridge and Flower Garden Banks areas (Figs. 3 and 4 and Table 3). More precisely, this study suggests that enlarging the existing Pulley Ridge HAPC and FGBNMS, or increasing harvest regulations within these existing MPAs, would offer substantial protection to many of the FSA-forming species of the grouper-snapper complex of the U.S. GOM. The Pulley Ridge HAPC had the highest spawner and CLS hotspot indices of all MPAs considered, which concurs with many anecdotal reports from fishers of grouper-snapper FSAs in the Pulley Ridge area (Hallock, 2007). Moreover, the FGBNMS had the highest juvenile hotspot index and the second largest CLS hotspot index, as the Flower Garden Banks area is an important sink of grouper and snapper larvae in the U.S. GOM (Schmahl, Hickerson, & Precht, 2008).

Both the Pulley Ridge HAPC and FGBNMS were primarily established to protect coral species. It has been recently discussed to expand both MPAs to better conserve corals and associated fish communities (Andradi-Brown et al., 2016; NMSP, 2018). In June 2018, the Gulf of Mexico Fishery Management Council voted for the expansion of restrictions on fishing activities both east and south of Pulley Ridge HAPC's previous borders (GMFMC, 2018). Our results suggest that expanding fishing restrictions north of Pulley Ridge HAPC's previous boundaries may also be beneficial to many FSA-forming grouper-snapper species (Figs. 3 and 4). Moreover, in May 2018, the Sanctuary Advisory Council recommended the inclusion of 14 additional (non-contiguous) reefs and banks in the FGBNMS; this recommendation is pending final federal approval (NMSP, 2018). Our study supports the recommended enlargement of the FGBNMS, since it will expand protection of critical life stages for many FSA-forming grouper-snapper species.

Our statistical modelling approach makes comprehensive use of available fisheries-independent and fisheries-dependent data, in contrast to most mechanistic models, which rely heavily on functional relationships (e.g., stock-recruitment relationships, relationships between weight-at-age and fecundity-at-age), many of which are typically uncertain. As illustrated above, the outputs of the approach can be directly employed for supporting existing or proposed resource management plans and envisioning new ones. They can also serve as inputs to conservation planning software packages identifying optimal MPA configurations based on biological, environmental and fisheries information (e.g., Marxan with zones; Metcalfe, Vaughan, Vaz, & Smith, 2015; Zonation; Leathwick et al., 2008). All that said, our statistical modelling approach should not be viewed as a substitute for, but rather as a complement to mechanistic models for guiding spatial protection efforts; specifically, our approach serves to identify critical life stage hotspots, and mechanistic models are useful for testing alternative management and environmental scenarios.

Though our statistical modelling approach relies on multiple fisheries-independent and fisheries-dependent datasets, we offer the caveat that sufficient monitoring might not be available to create predictions for the juveniles or spawners of all study species, as was the case in this study (Table 1). Yet, the list of those life stages for which monitoring data are lacking for developing spatial SDMs can be communicated to the institutions responsible for data collection or considered in simulation experiments aiming at optimizing monitoring program designs (Reich, Pacifici, & Stallings, 2018; Thorson, 2019), so as to enable data gaps to be filled in the future. In the case of the U.S. GOM, the use of monitoring data collected by state agencies at fixed sampling stations (along with some modifications in our statistical models) would also enable one to generate predictions for coastal species (e.g., red drum (*Sciaenops ocellatus*), black drum (*Pogonias chromis*)) that would be unattainable otherwise (Grüss et al., 2018). Moreover, it is important to note that the spawner hotspots predicted by our approach are not necessarily spawning areas, but could include pre-spawning areas that could be used for resting, feeding or courtship (Nemeth, 2012), or adult normal residence areas that are still populated during the spawning season by mature individuals skipping spawning (Rideout & Tomkiewicz, 2011). Nonetheless, if resource managers seek to protect spawning areas (e.g., the spawning sites of FSA-forming species), the spawner hotspots predicted by our approach represent valuable information for prioritizing the surveys aiming at identifying the actual spawning areas of species and species complexes within a large marine region (Grüss, Biggs, Heyman, & Erisman, 2018). More generally, we recommend our approach to be supplemented by field-verification studies for resource managers to garner more confidence in the predictions made with the approach.

An additional caveat to our statistical modelling approach is its reliance only on encounter/non-encounter data from monitoring programs. However, monitoring programs generally also collect count and biomass data. We recommend the development of an enhanced version of our approach with expanded capability to include count and biomass data (e.g., using an approximation to a compound Poisson-gamma process; Grüss & Thorson, 2019). This proposed enhanced version would allow one to both map biomass hotpots for individual life stages and predict trends in relative biomass for these life stages. This information would be employed for identifying the life stages or species with significant declining trends. These life stages or species would then be given more importance in spatial protection efforts and more weight in the calculation of hotspot indices (eqns 1 and 2). That said, we recognize that our approach is best suited for data-rich regions. For data-limited regions, we recommend a "light" version of our approach. This light version could consist of using only simpler and more flexible, spatial GAMs instead of a combination of geostatistical GLMMs and spatial GAMs, as geostatistical GLMMs usually require a relatively large number of data points to converge (Grüss et al., 2018). The light version of our approach for data-limited regions could be even simpler and consist of fitting spatial GAMs for the life stages of species complexes (instead of spatial GAMs for the life stages of the individual species comprising the species complexes), as is often done for informing the parameterization of ecosystem simulation models (Grüss, Chagaris, Babcock, & Tarnecki, 2018). For regions where monitoring data are extremely scarce, statistical modelling approaches using opportunistic information (e.g., counts by recreational divers) will need to be developed.

The number of MPAs is increasing and will continue to increase worldwide (Lubchenco & Grorud-Colvert, 2015; Boonzaier & Pauly, 2016). In this context, statistical modelling approaches making comprehensive use of available data such as the one presented in this study are urgently needed to support resource managers' ability to formulate sound and efficient spatial protection plans. MPA planning and complementary management decisions (e.g., harvest limits outside protected areas) assisted by robust tools such as our approach will allow resource managers to effectively protect biodiversity while supporting fisheries (Russell, Luckhurst, & Lindeman, 2012; Ban et al., 2014).

Authors' Contributions

AG conceived the study, developed the models, produced the maps, and wrote the first draft of the manuscript. All authors compiled the data, analyzed and discussed the results, assisted in writing the manuscript, and gave final approval for publication.

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Data availability statement

The monitoring data employed in this study that can be shared publicly are available via the Figshare Digital Repository https://doi.org/10.6084/m9.figshare.7439585.v1 (Grüss, 2018). The fisheries-dependent data collected by the National Oceanic and Atmospheric Administration (NOAA) used in this study are U.S. government data that are confidential and cannot be shared publicly. Please contact Dr. John Carlson (john.carlson@noaa.gov) to request the OBSGILL and SBLOP data; Dr. Elizabeth Scott-Denton (elizabeth.scott-denton@noaa.gov) to request the OBSLL, OBSSHRIMP and OBSVL data; and Dr. Lawrence Beerkircher (Lawrence.R.Beerkircher@noaa.gov) to request the POP data.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figures

Fig. 1. Map of the Gulf of Mexico (GOM). Depth contours are labeled in 20−, 40−, 60−, 100−, 200−, and 1000−m contours. The black dashed-dotted line delineates the U.S. exclusive economic zone. Important features are labeled and include: the Flower Garden Banks area, the West Florida Shelf, and the Pulley Ridge area. The existing marine protected areas (MPAs) of the U.S. GOM considered in this study include: the Flower Garden Banks National Marine Sanctuary (M1), the Madison-Swanson Marine Reserve (M2), Steamboat Lumps (M3), The Edges (M4), the Pulley Ridge Habitat Area of Particular Concern (M5), the Dry Tortugas Marine Reserve (M6), and the Florida Keys National Marine Sanctuary (M7). MS = Mississippi - AL = Alabama.

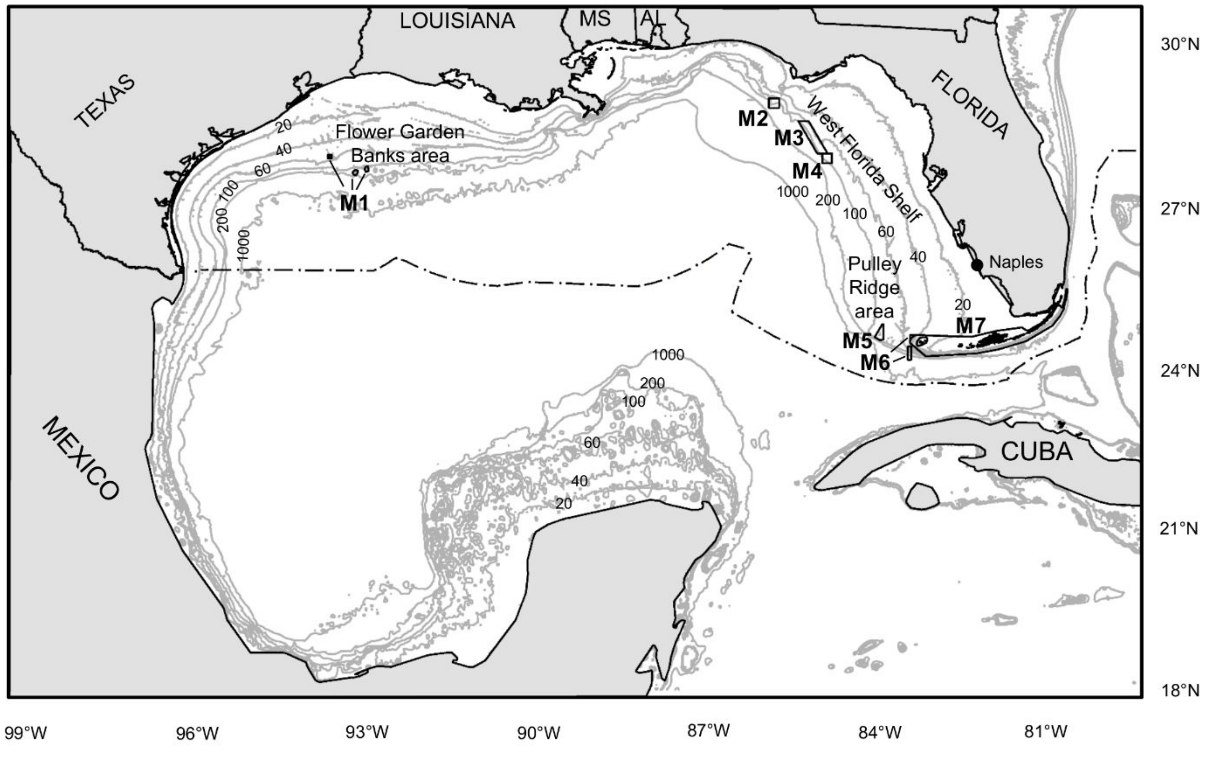


Fig. 2. Examples of (A-D) maps of encounter probability and (E-F) hotspot maps produced for the juveniles and spawners of the species of grouper-snapper complex of the U.S. Gulf of Mexico considered in this study. (A, B, E, F) are for gag (*Mycteroperca microlepis*), while (C, D, G, H) are for scamp (*M. phenax*). The rest of the maps generated in this study are provided in Fig. S5.

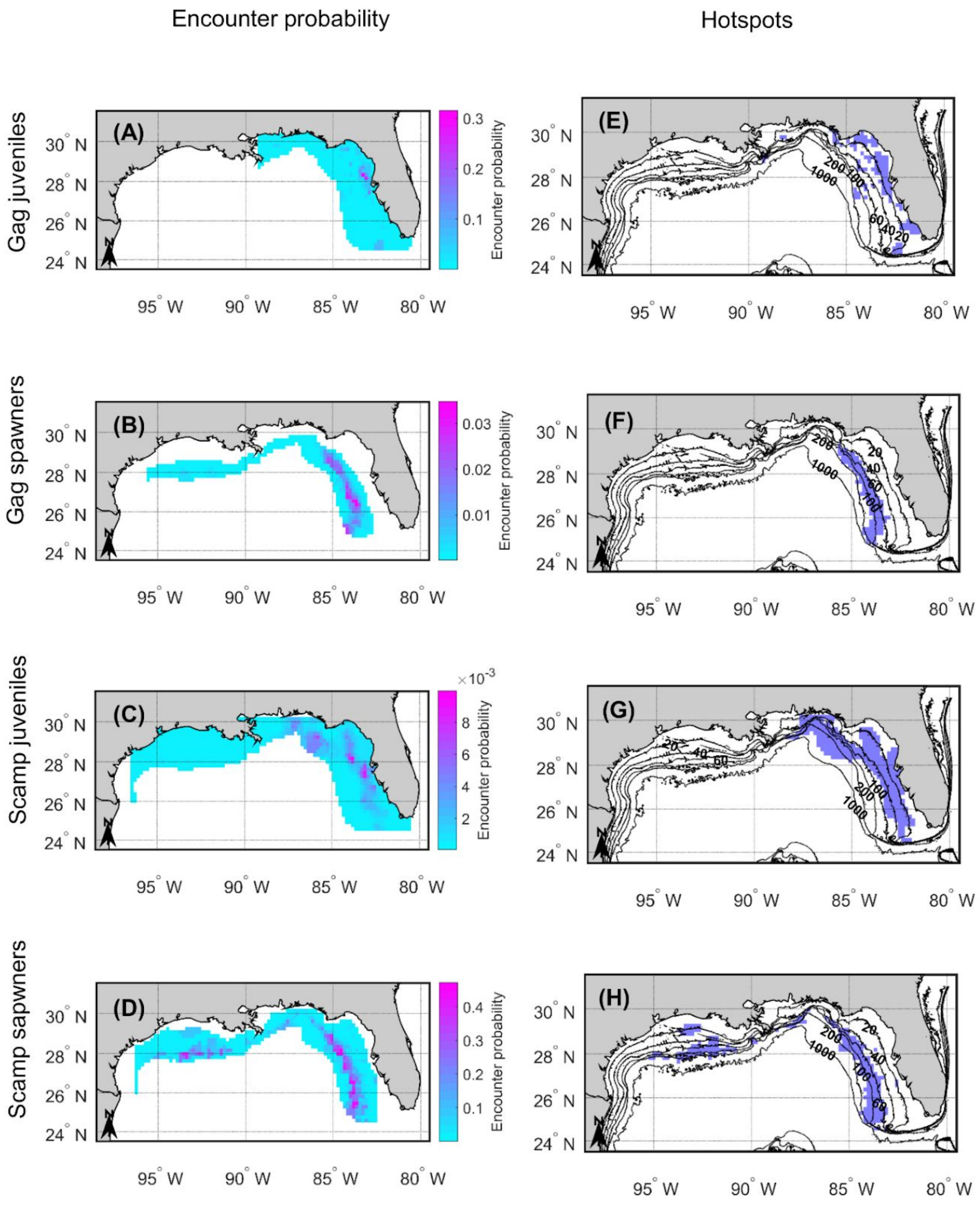


Fig. 3. (A) Juvenile hotspot indices, (B) spawner hotspot indices, and (C) critical life stage (CLS) hotspot indices for the vulnerable grouper-snapper complex of the U.S. Gulf of Mexico (GOM), all estimated using the statistical modelling approach employed in this study. The seven important existing marine protected areas (MPAs) of the U.S. GOM considered in this study are also shown here (black polygons), and the mean juvenile hotspot, spawner hotspot and CLS hotspot indices in these MPAs are provided in Table 3.

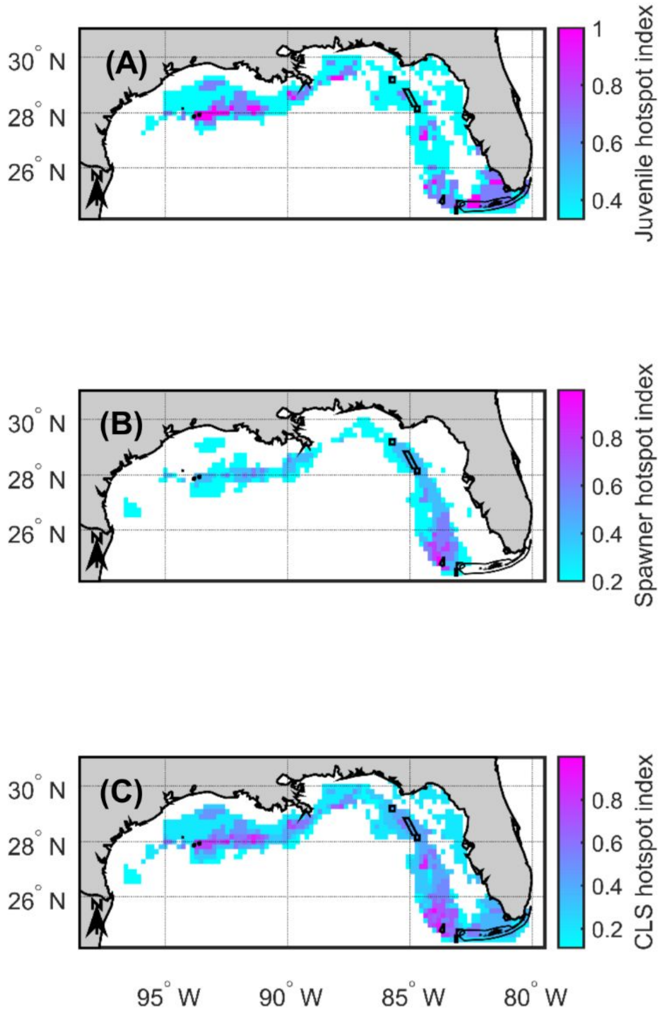
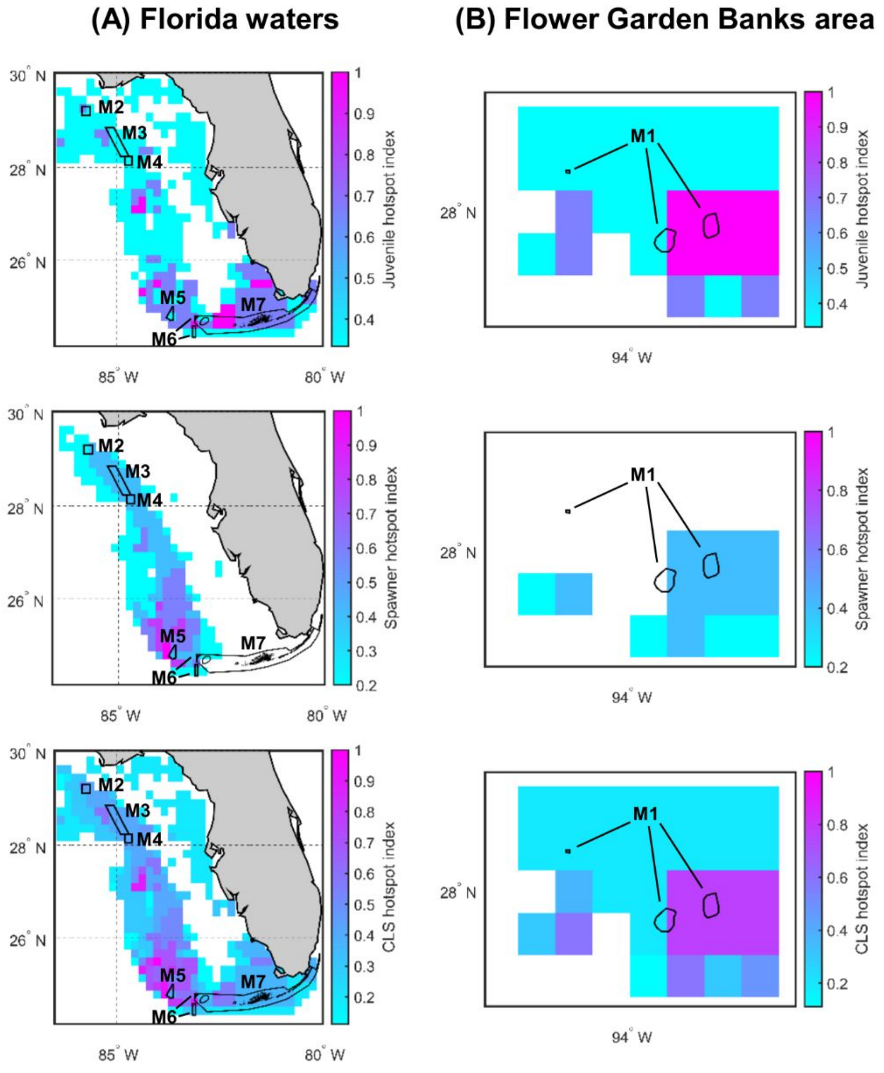


Fig. 4. Juvenile, spawner and critical life stage (CLS) hotspot indices for the vulnerable grouper-snapper complex of the U.S. Gulf of Mexico (GOM), all estimated using the statistical modelling approach employed in this study, in (A) Florida waters and (B) the Flower Garden Banks area. The seven important existing marine protected areas (MPAs) of the U.S. GOM considered in this study are also shown here (black polygons) and include: the Flower Garden Banks National Marine Sanctuary (M1), the Madison-Swanson Marine Reserve (M2), Steamboat Lumps (M3), The Edges (M4), the Pulley Ridge Habitat Area of Particular Concern (M5), the Dry Tortugas Marine Reserve (M6), and the Florida Keys National Marine Sanctuary (M7).


(A) Florida waters

(B) Flower Garden Banks area

Tables

Table 1. Grouper-snapper species of the U.S. Gulf of Mexico considered in this study, their total length at sexual maturity (from Biggs et al. (2018a)) and spawning months (from Biggs et al. (2018b)), and the spatial species distribution models fitted for these species. Spawners refer to adult individuals during the spawning season, except in the case of gag (*Mycteroperca microlepis*). Gag is a protogynous species that is relatively unique in that the adult females and males of the species are spatially segregated during most of the year; adult male gags stay at spawning sites year-round and are joined by adult females during the spawning season (Koenig & Coleman, 2012). Thus, in the case of gag, spawners refer to adult male individuals during both the spawning and non-spawning seasons. GLMM = generalized linear mixed model – GAM = generalized additive model.

Species	**Family**	**Total length at sexual maturity (cm)**	**Spawning months**	**Spatial species distribution models fitted**
Mutton snapper (*Lutjanus analis*)	Lutjanidae	50	May to August	Juveniles: Geostatistical GLMM Spawners: Spatial GAM
Cubera snapper (*Lutjanus cyanopterus*)	Lutjanidae	61	June to September	Juveniles: None Spawners: None
Black grouper (*Mycteroperca bonaci*)	Epinephelidae	86	December to April	Juveniles: Geostatistical GLMM Spawners: Spatial GAM
Gag (*Mycteroperca microlepis*)	Epinephelidae	54	January to April	Juveniles: Geostatistical GLMM Spawners: Geostatistical GLMM
Scamp (*Mycteroperca phenax*)	Epinephelidae	33	January to June	Juveniles: Geostatistical GLMM Spawners: Geostatistical GLMM
Yellowmouth grouper (*Mycteroperca interstitialis*)	Epinephelidae	43	January to December	Juveniles: None Spawners: None
Yellowfin grouper (*Mycteroperca venenosa*)	Epinephelidae	54	January to August	Juveniles: None Spawners: None
Goliath grouper (*Epinephelus itajara*)	Epinephelidae	120	June to October	Juveniles: Geostatistical GLMM Spawners: None
Nassau grouper (*Epinephelus striatus*)	Epinephelidae	40	December to February	Juveniles: None Spawners: None
Yellowedge grouper (*Hyporthodus flavolimbatus*)	Epinephelidae	55	February to November	Juveniles: Geostatistical GLMM Spawners: Geostatistical GLMM
Warsaw grouper (*Hyporthodus nigritus*)	Epinephelidae	81	April to November	Juveniles: Spatial GAM Spawners: Spatial GAM

Table 2. The seven important existing marine protected areas (MPAs) of the U.S. Gulf of Mexico considered in the present study. The geographical location of the seven MPAs is shown in Fig. 1.

MPA	MPA type and history	Comments
Flower Garden Banks National Marine Sanctuary	Partial-take year-round MPA (1992–); only the conventional hook and line gear is allowed within the MPA	Consists of three protected areas: (1) East Flower Garden Bank; (2) West Flower Garden Bank; and (3) Stetson Bank, which is located north of the two other protected areas and was added to the Sanctuary in 1996. The Sanctuary was designed to protect the benthic species (including corals) and fish species inhabiting the Flower Garden Banks area.
Madison-Swanson MPA	Partial-take seasonal MPA (2000–); only surface trolling targeting species other than reef fish species is allowed inside the MPA from May to October	Established to protect the fish spawning aggregations (FSAs) of reef fish species, particularly gag (*Mycteroperca microlepis*) and scamp (*M. phenax*).
Steamboat Lumps	Partial-take seasonal MPA (2000–); only surface trolling targeting species other than reef fish species is allowed inside the MPA from May to October	Established to protect the FSAs of reef fish species, particularly gag and scamp.
The Edges	No-take seasonal MPA (2009–); no fishing activities are allowed inside the MPA from January to April	Established to protect the FSAs of reef fish species, particularly gag and scamp.
Pulley Ridge Habitat Area of Particular Concern (HAPC)	Partial-take year-round MPA (2005–); longlines, bottom trawls, buoy gears, traps and pots are not allowed inside the MPA	Primarily designed for protecting deep sea corals.
Dry Tortugas Marine Reserve	No-take year-round MPA (2001–)	Consists of two separate protected areas. The Reserve was created in part to protect the FSAs of mutton snapper (*Lutjanus analis*).
Florida Keys National Marine Sanctuary	Year-round partial-take and no-take MPAs (1990–)	Comprises multiple zones under different fishing regulations. It was designed to protect the Florida Keys area from oil exploration, mining and all activities that could alter the seafloor, and to restrict anchoring and coral collection in the area.

Table 3. Mean juvenile hotspot index, mean spawner hotspot index, and mean critical life stage (CLS) hotspot index in seven important existing marine protected areas (MPAs) of the U.S. Gulf of Mexico, all estimated using the statistical modelling approach employed in this study. The species considered to produce all indices are the species of the grouper-snapper complex listed in Table 1, and the geographical location of the seven MPAs is shown in Fig. 1. The reader is referred to the main text for details on the calculation of the juvenile, spawner and CLS hotspot indices.

MPA	**Mean juvenile hotspot index**	**Mean spawner hotspot index**	**Mean CLS hotspot index**
Flower Garden Banks National Marine Sanctuary (M1 in Fig. 1)	0.71	0.23	0.52
Madison-Swanson MPA (M2)	0.67	0.20	0.48
Steamboat Lumps (M3)	0.33	0.40	0.41
The Edges (M4)	0.33	0.40	0.41
Pulley Ridge Habitat Area of Particular Concern (M5)	0.50	0.50	0.56
Dry Tortugas Marine Reserve (M6)	0.50	0.30	0.44
Florida Keys National Marine Sanctuary (M7)	0.61	0.03	0.36